Data-driven approaches and systems thinking to understand change in coastal environments

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Äidilleni.

’Eikä hän ollut käsittänyt, että meri saattoi olla niin ehdoton ja valtava kuin tällä hetkellä. Hänestä tuntui äkkiä, että ainoat oikeat ja ehdottomasti varmat seikat maailmassa olivat kuu, meri ja vene.’

Tove Jansson, Muumipappa ja meri (1965)

‘And never before had he grasped that the sea could be as absolute and enormous as he saw it now. All at once he had a feeling, that the only real and convincing things in existence were the moon and the sea and the boat.’

Tove Jansson, Moominpappa at Sea (1965)

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1 Introduction

Coastal environments are highly dynamic systems characterized by tight interconnections between land and sea (Abelson et al., 2020; Preston et al., 2025) and endowed with unique biodiversity (Ramírez et al., 2025; Roberts et al., 2002). Coastal regions are also the world’s most densely populated areas and coastal ecosystems provide essential benefits to societies and economies worldwide (Barbier et al., 2011; Small & Nicholls, 2003). However, coastal ecosystems are increasingly threatened by local and global anthropogenic stressors (Doney et al., 2012; Halpern et al., 2008; He & Silliman, 2019; Tuholske et al., 2021).

Coral reefs are among the most biodiverse and highly threatened coastal ecosystems (Bridge et al., 2013; Hughes et al., 2017). Coral reefs are particularly vulnerable to climate change impacts, including sea level rise, extreme marine heatwaves, and an increased magnitude and frequency of storms (Ban et al., 2014; van Hooidonk et al., 2016). On tropical islands, healthy coral reefs are a fundamental condition for human well-being: reef ecosystems provide coastal protection from storms and support key livelihoods such as fishing and pearl oyster farming (Andréfouët et al., 2022; Harris et al., 2018). The very existence of atoll islands depends on the continuation of biogenic reef accretion and sediment generation processes (Perry et al., 2015; Steibl et al., 2024).

Recent research suggests that local management action could support the resilience of island-reef systems to climate change (Barnett et al., 2022; Benkwitt et al., 2023; Gove et al., 2023). However, there are still major knowledge gaps about how different biophysical, anthropogenic, and ecological drivers shape island-reef systems and their capacity to adapt to the rapidly changing climate (Duvat & Magnan, 2019; Hédouin et al., 2020; Pérez-Rosales et al., 2021; Steibl et al., 2024). This is partly because tropical islands are distributed over vast geographies, making comprehensive field studies unfeasible (Andréfouët et al., 2022). Furthermore, long-term monitoring studies are few and primarily focused on the largest high volcanic islands with established research facilities, such as Hawai’i Island in the North Pacific and Mo’orea in the South Pacific (Grady et al., 2022; Hédouin et al., 2020; MCR LTER, 2024).

Remote sensing via satellites and drones has been proposed as a cost-effective method for monitoring tropical island-reef systems (Lefebvre et al., 2022). Remote sensing can be used to map the anthropogenic stressors imposed on these systems, their impact on environmental conditions, and the resulting ecological alterations (Hedley et al., 2016; Lutzenkirchen et al., 2024; Wedding et al., 2018). The spatial, spectral, and temporal resolutions of satellite data have drastically increased over recent years, opening new opportunities for environmental remote sensing (Li et al., 2022; Purkis, 2018). Drone surveys can complement satellite data by providing very high spatial resolution imagery (<10 cm^2) and avoiding uncertainties associated with atmospheric correction (Botha et al., 2013; Cillero Castro et al., 2020; Collin et al., 2018).

In this DPhil thesis, I develop conceptual and analytical tools to advance coral reef research and management, with a specific focus on remote sensing applications and the importance of cross-ecosystem nutrient flows and water quality in island-reef systems in the Pacific and the Caribbean. The ultimate aim of my research is to inform local management and restoration strategies that strengthen the resilience of island-reef systems to climate change. More broadly, the premise of my thesis is that in order to support the resilience of coastal ecosystems to climate change, we need to develop both 1) data-driven approaches (remote sensing and machine learning) to understand how coastal ecosystems are changing across wide geographies and over time; and 2) a conceptual framework to support the interpretation of that data (systems thinking).

In my first chapter, I used a combination of satellite and field data to assess concomitant changes in land-based pressures and coral reef benthic communities in an ecologically significant coastal region in northeastern Puerto Rico between 2000 and 2015. This exercise allowed me to identify opportunities and limitations associated with the use of satellite data to study land-sea connections. I found that the application of remote sensing to inform land-sea management of coral reefs is hindered by the lack of freely available, off-the-shelf algorithms and data products, especially in the marine environment. In particular, I found a need to develop improved satellite algorithms to map water quality in optically shallow and complex coastal waters. “Optically shallow” means that the optical signal detected by the remote sensing sensors is affected by reflectance from the water column and from the seafloor (Lee et al., 1999). “Optically complex” means that the signal from the water column is affected by several optically active water constituents, such as phytoplankton, colored dissolved organic matter, and suspended sediments (Phinn et al., 2005).

In my second chapter, I conducted a systematic literature review on the study of nutrient connectivity in tropical and subtropical coastal environments. In coral reef ecosystems, the management of nutrient connectivity across the land-sea interface has been identified as a promising strategy for enhancing resilience to climate change (Benkwitt et al., 2019, 2023; Mcleod et al., 2019; Speare et al., 2026). The review revealed a need for the development of a more predictive science of nutrient connectivity that can inform resilience-based coastal management. Additionally, the review highlighted that few studies have leveraged remote sensing or machine learning to study coastal nutrient connectivity. Building on the insights from the literature review, I proposed an integrated research approach, *nutrientscape ecology*, for the interdisciplinary study of coastal nutrient flows. Nutrientscape ecology combines landscape ecology and systems thinking and provides the necessary conceptual framework for integrating and interpreting data from multiple sources. The framework encourages the application of novel technologies, including remote sensing and machine learning, and promotes the development of a spatially explicit and predictive science of nutrient connectivity.

Together, the first two chapters formed the foundations and motivation for my third chapter, where I employed a new probabilistic machine learning method to advance remote sensing applications in optically complex and shallow marine environments, such as coral reefs. I developed a novel algorithm for estimating the concentrations of key water quality constituents (phytoplankton, minerals, and colored dissolved organic matter) in shallow reef environments from remotely sensed optical data. Mapping and monitoring water quality constituents can provide new insights into key ecological and biogeochemical processes taking place in coral reef ecosystems (Russell et al., 2019). For example, phytoplankton concentration can be used as a proxy for nutrient loading (Devlin & Schaffelke, 2009; Salgado-Hernanz et al., 2019). To support future applications and development of the algorithm, all data and code were made freely available via the Open Science Framework data repository and an associated GitHub repository (Palola, 2024).

The fourth and final chapter builds on the understanding of the importance of cross-ecosystem connectivity developed in the second chapter. I used satellite data to examine the “island mass effect” (i.e., the enhancement of primary production observed in nearshore waters surrounding islands) around Pacific atolls (Gove et al., 2016). These productive nearshore waters deliver important energy and nutrient subsidies into the atoll system (Radice et al., 2019; Skinner et al., 2021). The pelagic subsidies can support atoll reef resilience to marine heatwaves by providing an external food supply to corals during bleaching events (Fox et al., 2023). The fourth chapter provides the first characterization of variability in island mass effect and vulnerability to marine heatwaves across Pacific atolls, thereby contributing novel insights into atoll resilience to climate change.

2 Literature review

Coastal environments around the world are changing rapidly due to local human activities and global climate change (Doney et al., 2012; Halpern et al., 2008; He & Silliman, 2019; Tuholske et al., 2021). Designing effective coastal management strategies requires understanding how, where, and why coastal environments are changing (Hughes et al., 2017; Wedding et al., 2018). Poor site selection – due to a lack of data on environmental conditions and drivers of change – is a common reason for the failure of coastal restoration projects (Ward & Beheshti, 2023). Local managers and restoration practitioners need spatial data on the stressors imposed on the system (“pressures”), the consequent changes in environmental conditions (“state”), and the resulting ecological alterations (“impact”) (Delevaux, Jupiter, et al., 2018; Delevaux, Whittier, et al., 2018). Remote sensing using satellites and drones offers great potential for collecting such data (Hedley et al., 2016). However, collecting large environmental datasets alone is not sufficient – conceptual tools and theory are needed to support the interpretation of that data in a meaningful way (Coveney et al., 2016). To develop resilience-based management of coastal ecosystems, data-driven approaches need to be complemented by a theoretical understanding of system dynamics and resilience (Coveney et al., 2016; Mcleod et al., 2019; Scheffer et al., 2001).

In the next section, I will provide concise summaries of two key research fields that underpin the motivation and epistemological approach of my DPhil research. First, drawing from systems thinking, I briefly discuss the concept of ecosystem “resilience”. As the aim of my research is to provide information to support resilience-based management — and as ‘resilience’ is mentioned several times throughout the chapters of this DPhil — it is necessary to provide a formal definition of “resilience” in the context of this thesis. Second, I summarize the state-of-science and key challenges in coral reef remote sensing. While coral reef environments are the focal study system, many of the concepts and principles presented are broadly applicable to shallow coastal marine environments.

2.1 Resilience

A multifaceted concept, *resilience* has been defined and quantified in different ways in the literature (Henry & Ramirez-Marquez, 2012; Levin & Möllmann, 2015; Levin & Lubchenco, 2008; Palumbi et al., 2008; Scheffer et al., 2001). In a foundational paper, Holling (1973) defined resilience as the ability of the ecosystem to absorb perturbations without being pushed into an alternative *basin of attraction* (Holling, 1973). A basin of attraction can be understood as a "valley" in a "stability landscape", where the bottom of the valley is a stable state to which the system returns as it recovers from a perturbation (Anthony et al., 2015; van Nes & Scheffer, 2007). For example, stability landscapes of coral reef ecosystems are commonly described in terms of two alternative system states: coral-dominated and macroalgae-dominated (Hughes, 1994; Hughes et al., 2017; Mumby et al., 2007), although this dichotomy has been challenged as overly simplifying – there may be more than two stable states (Norström et al., 2009).

Examining the stability landscape, we can distinguish between two facets of resilience: first, the *resistance* of the system to change (i.e., the width of the basin of attraction) and second, the *rate of recovery* following a perturbation (i.e., the slope of the valley hill) (Figure 1) (Levin & Lubchenco, 2008; Palumbi et al., 2008; van Nes & Scheffer, 2007). Resistance can be understood as the ecosystem's ability to resist change (i.e., the magnitude of impact caused by a given perturbation) (Palumbi et al., 2008). For example, the resistance of a coral reef system to a marine heatwave could be quantified as the extent of coral mortality given some level of heat stress (Howells et al., 2025). The rate of recovery of a coral reef system from a marine heatwave could be measured as the time period required to return to pre-disturbance levels of live coral cover (Benkwitt et al., 2023).

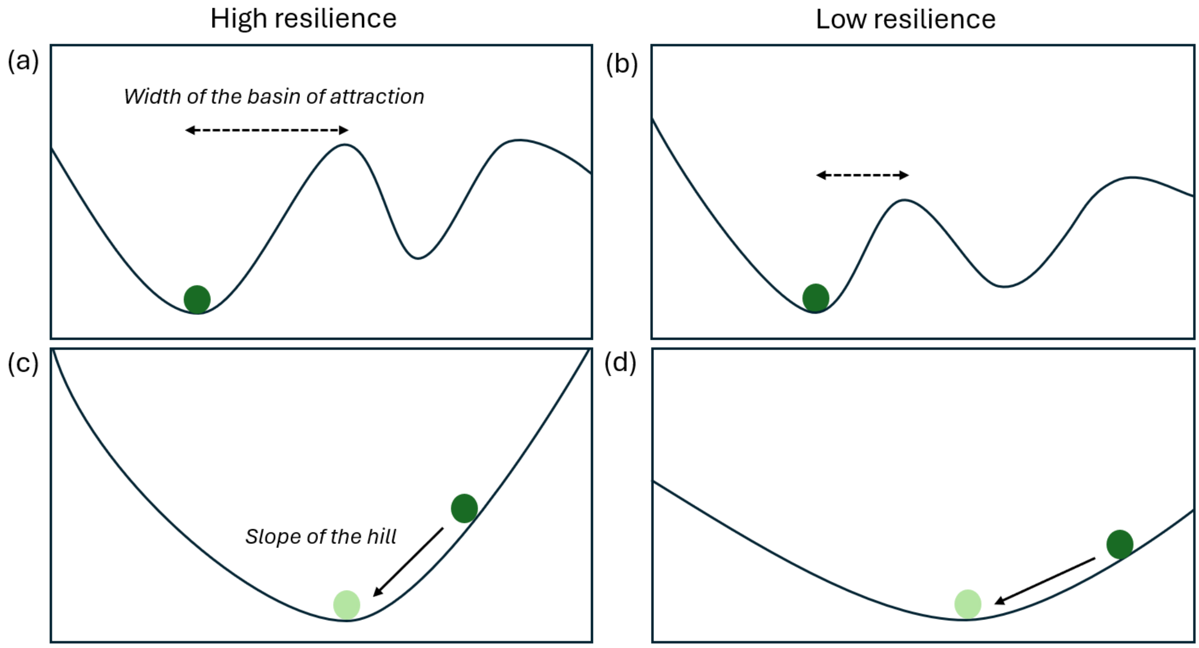

Figure 1. Illustration showing the system state (depicted by the ball) in the stability landscape of valleys and hills. Two facets of resilience are illustrated: resistance (a-b) and recovery (c-d). Based on van Nes & Scheffer (2007). In systems with higher resistance (a), a larger push is needed to tip the system state into a new basin of attraction. Systems with a higher recovery rate return to the stable state more quickly following a perturbation (c).

Resilience-based management aims at preventing the system from being pushed over a tipping point that separates basins of attraction (Mcleod et al., 2019). Avoiding the tipping point is critical due to *hysteresis*: once a tipping point has been breached, it is very difficult or impossible to restore the system back to its original state (Scheffer et al., 2001).

To avoid breaching a tipping point, resilience-based management can aim at supporting both ecosystem resistance and recovery (Hughes et al., 2017). For example, reducing land-based anthropogenic stressors (Chapters 1 and 2) can support coral reef resistance to and recovery from thermal stress (Gove et al., 2023; Graham et al., 2015). Restoring herbivorous fish populations can support the resistance of reefs to the negative impacts of excess anthropogenic nutrient loading by limiting macroalgae proliferation (Adam et al., 2015; Brandl et al., 2019).

The reality of nature is, however, complex. In the context of multiple interacting stressors affecting the ecosystem simultaneously, designing effective resilience-based management interventions is not evident (Côté et al., 2016; Côté & Darling, 2010). For example, increased turbidity, caused by coastal land-use change, is generally understood as harmful to coral reefs (Otaño-Cruz et al., 2019; Tuttle & Donahue, 2022). Yet, elevated turbidity can protect corals from thermal stress by providing "shading" from high irradiance and outweighing the harmful impacts of increased sediment loading on coral physiology (Cacciapaglia & van Woesik, 2016; Fabricius, 2005). Similarly, the impacts of increased nutrient loading on coral reefs are not always negative – in fact, the impacts depend on the nutrient subsidies' source, magnitude, and interactions with other stressors (Chapter 2) (Shantz & Burkepile, 2014; Speare et al., 2026). Restoring non-anthropogenic cross-ecosystem nutrient flows can promote faster reef recovery from the impacts of marine heatwaves (Chapters 2 and 4) (Benkwitt et al., 2023; Fox et al., 2023).

In summary, coastal ecosystems are complex, and management strategies must be based on systems thinking that takes into account feedback loops between different system components and drivers of change (Chapter 2) (Hughes et al., 2017; Williams et al., 2019). Combining the theoretical understanding of system dynamics with data-driven approaches, including remote sensing and machine learning, is key to understanding change in coastal environments in the 21st century (Chapters 1–4).

2.2 Coral reef remote sensing

Optical remote sensing is based on the measurement of electromagnetic radiation, and the optical sensors mounted on satellites or drones are designed to detect specific bands of the electromagnetic spectrum. Multispectral data is typically considered to consist of no more than ~10 spectral bands, while hyperspectral sensors can measure >100 spectral bands (Hedley et al., 2016). A suite of key terrestrial and marine variables associated with "pressures", "state", and "impact" on coral reefs could, in principle, be quantified using optical remote sensing (Figure 2) (Hedley et al., 2016). In practice, however, generally applicable (i.e., transferable beyond a local study site) remote sensing algorithms for many of the marine variables in Figure 2 only exist for optically deep waters (Werdell et al., 2018). Developing generally applicable remote sensing algorithms for optically shallow and complex coral reef environments has proved to be challenging (Dekker et al., 2011; Hondula et al., 2024; Theenathayalan & Shanmugam, 2021).

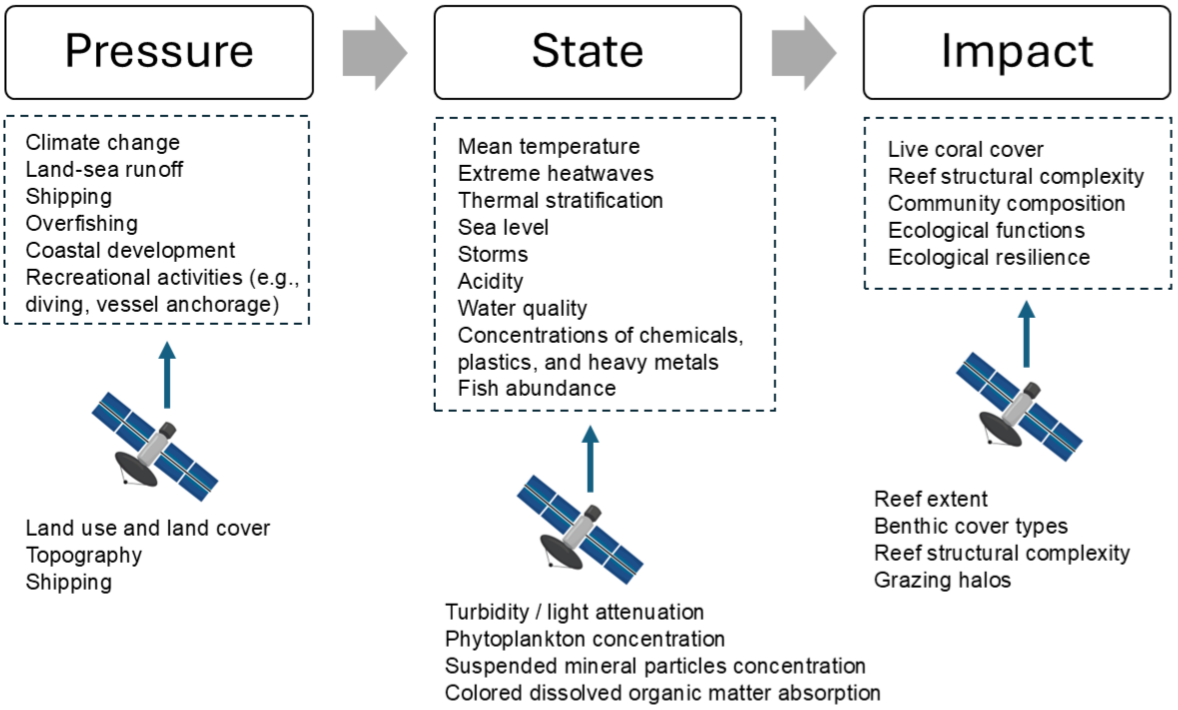

Figure 2. To understand change in coral reef environments, we need spatial information on pressures, state, and impact. Non-exhaustive lists of key variables associated with pressures, state, and impact are provided in the dashed-line boxes. Several of these variables, listed under the satellite illustrations, can be estimated using remote sensing.

Hyperspectral data analysis has revealed that different benthic cover types, such as coral and algae, have distinct spectral signatures and therefore could be mapped using remotely sensed optical data (Hochberg et al., 2003; Lucas & Goodman, 2014). However, reliably distinguishing between different benthic cover types remains challenging for a number of reasons (Kutser et al., 2020; Lutzenkirchen et al., 2024). First, the optical signal is confounded by optically active water constituents, such as suspended sediments (Bell et al., 2020; Theenathayalan & Shanmugam, 2021). Accurately correcting for the water column is hindered by the limited understanding of spatial-temporal variability in water column optical properties in coral reef systems (Hochberg et al., 2020; Russell et al., 2019), and algorithms tend to rely on simplifying assumptions (Bajjouk et al., 2019; Li et al., 2022). Second, in spatially heterogeneous reef environments, a single satellite pixel typically contains multiple benthic substrates, posing the problem of spectral mixing of different cover types (Hedley et al., 2016; Joyce et al., 2013). Conducting spectral unmixing is challenging due to spectral similarities between some benthic classes, such as green algae and seagrass (Davies et al., 2023; Hochberg et al., 2003). Furthermore, the bands most useful for distinguishing between classes are often in the green/red spectral range where water strongly absorbs light (Davies et al., 2023). Other challenges for spectral unmixing include within-class variation in the spectral signatures of benthic substrates, as well as heterogeneity in water column optical properties that alter the observed optical signal (Purkis, 2018). Third, while leveraging hyperspectral data could enable more accurate benthic classification, satellite sensors face a trade-off between spectral and spatial resolutions (Holden & LeDrew, 2001; Muller-Karger et al., 2018). Thus, hyperspectral satellite sensors may not provide a sufficient spatial resolution for fine-scale coastal applications (Dierssen et al., 2021). Fourth, the optical signal from the water surface is weak compared to the signal from the atmosphere, making the analysis sensitive to minor errors in atmospheric correction (Mouroulis et al., 2008; Purkis, 2018).

Due to these challenges, satellite-derived benthic maps tend to have limited thematic resolution – that is, a limited number of distinct habitat or substrate classes – and suffer from large uncertainties, especially when spatial and temporal variation in water column optical properties is significant (Collin et al., 2021; Lutzenkirchen et al., 2024; Purkis, 2018). Studies with higher thematic resolutions (multiple classes including coral, algae, seagrass, sand, and their mixtures) have achieved good classification accuracies when applying very high spatial resolution (<3.5 m^2) hyperspectral data from airborne sensors (Bajjouk et al., 2019; Kobryn et al., 2013). Because of the trade-off between spatial and spectral resolutions associated with spaceborne sensors, such data cannot currently be retrieved using satellites (Dierssen et al., 2021). Satellites can nevertheless be used to derive maps of reef extent and bathymetry in sufficiently clear and shallow waters (Kennedy et al., 2021; Li et al., 2021; Lyons et al., 2024). Even grazing halos (i.e., circular zones of cleared vegetation around reef patches created by herbivorous fish) can be detected from very high-resolution satellite imagery (0.5 m^2 resolution) (Franceschini et al., 2023; Madin et al., 2019). Drone data can be used to create very fine scale (<10 cm^2), thematically detailed benthic maps (Contini et al., 2025; Ventura et al., 2023). However, in contrast to satellites with consistent revisit times and near-global coverage, drones can only cover a limited spatial extent and require calm weather conditions (Casella et al., 2016). Furthermore, drone surveys require in-person operation and therefore cannot feasibly be used for long-term monitoring of remote reefs (Cillero Castro et al., 2020; Obura et al., 2019).

In addition to mapping the benthos, optical remote sensing can be used to retrieve key water constituents, including phytoplankton, suspended sediments, and colored dissolved organic matter (Mobley, 1994). Metrics describing light attenuation in the water column, such as the diffuse attenuation coefficient and turbidity, can also be quantified (Hochberg et al., 2020; Li et al., 2022). However, most satellite algorithms for water quality mapping have been designed for deep waters where the optical signal is not confounded by bottom reflectance (Werdell et al., 2018). When applying ocean color products, pixels shallower than 30 m should be masked to ensure reliable estimates (Gove et al., 2016; Messié et al., 2022). Additionally, the coarse spatial resolution of currently available ocean color data (e.g., 4 km^2 for MODIS Aqua, 750 m^2 for VIIRS) limits their application very close to the shore due to land-adjacency effects (Feng & Hu, 2017). Consequently, a typical approach for the satellite-based mapping of water quality in reef environments has been to retrieve ocean color data from deep offshore waters *near* the shallow reefs (Adam et al., 2021; Devlin & Schaffelke, 2009; Wedding et al., 2018). Indeed, while satellite remote sensing has enabled the study of regional-scale patterns in coastal water quality at a coarse spatial resolution (Devlin & Schaffelke, 2009; Wedding et al., 2018), we lack water quality algorithms and data products designed for shallow nearshore environments (Werdell et al., 2018).

To my knowledge, the only off-the-shelf satellite-derived water quality product currently available for optically shallow coastal waters is the Allen Coral Atlas turbidity data (Li et al., 2022). The algorithm presented by Li et al. (2022) is based on estimating water column optical properties from nearby optically deep waters. These estimates are then used to calculate depth and benthic cover at the shallow study site, and turbidity is approximated based on those estimates (Li et al., 2022). Thus, the algorithm assumes spatial homogeneity in water column optical properties between deep and shallow waters (Li et al., 2022). Yet, water constituent concentrations vary within the reef system across reef geomorphic zones due to biogenic processes and patterns of wave- or tide-driven circulation (Dekker et al., 2022; Russell et al., 2019). Coral reef waters are also characterized by high temporal variability, for example due to wind- and wave-driven resuspension of sediments and sediment plumes from land to sea (Adam et al., 2021; Andréfouët et al., 2001; Bessell-Browne et al., 2017; Fong et al., 2020). Thus, the Allen Coral Atlas turbidity data should be interpreted with caution (Li et al., 2022).

3 Article-based thesis: status of manuscript submissions

This thesis follows the paper-route (i.e., an article-based format) and comprises four academic papers that have been submitted for publication in peer-reviewed journals. The status of each manuscript submission is detailed below.

Chapter 1: From ridge to reef: combining remote sensing and field surveys to inform coral reef conservation

Status: Re-submitted to *Remote Sensing in Ecology and Conservation* following reviewer feedback.

Chapter 2: Nutrientscape ecology: a whole-system framework to support the understanding and management of coastal nutrient connectivity

Status: Published in *Landscape Ecology*.

Full reference: Palola, P., Pittman, S. J., Collin, A., Benkwitt, C. E., Thomson, E., Malhi, Y., Graham, N. A. J., & Wedding, L. M. (2025). Nutrientscape ecology: a whole-system framework to support the understanding and management of coastal nutrient connectivity. *Landscape Ecology*, *40*(3), 48. https://doi.org/10.1007/s10980-025-02060-w

Chapter 3: Simulation-based inference advances water quality mapping in shallow coral reef environments

Status: Published in *Royal Society Open Science*.

Full reference: Palola, P., Theenathayalan, V., Schröder, C., Martinez-Vicente, V., Collin, A., Wright, R., Ward, M., Thomson, E., Lopez-Garcia, P., Hochberg, E. J., Malhi, Y., & Wedding, L. M. (2025). Simulation-based inference advances water quality mapping in shallow coral reef environments. *Royal Society Open Science*, *12*(5), 241471. https://doi.org/10.1098/rsos.241471

Chapter 4: Variability in island mass effect and vulnerability to marine heatwaves across South Pacific atolls

Status: Submitted to *Remote Sensing of Environment*, in review.

4 Chapter 1

A range of earth observation products are now freely available to the scientific community and environmental practitioners. In this first chapter, I explored the extent to which these satellite products can be used to map long-term changes in a tropical coastal environment with coral reefs. In the context of my personal development as a researcher, this chapter was my first experience working with satellite imagery and machine learning. As such, this chapter allowed me to develop the necessary foundations for the more advanced remote sensing applications in the subsequent chapters (Chapters 3 and 4).

From Ridge to Reef: Combining Remote Sensing and Field Surveys to Inform Coral Reef Conservation

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Abstract

Multiple land-based and sea-based stressors threaten coral reefs, and spatial data is needed to inform integrated land-sea management that reduces these threats. This study explored the use of freely available satellite products to examine long-term patterns of change across the land-sea continuum. We focused on northeastern Puerto Rico, where previous studies documented drastic coral cover decline in the late 20th century despite concomitant watershed reforestation and associated reduction in estimated land-based pressure. The aims of this study were 1) to examine whether these trends continued in 2000-2015 and 2) to synthesise the opportunities and limitations associated with using satellite data to inform land-sea management. We applied a Random Forest classifier on Landsat 7 satellite imagery to assess changes in land cover and landscape development intensity, a spatial index to estimate land-based pressure on nearshore marine habitats. We used field monitoring data to quantify coral reef benthic community change. We found that reforestation continued in 2000-2015 (+20%), suggesting reduced land-based pressure on adjacent reefs in both northern (Luquillo) and eastern (Ceiba-Fajardo) watersheds. Concomitantly, we observed a ubiquitous coral cover decline and aggressive peyssonnelid algal crust (PAC) expansion. Clustering analysis indicated that benthic monitoring sites in the same region (nearshore/offshore, east/west) followed similar community composition trajectories over time. Based on our results, the continued reforestation and estimated reduction in land use-based pressure has not been sufficient to halt coral cover decline in northeastern Puerto Rico. Our findings also raise the need for considering an alternative system state dominated by PAC, beyond conventional coral-macroalgae phase shifts. Finally, we identified developments needed in the field of environmental remote sensing, in particular the need for water quality algorithms designed for

optically shallow waters. To monitor and mitigate land-based stressors on coral reefs, a strategic combination of remote sensing and targeted field surveys is required.

1 Introduction

Coral reefs are highly diverse ecosystems that provide valuable benefits to people (Sing Wong, Vrontos and Taylor, 2022). However, coral reefs are vulnerable to climate change impacts, such as extreme marine heatwaves, increased magnitude and frequency of storms, and ocean acidification (van Hooidonk *et al.*, 2016). In addition to global climate change impacts, coral reefs are threatened by local land-based and sea-based pressures (Burke *et al.*, 2011; Ban, Graham and Connolly, 2014), such as increased sediment and nutrient runoff to coastal waters from agricultural lands and built-up areas (Bartley *et al.*, 2014; Bégin *et al.*, 2014; Bainbridge *et al.*, 2018). High rates of anthropogenic nutrient loading negatively impact coral reefs (Vega Thurber *et al.*, 2014), causing decreased rates of coral calcification and fertilization (Fabricius, 2005) and reduced resistance to thermal stress (Wooldridge, 2020). While environmental managers cannot sufficiently alleviate global stressors, local management action can reduce local stressors and support coral reef resilience to climate change impacts (Hughes *et al.*, 2017).

The need to identify and mitigate local stressors and an increased understanding of land-sea interconnections have given rise to calls for integrated land-sea management (Oleson *et al.*, 2017; Sandin *et al.*, 2022; Palola *et al.*, 2025a). To support integrated land-sea management and restoration, we must develop efficient ways to collect and synthesize meaningful spatial data on the ecosystem state and anthropogenic stressors across the land and sea interface (Wedding *et al.*, 2018; Carlson *et al.*, 2021). Integrated management of coral reefs incorporates land and sea management into a single framework (Álvarez-Romero *et al.*, 2011; Makino *et al.*, 2013). To inform integrated land-sea management, concomitant monitoring of terrestrial and marine ecosystems is of utmost importance (Halpern *et al.*, 2009; D'Angelo and Wiedenmann, 2014). However, many coastal studies and monitoring programs still focus efforts on either land or sea (Collin *et al.*, 2021; Williams *et al.*, 2022) and implementing integrated land-sea management is in many regions hindered by a lack of data at meaningful spatial-temporal scales (Jupiter *et al.*, 2017; Carlson *et al.*, 2021).

Integrating remote sensing and field surveys can help link patterns and processes across land and sea and avoid scale mismatches between the geographic extents of different stressors, ecological consequences, and their scientific investigation and management (Lutzenkirchen, Duce and Bellwood, 2024). Yet, only 3% of coral reef ecological studies published between 2012-2021 integrated both remote sensing and in-situ observations (Lutzenkirchen, Duce and Bellwood, 2024). Field surveys provide detailed information on ecological community compositions at very fine taxonomic scales (genus, species) and allow the classification of terrestrial and marine habitat types at high thematic resolutions (Kerr and Ostrovsky, 2003; Lutzenkirchen, Duce and Bellwood, 2024). However, field surveys alone typically only cover a limited area and tend to be spatially biased towards a few easily accessible focal sites of special interest (Rhodes *et al.*, 2015; Lutzenkirchen, Duce and Bellwood, 2024). In contrast, satellite remote sensing provides a rapid and cost-efficient tool for monitoring environmental change across landscapes and seascapes albeit at lower spatial and taxonomic resolutions (Shiklomanov *et al.*, 2019; Thomson *et al.*, 2021). Thus, combining remote sensing with field surveys can enable mapping of environmental change across spatial, temporal, and taxonomic scales (Palola *et al.*, 2025a), and inform the design of targeted field surveys to fill critical knowledge gaps that satellite data cannot exclusively address (Lutzenkirchen, Duce and Bellwood, 2024).

In this study, we explore the extent to which currently available optical satellite products can be used and combined with field monitoring data to examine long-term patterns of change in coastal environments with coral reefs. To achieve a rapid and cost-effective integrative methodology, our requirements for the choice of satellite products were that 1) satellite datasets are freely available; 2) no field data collection for calibration, training, or validation of satellite algorithms is needed; 3) any satellite data pre-processing and analyses are conducted using off-the-shelf tools available via free platforms. We focus our study on northeastern Puerto Rico, where coral reefs have been in decline for decades (Burke *et al.*, 2011; Gutierrez *et al.*, 2024), land-based pressure is considered a major driver of coral reef degradation (Otaño-Cruz *et al.*, 2019; Rogers and Ramos-Scharron, 2022), and managers are advancing integrated land-sea management (Carriger et al., 2013; Pittman et al., 2017; Smith et al., 2017). To better manage connected landscapes and seascapes in the region, the integrated management plan for the Northeast Marine Corridor, a large land-sea reserve network, was launched in 2017 (NOAA, 2017).

Long-term monitoring data is important to understand changes in the watersheds and marine water conditions in the region that may impact coral reefs and provides important historical context for future land-sea management strategies (Pittman et al., 2017; Rogers and Ramos-Scharron, 2022). Ramos-Scharrón, Torres-Pulliza and Hernández-Delgado (2015) documented concomitant changes in watershed land cover and coral reefs in Puerto Rico in 1978-2004. They observed an increase in forested area, suggesting reduced nutrient and sediment runoff to nearshore waters. Yet, over the same time period, they found a significant decline in living coral cover.

Sediment eroded from hillslopes and deposited in valleys may support increased sediment discharge to coastal waters even decades after agricultural lands have been abandoned and reforested (Larsen and Santiago Román, 2001; Gellis *et al.*, 2006). Due to this lag effect, reduced impacts on nearshore reefs may not be immediately observed.

In this study, we build on the work of Ramos-Scharrón, Torres-Pulliza and Hernández-Delgado (2015) and assess whether the trends of watershed reforestation and coral reef decline continued in 2000-2015. We use a spatial land use-based index to estimate changes in potential land-based anthropogenic pressure on adjacent coral reefs (Oliver, Lehrter and Fisher, 2011). We expect that if the estimated land use-based anthropogenic pressure on nearshore reefs continued to decline in 2000-2015, positive impacts of reduced sediment and nutrient loading associated with decades of reforestation should start to become apparent on the nearshore reefs (Ramos-Scharrón, Torres-Pulliza and Hernández-Delgado, 2015). Through our study in northeastern Puerto Rico, we identify opportunities and highlight limitations in applying satellite remote sensing and in-situ monitoring data to inform integrated land-sea management of coral reefs.

2 Materials and methods

2.1 Study site and benthic data

The study area comprises two watersheds in northeastern Puerto Rico: Luquillo and Fajardo-Ceiba (Figure 1). Large-scale deforestation due to agricultural expansion led to elevated rates of erosion and sediment runoff island-wide in the 19th and 20th centuries, with detrimental consequences to nearshore reefs (Larsen and Santiago Román, 2001; Larsen and Webb, 2009; Ramos-Scharrón, Torres-Pulliza and Hernández-Delgado, 2015). In recent decades, concern over coastal development associated with mass tourism has been increasing (Hernández-Delgado *et al.*, 2012).

We used biological field survey data from 2000-2015 to assess change in coral reef communities. Coral reef benthic communities were surveyed at eight nearshore monitoring sites (<400 meters from the mainland) and five offshore monitoring sites (>1,000 meters from the mainland) (Figure 1). Benthic surveys were conducted at the same sites every five years between 2000 and 2015, yielding data from four survey years (2000, 2005, 2010, 2015). Eight random replicate point count transects were conducted at each site using digital video imaging (60 points per transect). Each transect was 30 meters long and located at a depth of up to 10 meters. The substrate was identified to coral species level, or to other categories of benthic substrate (e.g., sponge, cyanobacteria, crustose coralline algae, *Halimeda* – see Appendix A for the full list of substrates). The average percent cover of the eight replicates for each site was used in the subsequent analyses.

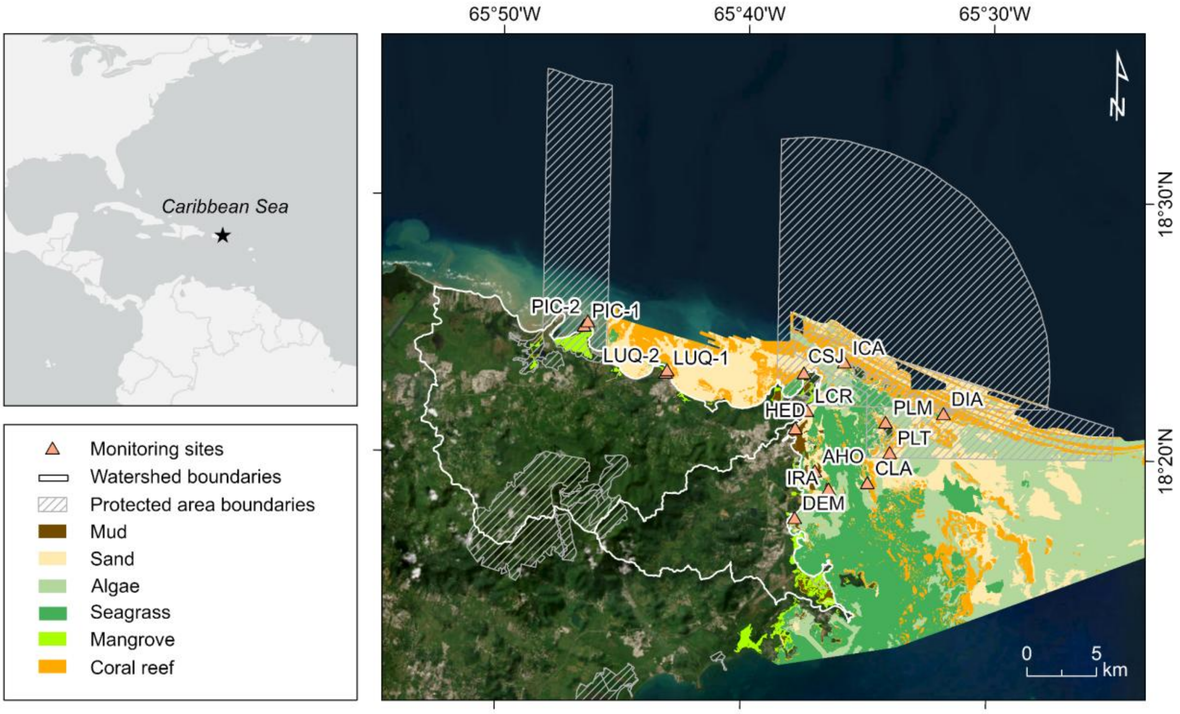

Figure 1. Map of the study region showing the benthic monitoring sites and watershed boundaries of Luquillo (northern coast) and Ceiba-Fajardo (eastern coast). Several important coastal habitat types (NCCOS, 2025) and marine and terrestrial protected areas are located within the study region (UNEP-WCMC and IUCN, 2025). Satellite image credit: ESRI, TomTom, FAO, NOAA, USGS, Earthstar Geographics.

2.2 Benthic analysis

All statistical analyses were performed using R v4.3.0 (R Core Team, 2024). To assess differences in community composition between sites and across years, we used the beta diversity metric Bray-Curtis on square-root transformed site-level benthic cover data. We then performed PERMANOVA analysis with 999 permutations on the Bray-Curtis matrix to assess whether the change in community composition across sites over time was statistically significant (R package *vegan* version 2.6) (Oksanen *et al.*, 2024). To identify similarities in temporal patterns of benthic community composition change between sites, we conducted bootstrap hierarchical clustering analysis on the same matrixed data using the ‘clusterboot’ function from the R package *fpc* (version 2.2) (Hennig, 2024). Ordination plots were drawn by non-metric multidimensional scaling (NMDS) using the ‘metaMDS’ function from the R package *vegan* with distance set to “bray” to visualize each site's clustering and community composition changes across time and space. The ‘metaMDS’ function automatically applies a Wisconsin Double Standardisation and square-root transformation to standardize the data and downweigh high abundance values. All the statistical analyses were carried out at the highest available taxonomic resolution (see section 2.1 and Appendix A). Additionally, we synthesised broad patterns of change among key taxon groups (hard coral, soft coral and sponge, macroalgae, turf, peyssonnellia algal crust, and other) in a bar plot (see e.g. Lange *et al.*, 2021).

2.3 Land cover change analysis

We used open access, freely available multispectral satellite imagery (30-meter resolution Landsat 7 ETM+) to analyse historical land cover change from 2000 to 2015. All satellite data analyses were conducted in Google Earth Engine, a cloud-based platform for geospatial data analysis (Gorelick *et al.*, 2017). We applied a machine learning decision tree algorithm, the Random Forest (Breiman, 2001), for the supervised classification of Landsat data. Random Forests work well in land cover classifications of heterogeneous environments (Jin *et al.*, 2018; Xu *et al.*, 2018). Random Forest classifiers can incorporate different types of ancillary variables in addition to spectral information, allowing for more accurate separation of spectrally similar classes (Kennaway and Helmer, 2007; Jin *et al.*, 2018). We included seven land cover types defined by similar physiognomy and moisture: “forest”, “woodland and shrubland”, “flooded coastal forest”, “non-forest vegetation”, “plantations”, “urban” and “water” (Appendix A) (Gould *et al.*, 2008, 2012).

The satellite imagery of the USGS GAP 2001 classification dated from 1999 to 2003 (Gould *et al.*, 2008), and we used Landsat 7 imagery from the same time period to create a cloud-free composite image. We overlaid polygons corresponding to each of the land cover type on the composite image, ensuring sampling over large parts of the study region, as well as a good representation of within-class variation (Appendix A) (Horning, Leutner and Wegmann, 2016; Wadoux *et al.*, 2021). Then, we extracted random samples from the polygons to create training and validation datasets for the supervised classification. We used separate polygons for the two datasets to ensure training and validation data independence and avoid spatial autocorrelation issues (Ploton *et al.*, 2020; Wadoux *et al.*, 2021). The number of sampled data points for each of the seven land cover types were 980 (70%) and 420 (30%) for training and validation, respectively. In addition to Landsat 7 spectral data, we derived elevation and slope from the Shuttle Radar Topography Mission digital elevation data (Farr *et al.*, 2007) and added them as ancillary variables. The classification accuracy was assessed using confusion matrices that compare predicted and actual values of pixels (Foody, 2002).

We used Landsat 7 imagery to create three 5-year cloud-free composite images: 2000-2005, 2005-2010, and 2010-2015. We applied the trained and hyperparameter-tuned Random Forest to each composite. The resulting three land cover maps were then used to map reforestation and deforestation over time.

2.4 Landscape development intensity (LDI) index

Environmental indices provide a means to synthesize complex information about the state of the environment in a way that is easy to measure, communicate, and apply in management (Dale and Beyeler, 2001; Gergel *et al.*, 2002). LDI is a spatial land use-based index to assess potential land-based anthropogenic pressure on coastal marine ecosystems (Brown and Vivas, 2005; Oliver, Lehrter and Fisher, 2011). We calculated the LDI index for both watersheds for each time point as follows: $LDI_{watershed} = (\sum \% LC_i \times LDI_i)/100$, where $\%LC_i$ is the percent cover of land cover type i, and LDI_i is the corresponding LDI coefficient (Appendix A) (Brown and Vivas, 2005; Oliver, Lehrter and Fisher, 2011). The LDI coefficients range from 1 to 5, with the largest values assigned to land cover types associated with the greatest runoff potential (i.e., impervious surfaces associated with urban land cover) (Oliver, Lehrter and Fisher, 2011).

3 Results

3.1 Watershed change

The Random Forest performed well (validation accuracy: 0.86; kappa coefficient: 0.83). “Urban” and “Water” land cover types were classified most accurately, while the land cover types with similar, closed forest physiognomy (“Plantations” and “Forest”) were most difficult to distinguish (Table 1).

Table 1. Confusion matrix. The rows represent actual values, and columns represent predicted values. If no pixels were misclassified, all values would fall on the diagonal line (in gray). PA = Producer’s Accuracy. UA = User’s Accuracy.

	Forest	Woodland and Shrubland	Flooded Coastal Forest	Non-forest vegetation	Plantations	Urban	Water	PA
Forest	268	20	5	9	11	2	0	85%
Woodland and Shrubland	21	13	2	11	1	1	0	27%
Flooded Coastal Forest	1	0	114	0	0	0	0	99%
Non-forest vegetation	20	6	0	163	0	0	0	86%
Plantations	28	0	27	0	56	0	0	50%
Urban	0	0	0	12	0	174	0	93%
Water	0	0	0	0	0	0	281	100 %
UA	79%	33%	77%	84%	82%	98%	100%	

In both Luquillo and Ceiba-Fajardo watersheds, non-forest vegetation decreased (-10% and -11%, respectively) while forested land cover types (“Forest”, “Flooded Coastal Forest”, and “Plantations”) increased (see Appendix B for additional results). The observed forest regrowth occurred mainly inland and outside protected areas, in a belt between the steep, forested mountainous regions inland and the urbanized areas of the coastal flats (Figure 2A). Some reforested patches were observed at the land-sea interface, particularly in the non-urban region between the towns of Luquillo and Fajardo (Figure 2A). These nearshore-reforested patches were classified as coastal flooded forests (mangrove forests and Pterocarpus swamp, Appendix A). The areas where non-forest vegetation increased were mainly located around built-up regions or by the coast (Figure 2A). Urban cover remained stable over time in both watersheds (Figure 2B). The relative proportion of different land cover types and LDI levels were similar in both watersheds (Figure 2B; Table 2). Due to the observed reforestation, LDI decreased in both watersheds between 2000 and 2015 (Table 2).

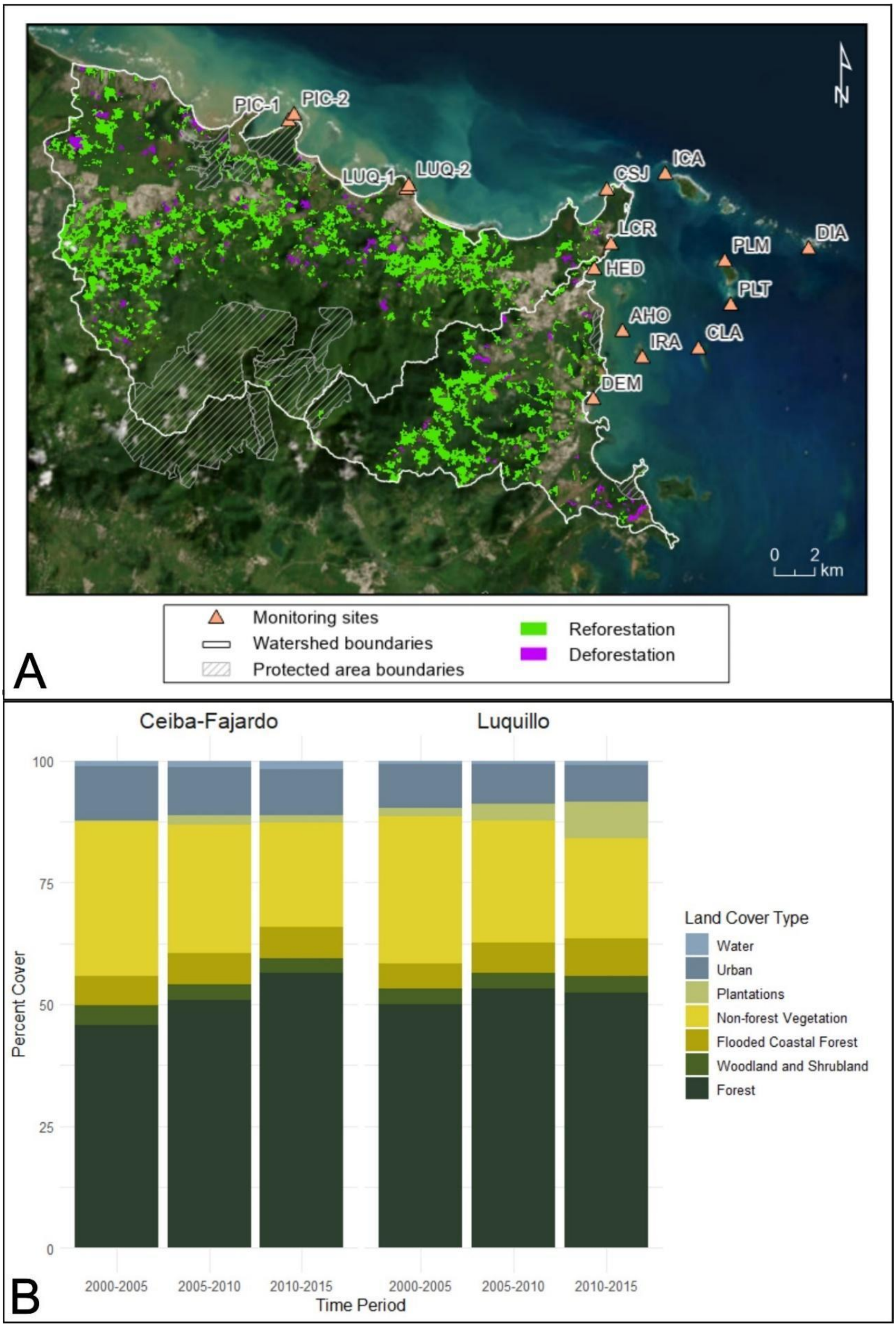

Figure 2A. A map of reforestation and deforestation in the Luquillo and Fajardo-Ceiba watersheds between 2000 and 2015. Here, “Forested” is the sum of forested land cover classes ("Forest", "Flooded Coastal Forest", and "Plantations"). Satellite image credit: Earthstar Geographics. 2B. Percent land cover change in the Luquillo and Fajardo-Ceiba watersheds between 2000 and 2015.

Table 2. Change in landscape development intensity index in the Luquillo and Fajardo-Ceiba watersheds between 2000 and 2015.

LDI index	**Luquillo**	**Fajardo-Ceiba**
2000 to 2005	2.05	2.18
2005 to 2010	1.91	2.00
2010 to 2015	1.80	1.88

3.2 Benthic community change

As a general pattern, at the start of the study period in 2000, sites located far (>1,000 meters) from mainland were characterized by higher hard coral cover (25%) and lower macroalgae and turf cover (47%) compared to sites located in close proximity (<400 meters) to mainland (10% and 68%, respectively). Soft coral cover and peyssonnelid algal crust (PAC) were observed at low levels (<15%) at all sites in 2000. We observed a significant change in community composition across sites between 2000 and 2015 (PERMANOVA: $F = 9.33$, $p < 0.001$). PAC became more dominant at all sites, increasing by 3-14-fold between 2000 and 2015.

To quantitatively assess dissimilarity in patterns of community composition change between sites, we used bootstrap analysis and identified four clusters (Figure 3A). Figure 3B shows the movement of community compositions towards a PAC-dominated state (the top left corner of the NMDS plot) over time from different starting compositions (the bottom of the plot: more hard coral; the right side of the plot: more macroalgae). The clustering broadly corresponds to a geographical division of the sites to northern nearshore (near the Luquillo watershed), eastern nearshore (near the Fajardo-Ceiba watershed), offshore, and Playa Hedionda. Hereafter, we refer to the clusters using these geographical divisions. The main difference between the northern and eastern nearshore clusters was that northern nearshore sites had higher macroalgae cover, while eastern nearshore sites had higher turf cover (Figure 3). Additionally, northern nearshore sites were the only sites where the decrease in macroalgae had already started in 2000-2005; for other sites, the decreasing trend only started after 2005. However, interestingly, one of the offshore sites (Cayo Ahogado), one of the northern nearshore sites (Luquillo 2), and one of the eastern nearshore sites (Bahia Demajagua) stand out from the overall geographic pattern (Figure 3).

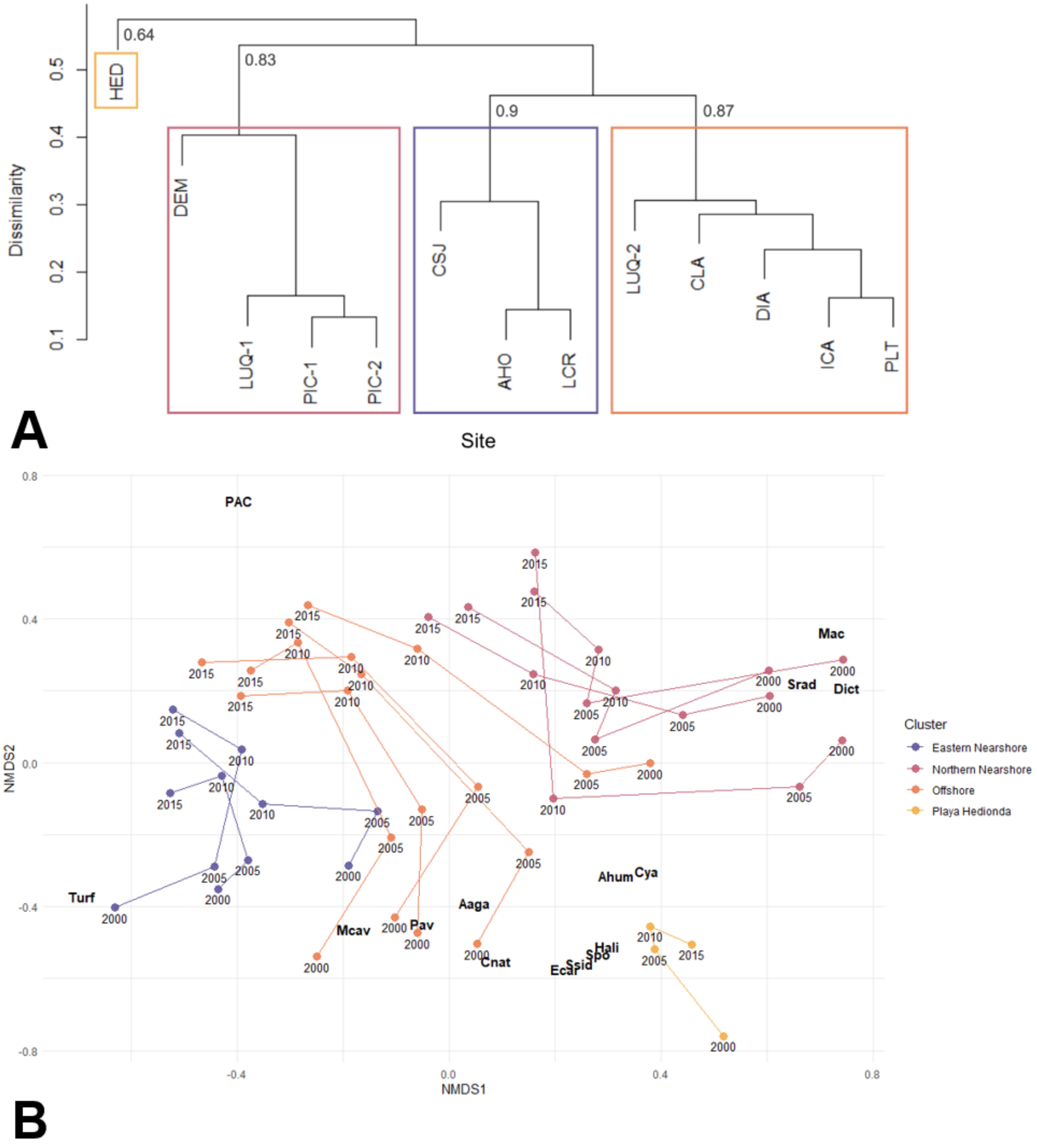

Figure 3A. Dendrogram highlighting the clusters identified from bootstrapping (k=4) and (Bray-Curtis) dissimilarity between the sites. Site abbreviations: AHO = Cayo Ahogado, CLA = Cayo Largo, CSJ = Cabezas de San Juan, DEM = Bahia Demajagua, DIA = Cayo Diablo, HED = Playa Hedionda, ICA = Cayo Icacos, LCR = Las Croabas, LUQ = Luquillo, PIC = Las Picuas, PLT = Cayo Palominitos. 3B. NMDS plot with sites (points) plotted according to Bray-Curtis dissimilarity of taxa composition and labelled with the year of data collection. The direction of the vectors between the points (years) indicates the compositional shift of each community at each site. The taxa displayed in black text had the most significant influence ($p =/< 0.01$) on the changes in community composition. Sites are coloured according to the cluster assigned by bootstrap analysis. Abbreviations: Aaga = *Agaricia agaricites*, Ahum = *Undaria humilis*, Cya = Cyanobacteria, Cnat = *Colpophyllia natans*, Dict = *Dictyota spp.*, Ecar = *Erythropodium caribaeorum*, Hali = *Halimeda*, Mac = Macroalgae, Mcav = *Montastraea cavernosa*, PAC = Peyssonnellia Algal Crust, Pav = Pavement, Spo = Sponge, Srad = *Siderastrea radians*, Ssid = *Siderastraea siderea*, Turf = Algal turf.

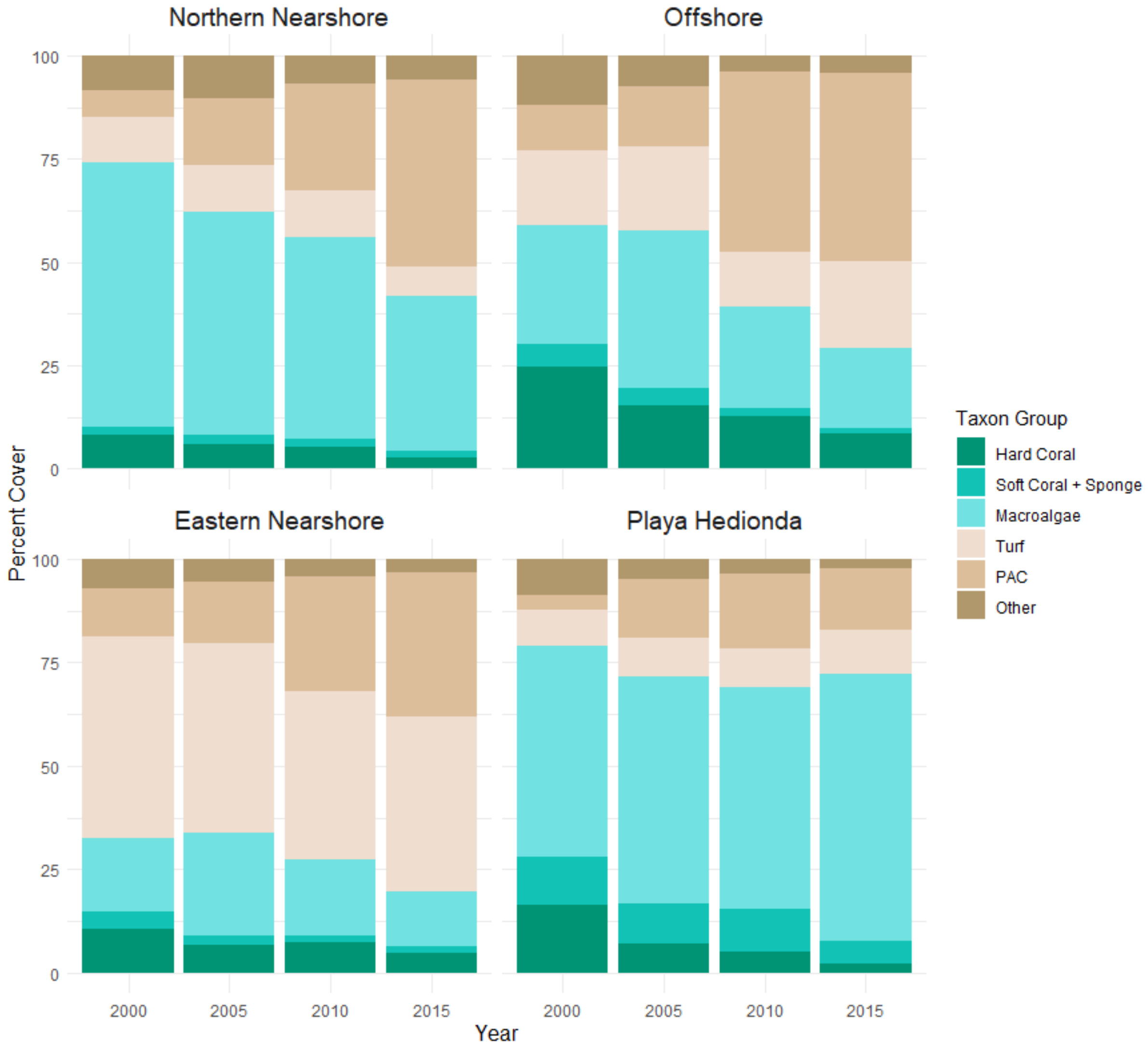

Figure 4. Community composition is indicated by the percent cover of each taxon group in each cluster, between 2000 and 2015.

4 Discussion

In the face of accelerating climate change and multiple local stressors, it may not be possible to return to the past reef systems characterized by high diversity and abundance of corals (Hughes *et al.*, 2018; Woodhead *et al.*, 2019). Well-designed environmental management and restoration action will be needed to steer the transformation of reef ecosystems in a direction that maintains ecological and social values (Hughes *et al.*, 2017; Bellwood *et al.*, 2019). To support effective coral reef management and restoration, continuous monitoring of anthropogenic pressures and their ecological impacts across land and sea is critically needed. In this study, we used a combination of field monitoring and remote sensing to examine environmental change on land and at sea from 2000 to 2015 in northeastern Puerto Rico, where efforts for integrated coral reef management are underway.

Building on the work of Ramos-Scharrón, Torres-Pulliza and Hernández-Delgado (2015), who documented trends of reforestation and coral cover decline in Puerto Rico in 1978-2004, we showed that both trends continued in the northeastern region in 2000-2015. In the next sections, we discuss our results and their implications to integrated land-sea management in the region. We identify future research needs to advance the use of remote sensing to inform land-sea management, and to establish the causal links between changes in land cover and coral reef communities.

4.1 Land cover change

Northeastern Puerto Rico has been recognized as an important land-sea ecological corridor with considerable conservation concern over land-based pollution linked to land use changes (Pittman *et al.*, 2017). In this study, we detected reforestation in both Luquillo and Fajardo-Ceiba watersheds between 2000 and 2015. Previous studies have documented large-scale deforestation in Puerto Rico in the early 20th century, followed by a shift to reforestation from the 1950s onwards (Kennaway and Helmer, 2007; Ramos-Scharrón, Torres-Pulliza and Hernández-Delgado, 2015; Wang, Yu and Gao, 2017). Thus, our results indicate that the reforestation trend continued in northeastern Puerto Rico in the early 21st century.

Historical deforestation and recent reforestation patterns are common in many tropical Caribbean islands and beyond (Lugo and Helmer, 2004; Farrant *et al.*, 2023; Gobierno de Canarias, 2023). Reforestation has typically resulted from the abandonment of agricultural lands (Murphy and Stallard, 2012; Farrant *et al.*, 2023). Agricultural land abandonment could explain the increase in forested areas observed in this study. However, recent food security plans to increase domestic agricultural production in Puerto Rico suggest widespread agricultural land abandonment is no longer occurring (Comas, 2013; Keck, 2015). Additionally, hurricanes play an important role in shaping vegetation patterns in Puerto Rico (Murphy and Stallard, 2012; Van Beusekom *et al.*, 2014). In fact, in their island-wide study, Wang *et al.* (2017) found that reforestation between 2000 and 2010 was mainly concentrated in eastern Puerto Rico, following widespread damage to vegetation by Hurricane George in September 1998. Thus, the reforestation observed in the Luquillo and Fajardo-Ceiba watersheds could be due to post-hurricane forest recovery (Wang, Yu and Gao, 2017). The deforested patches were characterized by increased non-forest vegetation rather than built-up land as a result of localized land clearance for golf courses and agriculture (Hernández-Delgado *et al.*, 2012). However, further research is needed to confirm the drivers of the observed land cover changes.

Urban expansion in coastal regions has been a key concern for land-sea management in Puerto Rico (Hernández-Delgado *et al.*, 2012). Previous studies have documented significant increases in human population and urban land in the 20th century in coastal regions around Puerto Rico (López, Aide and Thomlinson, 2001; Parés-Ramos, Gould and Aide, 2008; Ramos-Scharrón, Torres-Pulliza and Hernández-Delgado, 2015). In northeastern Puerto Rico, a ten-fold increase in urban land was reported between 1936 and 2004 (Ramos-Scharrón, Torres-Pulliza and Hernández-Delgado, 2015). While urban expansion continued between 2000 and 2010 on an island-wide scale (Wang, Yu and Gao, 2017), our results indicate that no significant change in the proportion of urban cover occurred in the Luquillo and Ceiba-Fajardo watersheds over the study period. This finding aligns with reported population declines in the municipalities of Luquillo, Fajardo, and Ceiba (United States Census, 2018).

4.1 Estimated land-based pressure on coral reefs

The observed reforestation and lack of urban expansion corresponded to decreased LDI, signalling an estimated reduction in land use-based pressure on adjacent coral reefs (Oliver, Lehrter and Fisher, 2011). However, the concomitant reduction in coral cover suggests that the continued decline in land use-based pressure has not been sufficient to halt the loss of corals in northeastern Puerto Rico.

The LDI assessment did not indicate any important differences between the Luquillo and Ceiba-Fajardo watersheds in the potential exposure risk of monitored coral reefs to land-based sources of pollution. However, LDI does not account for point sources of pollution, such as wastewater outlets, that can significantly impact local nearshore water quality (Santavy *et al.*, 2023). Additionally, the watershed-scale LDI assessment does not capture finer-scale patterns, such as potential spatial clustering of land-based pollution close to river mouths (Brown *et al.*, 2017, 2019). For example, two nearshore benthic monitoring sites in our study, Playa Hedionda and Bahia Demajagua, are located close to the mouths of major rivers along the eastern coast (Río Fajardo and Río Demajagua, respectively) and likely experience elevated sediment and nutrient loading compared to the other nearshore sites (Ramos-Scharrón, Torres-Pulliza and Hernández-Delgado, 2015). The coral reef community compositions at these two monitoring sites stood out from the overall geographic pattern – i.e., they were not clustered along with the other nearshore eastern sites. Our findings raise the need for further research to determine the causal drivers of the observed patterns in community composition, and the extent to which the benthic communities are shaped by differences in exposure to land-based pollution.

Similarly to Ramos-Scharrón, Torres-Pulliza and Hernández-Delgado (2015), our study does not assert causality between the changes in land cover and coral reef communities. Determining changes in water quality is the missing link in the causal chain from land cover change to coral reefs (Brown *et al.*, 2017). However, no water quality data, neither field-measured nor remotely sensed, was available for our study region and time period. Additionally, we emphasise that coral reefs in Puerto Rico are subject to multiple stressors (Lessios, Robertson and Cubit, 1984; Hughes, 1994). Thus, as discussed below, the impacts of land-based pressure on coral reef communities should be understood in the context of simultaneous impacts from, *inter alia*, climate change, hurricanes, and coral diseases (Ellis *et al.*, 2019; Ramos-Scharrón, Torres-Pulliza and Hernández-Delgado, 2015).

4.2 Coral reef change

Over the past decades, multiple disturbances and anthropogenic stressors have impacted Caribbean coral reefs (Lessios, Robertson and Cubit, 1984; Hughes, 1994). Subjected to stress, Caribbean reefs can exhibit hysteresis: the inability of coral-dominated communities to recover from disturbances due to altered system dynamics (Hughes, 1994; Scheffer *et al.*, 2001). This study assessed coral reef community dynamics between devastating hurricanes that hit Puerto Rico in 1998 and 2017. The resilience of many reef ecosystems might have already been undermined before Hurricane George in 1998 due to the loss of herbivores, the spread of coral diseases, and high levels of land-based pollution, sedimentation, and anthropogenic nutrient loading (Lessios, Robertson and Cubit, 1984; Ramos-Scharrón, Torres-Pulliza and Hernández-Delgado, 2015). This loss of resilience likely precluded the reef ecosystems from fully recovering from the 1998 hurricane and possibly made them more vulnerable to PAC expansion (Wilson, Fan and Edmunds, 2020). Indeed, at all benthic sites in this study, hard coral cover was low at the beginning of the study period, suggesting that the reefs had already undergone a regime shift to coral-poor states dominated by macroalgae and turf.

4.2.1 Patterns of change in hard coral

At the start of the study period, we observed higher hard coral abundance at offshore sites compared to nearshore sites, which could be linked to greater historical exposure to land-based sources of stress (García-Sais *et al.*, 2008). By 2015, differences in hard coral abundance between sites were less pronounced, as hard coral cover had plummeted at all sites. Reefs in Puerto Rico experienced a major bleaching event in 2005, with extensive bleaching reported in eastern Puerto Rico (García-Sais *et al.*, 2008; Wilkinson and Souter, 2008). Our data showed a continued decline in hard coral cover throughout the study period, with no indication of recovery from the 2005 bleaching event.

4.2.2 Widespread proliferation of peyssonnelid algal crust

Concomitantly with the continued decline of hard coral cover, we observed a ubiquitous shift in benthic community composition to PAC domination across both nearshore and offshore sites. PAC are crustose red algae native to the Caribbean (Taylor and Arndt, 1929; Pueschel and Saunders, 2009) that have expanded considerably across Caribbean reefs since the early 2000s (Eckrich and Engel, 2013; Edmunds, Zimmermann and Bramanti, 2019). The mechanisms behind recent PAC proliferation are poorly understood, with suggestions that macroalgae-dominated coral communities – such as our study sites in 2000 – may be more vulnerable to PAC proliferation (Wilson, Fan and Edmunds, 2020). In northeast Puerto Rico, PAC proliferation occurred while both macroalgae and corals declined in relative abundance between 2000 and 2015. Thus, our findings raise the need for rethinking the possible range of alternative states on Caribbean coral reefs beyond the conventional coral-macroalgae phase shifts, and consider an alternative system state dominated by PAC. PAC is less negatively affected by ocean acidification and exposure to high irradiance compared to other coralline algae, contributing to a competitive advantage in a changing climate (Dutra *et al.*, 2016; Cornwall, Diaz-Pulido and Comeau, 2019; Edmunds, Schils and Wilson, 2023). Furthermore, PAC actively deter the settlement of coral larvae, likely leading to hysteresis as corals are unable to re-establish (Wilson, Fan and Edmunds, 2020). More information about PAC ecology and physiology is needed to understand the mechanisms that underlie the recent aggressive expansion of these encrusting algae (Hollister *et al.*, 2021; Stockton and Edmunds, 2021), and to identify management interventions that could be used to limit further PAC expansion (Edmunds, Schils and Wilson, 2023).

5 Remote sensing to inform integrated land-sea management

Thanks to technological and analytical advancements, a range of Earth observation satellite products are now freely available to the scientific community and environmental practitioners. In this study, we explored the extent to which these satellite products can be used to map long-term changes in a tropical coastal environment with coral reefs. We monitored terrestrial environmental change using freely available satellite imagery and a Random Forest classifier. This allowed us to examine watershed-scale patterns of land cover change and estimate how potential land-based pressure on nearshore reefs changed over time. However, the watershed-scale analysis did not capture finer-scale spatial variability in land-sea runoff and missed potentially important point-based sources of pollution, such as wastewater outlets, that cannot be detected from satellite imagery (Santavy *et al.*, 2023). Quantitative modelling of land-sea runoff rates would require complementing the land cover data with a digital elevation model, precipitation data, and information on soil hydraulic properties (Álvarez-Romero *et al.*, 2016; Delevaux *et al.*, 2018). While satellite-derived digital elevation models are freely available and have near-global coverage (Farr *et al.*, 2007), precipitation data and soil hydraulic properties must be measured *in situ* and are rarely available at relevant resolution and extent for watersheds.

Applying marine remote sensing to monitor change in northeastern Puerto Rico proved more challenging compared to terrestrial remote sensing. Different benthic cover types have distinct spectral signatures and could be mapped using remotely sensed optical data (Hochberg, 2003). However, distinguishing between benthic cover types, such as coral and algae, remains challenging due to the optical complexity of the underwater light field in shallow reef environments (Bell *et al.*, 2020; Kutser *et al.*, 2020) and therefore satellite-derived benthic maps have limited thematic resolution and significant uncertainties (Andréfouët *et al.*, 2024; Lutzenkirchen, Duce and Bellwood, 2024). Additionally, most satellite-derived benthic maps are currently only available at a single time point and cannot be used to detect environmental change (Allen Coral Atlas, 2022). In areas characterized by turbid conditions, such as the benthic monitoring sites situated near river mouths in this study, the optical signal from the benthos may not be detectable. Due to the limited thematic resolution, lack of temporal data, and data uncertainties, we relied on traditional field surveys to assess change in the benthic environment.

In addition to mapping the benthos, satellite remote sensing could be used to map key water quality parameters, such as suspended sediment concentration or turbidity (Mobley, 1994; Palola *et al.*, 2025b). However, most satellite algorithms for water quality mapping have been developed in deep waters where the signal is not confounded by bottom reflectance (Werdell *et al.*, 2018). To our knowledge, Allen Coral

Atlas turbidity data is the only available off-the-shelf satellite product suitable for nearshore, shallow coral reef waters (Li *et al.*, 2022). However, this turbidity dataset does not cover our study period (2000-2015). Furthermore, the Allen Coral Atlas turbidity data is characterized by high uncertainty as it assumes spatial homogeneity in water column optical properties. Encouragingly, recent analytical advancements leveraging probabilistic, physics-informed machine learning are enabling water quality mapping in optically shallow coral reef environments without assuming spatial homogeneity (Palola *et al.*, 2025b).

In summary, despite the great potential of remote sensing to inform integrated land-sea management, we found that its application in practice is hindered by the lack of freely available, off-the-shelf algorithms and data products, especially in the marine environment. We highlight here the need for further research developments and technological innovations, including user-friendly tools for mapping key water quality parameters from satellite imagery in optically shallow coastal waters. Accurately estimating water constituents would also improve the accuracy of satellite-derived benthic maps (Theenathayalan and Shanmugam, 2021). Critically, not all variables important for land-sea management can be quantified from optical data, and there is a need to strategically combine remote sensing with in-situ field surveys. On land, to quantitatively model sediment and nutrient runoff, satellite-derived land cover and topography data must be complemented with precipitation and soil hydraulic data measured in the field. At sea, ecological field surveys are still needed to identify the presence or absence of specific species in Puerto Rico, for example, to detect and track PAC proliferation. Additionally, field surveys will remain necessary in highly turbid conditions, where the optical signal of the benthos is not detectable from the water surface. Finally, laboratory experiments may help establish the specific mechanisms underlying the combined impacts of multiple stressors on coral reefs and quantify potential time lags for biological responses to environmental change.

6 Conclusions

A range of terrestrial and marine stressors threaten coral reefs around the world. In northeastern Puerto Rico, we observed drastic declines in coral cover despite a concomitant reduction in landscape development intensity in the adjacent watersheds. Our findings signal that continued reforestation and associated decline in land use-based pressure has not been sufficient to halt the loss of corals in northeastern Puerto Rico. In addition to land use-based pressure, coral reefs in Puerto Rico have been affected by the loss of herbivores, the spread of coral diseases, hurricanes, and heatwaves. It is therefore essential to consider the potential impacts of land cover change in the context of multiple interacting stressors. Our results underline the need to better understand the spatial and temporal patterns of multiple land-based and sea-based stressors and their combined impact on reef ecosystems in Puerto Rico and beyond.

Compared to expensive field studies of limited extent, remote sensing enables low-cost mapping of environmental change and anthropogenic stressors over time and across a broad spatial extent. A range of satellite data products, especially in the terrestrial realm, are already freely available and provide an important source of environmental information for local management. However, in marine remote sensing, shallow coral reef waters still pose a formidable challenge due to the optical complexity of the underwater light field. While both sensor technologies and analytical approaches are rapidly advancing, remote sensing approaches cannot provide the same level of detailed ecological information that can be acquired via traditional field surveys. The high spatial and temporal variability in water column and benthic optical properties in reef environments make it extremely challenging to develop global and regional remote sensing products that have sufficient local accuracy. Nevertheless, recently developed algorithms, such as the SIMA algorithm for water quality mapping in shallow reef environments (Palola *et al.*, 2025b), suggest that what was not possible over our study period (2000-2015) may be possible in the future. We call for a strategic and coordinated combination of field surveys and remote sensing to support integrated land-sea management.

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8 Author Contributions Statement

PP conceived the ideas and designed methodology; EHD collected the data; PP and SH analyzed the data; PP led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Our study brings together authors from different countries, including scientists based in the country where the study was carried out. Where relevant, literature published by scientists from the region was cited and efforts were made to consider relevant work published in the local language.

9 Data accessibility

The Google Earth Engine script for the satellite data analyses and the R scripts for the benthic analyses are freely available in an Open Science Framework repository (please see the link here). The benthic dataset is available upon request from Edwin Hernández-Delgado (email address: edwin.hernandezdelgado(at)gmail.com).

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Appendix A – Full details on the benthic surveys, land cover classification, and landscape development intensity index calculation

Contents

1 Benthic surveys

Table A1 Data items recorded in the benthic surveys.

Code	Species
Acer	*Acropora cervicornis*
Apal	*Acropora palmata*
Aaga	*Agaricia agaricites*
Afra	*Agaricia fragilis*
Agra	*Agaricia grahamae*
Ahum	*Undaria humilis*
Alam	*Agaricia lamarcki*
Aund	*Agaricia undata*
Aten	*Undaria tenuifolia*
Basb	*Briareum asbestinum*
CCA	Crustose coralline algae
Cnat	*Colpophyllia natans*
Cya	Cyanobacteria
Dcyl	*Dendrogyra cylindrus*
Dict	*Dictyota spp.*
Dlab	*Diploria labyrinthiformis*

Dsto	*Dichocoenia stokesii*
Pcli	*Pseudodiploria clivosa*
Pstr	*Pseudodiploria strigosa*
ECA	Erect calcareous algae
Ecar	*Erythropodium caribaeorum*
Efas	*Eusmilia fastigiata*
Ffra	*Favia fragum*
Hali	*Halimeda spp.*
Isin	*Isophyllia sinuosa*
Lcuc	*Helioceris cucullata*
Lob	*Lobophora*
Maur	*Madracis auretenra*
MAC	Macroalgae
Mali	*Mycetophyllia aliciae*
Malc	*Millepora alcicornis*
Mcav	*Montastraea cavernosa*
Mcom	*Millepora complanata*
Mdan	*Mycetophyllia danaana*
Mdec	*Madracis decactis*
Mfer	*Mycetophyllia lamarckiana*
Mlam	*Mycetophyllia ferox*
Mmea	*Meandrina meandrites*
Msqu	*Millepora squarrosa*
Oann	*Orbicella annularis*
Ofav	*Orbicella faveolata*
Ofra	*Montastraea franksi*
Odif	*Oculina diffusa*
PAC	Peyssonnellia Algal Crust
Past	*Porites astreoides*

Pav	Pavement
Pdiv	*Porites divaricata*
Pfur	*Porites furcata*
Ppor	*Porites porites*
Rub	Rubble
Sand	Sand
Spo	Sponge
Ssid	*Siderastraea siderea*
Srad	*Siderastrea radians*
Sros	*Stylaster roseus*
Slac	*Scolymia lacera*
Taur	*Tubastraea aurea*
Turf	Algal turf
Zoa	Zoanthid

2 Land cover classification scheme

51 of the 70 land cover classes described in the United States Geological Survey Gap Analysis Project occur in eastern Puerto Rico (Gould *et al.*, 2008; Gould, Martinuzzi and Páres-Ramos, 2012). These 51 land cover classes were divided into seven simplified categories according to their site features (physiognomy and moisture) described by Gould *et al.* (2008, pp. 143-149): “forest”, “woodland and shrubland”, “flooded coastal forest”, “non-forest vegetation”, “plantations”, “urban” and “water” (Table A2). To ensure good representation of within-type variation, samples were collected from each of the 51 land cover classes.

Table A2 Land cover classification scheme: seven land cover types and the corresponding subclasses (Gould *et al.*, 2008; Gould, Martinuzzi and Páres-Ramos, 2012).

1. Forest
Lowland dry riparian forest
Young secondary moist limestone evergreen and semi deciduous forest
Mature secondary moist limestone evergreen and semi deciduous forest
Mature secondary lowland dry alluvial semi deciduous forest
Young secondary montane wet alluvial evergreen forest
Mature secondary montane wet alluvial evergreen forest
Lowland moist riparian forest
Mature primary and secondary montane wet non-calcareous evergreen elfin woodland cloud forest
Young secondary lowland dry alluvial semi deciduous forest
Mature secondary lowland dry non-calcareous semi deciduous forest
Mature secondary lowland moist evergreen alluvial forest
Young secondary lowland dry noncalcareous semideciduous forest
Young secondary lowland moist evergreen alluvial forest
Mature primary and secondary montane wet non-calcareous evergreen Sierra Palm forest
Mature secondary montane wet noncalcareous evergreen forest

Mature primary and secondary montane wet non-calcareous evergreen Palo Colorado cloud forest
Young secondary montane wet noncalcareous evergreen forest
Mature primary and secondary montane wet noncalcareous evergreen Tabonuco forest
Mature secondary lowland moist evergreen noncalcareous forest
Young secondary lowland moist evergreen noncalcareous forest
2. Woodland and shrubland
Lowland dry riparian shrubland and woodland
Moist limestone shrubland and woodland
Montane wet alluvial shrubland and woodland
Lowland dry alluvial shrubland and woodland
Lowland moist riparian shrubland and woodland
Lowland dry noncalcareous shrubland and woodland
Lowland moist alluvial shrubland and woodland
Montane wet evergreen noncalcareous shrubland and woodland
Lowland moist noncalcareous shrubland and woodland
3. Flooded coastal forest
Mangrove forest and shrubland (mixed closed and open)
Freshwater Pterocarpus swamp (closed forest)

4. Non-forest vegetation
Emergent herbaceous saline wetlands (Herbaceous)
Emergent herbaceous non-saline wetlands (Herbaceous)
Dry grasslands and pastures
Seasonally flooded herbaceous saline wetlands (Grassland)
Hay and row crops (Herbaceous)
Seasonally flooded herbaceous non-saline wetlands (Grassland)
Moist grasslands and pastures
5. Plantations
Woody agriculture and plantations: Palm plantations
Lowland moist abandoned and active coffee plantations
Montane wet evergreen abandoned and active coffee plantation
6. Urban
High-density urban development (Developed)
Low-density urban development (Developed)
Artificial barrens (Barrens)
7. Water
Freshwater
Salt water

3 Landscape development intensity index calculation

We calculated the landscape development intensity (LDI) index as follows: $LDI_{watershed} = (\sum \% LC_i \times LDI_i)/100$, where $\%LC_i$ is the percent cover of land cover type i, and LDI_i is the corresponding LDI coefficient (Table A3) (Brown and Vivas, 2005; Oliver, Lehrter and Fisher, 2011). The largest values LDI coefficients are assigned to land cover types associated with the greatest runoff potential (i.e., impervious surfaces associated with urban land cover) (Oliver, Lehrter and Fisher, 2011).

Table A3. Coefficients used for each land cover type in the landscape development intensity index calculations (Oliver, Lehrter and Fisher, 2011).

Forest	Woodland and Shrubland	Flooded Coastal Forest	Non-forest vegetation	Plantations	Urban	Water
1	2.06	1	3.17	1	5.065	1

4 References

Brown, M.T. and Vivas, M.B. (2005) ‘Landscape Development Intensity Index’, *Environmental Monitoring and Assessment*, 101(1), pp. 289–309. Available at: https://doi.org/10.1007/s10661-005-0296-6.

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Appendix B – Additional results

Table B1. Land cover change in the Luquillo watershed between 2000 and 2015. The units are in square kilometers.

	Forest	Woodland and Shrubland	Flooded Coastal Forest	Non-forest vegetation	Plantations	Urban	Water	Total
2000-2005	134.0	8.3	13.9	80.8	4.6	24.2	1.9	267.8
2005-2010	142.2	8.8	16.4	67.3	9.2	22.0	1.7	267.8
2010-2015	140.4	8.9	20.5	55.4	19.8	20.5	2.3	267.8

Table B2. Land cover change in the Fajardo-Ceiba watershed between 2000 and 2015. The units are in square kilometers.

	Forest	Woodland and Shrubland	Flooded Coastal Forest	Non-forest vegetation	Plantations	Urban	Water	Total
2000-2005	48.2	4.4	6.3	33.6	0.2	11.6	1.3	105.6
2005-2010	53.6	3.4	6.9	27.8	2.0	10.2	1.5	105.6
2010-2015	59.5	3.2	6.9	22.6	1.5	10.0	1.8	105.6

5 Chapter 2

Literature reviews can play an important role in advancing science (Baumeister & Leary, 1997; Fausch et al., 2002). Literature reviews can describe and synthesize prevalent methodological approaches (Suárez-Castro et al., 2018; Tornwall et al., 2015; Uroy et al., 2021; Zeller et al., 2012), outline new research tools and opportunities (Erős & Lowe, 2019; Torgersen et al., 2021; Yu et al., 2019), and provide guidance on the selection and application of methods for data collection and analysis (Galpern et al., 2011; Tischendorf & Fahrig, 2000). Identifying and summarizing promising methodological approaches is particularly important in the context of rapid technological advancements, which increasingly enable data collection and analysis at multiple spatial and temporal scales (Erős & Lowe, 2019; Torgersen et al., 2021).

The aim of Chapter 2 was to review the dominant approaches to the scientific study of coastal nutrient connectivity in tropical and subtropical environments. Based on the results of the review, I identified 15 future research needs for coastal nutrient connectivity research. Finally, to help address these research needs, I presented an integrated, spatially explicit, and multi-scale research approach for nutrient connectivity studies called “nutrientscape ecology”.

Nutrientscape ecology: a whole-system framework to support the understanding and management of coastal nutrient connectivity

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Keywords

landscape ecology; nitrogen; phosphorus; seascape; social-ecological systems; systematic literature review

Abstract

Context

Nutrient connectivity across landscapes and seascapes plays a fundamental role in shaping the structure and function of coastal ecosystems. A whole-system understanding of the spatial-temporal dynamics and ecological significance of nutrient connectivity is essential for developing more effective coastal management strategies.

Objectives

The aim of this study is to summarize the recent state-of-science in coastal nutrient connectivity research and identify future research needs. We then propose an integrated and solution-oriented scientific framework to advance a landscape ecology approach to address the research needs.

Methods

We conducted a systematic literature review of 77 studies on nutrient flows in tropical and subtropical coastal marine environments (coral reefs, mangroves, and seagrasses) that have been conducted over the past decade.

Results

Few studies considered interlinkages between multiple coastal habitats. Most (73%) studies that examined ecological impacts of nutrient connectivity focused on anthropogenic terrestrial runoff and indicated negative ecological responses to nutrients. Few studies adopted landscape ecology concepts and methods. We identified 15 research needs for advancing coastal nutrient connectivity research. Urgent research needs include the impacts of climate change on nutrient connectivity, the interactions between multiple nutrient pathways across habitats, and the social-economic drivers and impacts of change. An integrated framework that we term nutrientscape ecology is presented as a way forward.

Conclusions

The nutrientscape ecology framework emphasizes the spatially explicit study of pattern-process relationships across multiple scales and leverages concepts and methods from landscape ecology and systems thinking. We seek to inspire interdisciplinary research collaborations and the development of a predictive science of nutrient connectivity that informs coastal management.

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1 Introduction

Nutrients are the critical building blocks of all living organisms (Fennel & Testa, 2019; Vitousek & Howarth, 1991). In both terrestrial and aquatic environments, the availability of key nutrients such as nitrogen and phosphorus is the most common limiting factor for primary productivity (Bristow et al., 2017; Elser et al., 2007; Ryther & Dunstan, 1971). Indeed, nutrient availability can produce cascading effects in the food web from primary producers to higher trophic levels, thereby fundamentally shaping ecosystem structure and function (Peñuelas et al., 2020; Vitousek & Howarth, 1991). Nutrient availability is often determined by nutrient connectivity, defined here as the nutrient flows that connect locations in space and time, forming spatial-temporal linkages between entities such as food webs, habitats, and ecosystems (Galloway et al., 2004; Loreau et al., 2003; Tuerena et al., 2022). Nutrient flows within and across ecosystems are highly complex as they operate and interact across multiple spatial and temporal scales (Adam et al., 2020; Fong & Fong, 2018; Graham et al., 2018; Shantz et al., 2015; Wang et al., 2018b).

Human activities have significantly modified the flow of nutrients over millennia (Doughty et al., 2016; Peñuelas et al., 2020). Changes to nutrient connectivity across ecosystems include the disruption of animal-vectored nutrient pathways. For example, seabirds foraging at sea transport nutrients through guano to land where they roost and nest (Croll et al., 2005). These seabird-vectored nutrient subsidies can subsequently leach into adjacent coastal waters (Benkwitt et al., 2021a; Graham et al., 2018; Savage 2019). However, on many tropical islands, seabird populations have drastically declined due to the introduction of invasive rats by humans (Dias et al., 2019; Jones et al., 2008). As a result, the magnitude of seabird-vectored nutrient flows between land and sea has diminished (Benkwitt et al., 2021a). In addition to the disruption of animal-vectored nutrient pathways, new anthropogenic sources of nutrients have been created through, for example, the runoff of industrial fertilizers from agriculture, the release of wastewater, fossil fuel combustion, amplified fire regimes, and aquaculture (Peñuelas et al., 2020; Seitzinger et al., 2010; Tang et al., 2021; Wang et al., 2020). Furthermore, various human modifications of the landscape and seascape, such as the building of channels, impervious surfaces, and dredging, have altered the location and speed of nutrient flows (McCann et al. 2021). The human-induced changes in the location, timing, magnitude, and interactions of nutrient flows have had significant and cascading impacts on both terrestrial and aquatic ecosystems (Borer et al., 2014; Galloway et al., 2003). For example, in coral reef ecosystems, changes in nutrient connectivity have altered coral reef biogenic structure, community composition, and ecological functions (Benkwitt et al., 2021b; Fabricius, 2005; Shantz et al., 2015).

Changes in nutrient connectivity may lead to irreversible changes in ecosystems (Breitburg et al., 2018; Steckbauer et al., 2011). For instance, increased anthropogenic nutrient loading to coastal waters has resulted in widespread eutrophication and higher rates of organic matter deposition to the seafloor (Maúre et al., 2021). In some cases, eutrophication has resulted in extreme deoxygenation and the formation of “dead zones”, as documented, for example, in the northern Gulf of Mexico (Dodds, 2006; Rabalais & Turner, 2019). Once a certain threshold of deoxygenation is breached, the resulting biogeochemical feedbacks may lead to hysteresis, i.e. the inability of the ecosystem to recover even when the nutrient load to coastal waters is decreased (Steckbauer et al., 2011). These “dead zones” are becoming increasingly widespread in coastal ecosystems worldwide (Diaz & Rosenberg, 2008; Malone & Newton, 2020; Rabalais & Turner, 2019). The magnitude and geographical extent of eutrophication and hypoxia in coastal waters globally suggest that humanity has already crossed the planetary boundary for biogeochemical flows, increasing the risk of broad-scale abrupt or irreversible environmental changes (Bunsen et al., 2021; Richardson et al., 2024; Rockström et al., 2009; Rose et al., 2024) and indicating an urgent need for improved management of nutrient connectivity worldwide (Nash et al., 2017). Altered nutrient connectivity is a key driver of marine ecosystem regime shifts globally, with impacts compounded by multiple interacting stressors, including global warming and overfishing (Levin & Möllmann, 2015; Rocha et al., 2015).

Recent research has shown that effective management of nutrient connectivity and restoration of beneficial animal-vectored nutrient flows and feedbacks could strengthen the resilience of coastal ecosystems to other stressors, such as the increased frequency and magnitude of extreme weather events caused by climate change (Benkwitt et al., 2024; Gove et al., 2023; Mcleod et al., 2019). Due to the contrasting ecological impacts of nutrient flows from anthropogenic and non-anthropogenic sources, the management of coastal nutrient connectivity would ideally consist of mitigative and restorative actions. For example, a mitigative intervention could be the reduction of anthropogenic nutrient runoff from land to sea to decrease detrimental effects on coral reef physiology (D'Angelo & Wiedenmann, 2014; Fabricius, 2005). An example of a land-sea restorative intervention is the restoration of seabird populations and the associated beneficial seabird-vectored nutrient flows, which can enhance coral reef ecosystem functions and support the recovery of coral reefs from extreme heat waves (Benkwitt et al., 2021b, 2024).

It is increasingly recognized that developing improved management of nutrient connectivity and effective resilience-based management of coastal ecosystems requires a whole-system understanding of the context-specific effects of nutrient flows and their various sources and interactions across multiple spatial-temporal scales (Malagó & Bouraoui, 2021; Shantz & Burkepile, 2014; Vigouroux & Destouni, 2022). However, traditional field-based surveys are typically characterized by data collection at a single spatial scale within a narrow temporal window, thereby only forming a collection of snapshots of the system's patterns and processes (Knee et al., 2016; Wang et al., 2018a). Furthermore, Sitters et al. (2015) suggested that research has largely focused on unidirectional flows of nutrients, with limited consideration of reciprocal nutrient flows between spatially connected ecosystems. Indeed, our understanding of nutrient connectivity, particularly its spatial-temporal patterns, ecological significance, and causative pathways linked to recent human activities, still presents important knowledge gaps (Fong & Fong, 2018; Nash et al., 2017; Sitters et al., 2015). To better inform resilience-based environmental management and restoration strategies, integrated research approaches that seek to understand nutrient connectivity from a whole-system perspective are needed (Riechers et al., 2021). Although calls for a more integrated land-sea management are many, a concomitant shift is lacking in the scientific framework and the major funding programs to provide the integrated science at spatial and temporal scales that are required for whole-system decision-making (Álvarez-Romero et al., 2011; Beger et al., 2010).

In this study, we conducted a systematic literature review to understand the dominant approaches to the scientific study of coastal nutrient connectivity, evaluate key knowledge gaps, and systematically identify future research needs. We were especially interested in evaluating the application of landscape ecology concepts and methods to coastal nutrient connectivity. We focused the scope of this study on three major marine coastal habitat types in tropical and subtropical environments: coral reefs, seagrass meadows, and mangroves. These coastal habitat types support high biodiversity and provide essential ecosystem services, yet they are degrading rapidly due to multiple anthropogenic drivers of change (Barlow et al., 2018; Duarte, 2002; Goldberg et al., 2020). We anticipate, however, that many of the general recommendations emerging from our literature review will also be applicable to temperate coastal ecosystems (Lønberg et al. 2021). We addressed the following research questions in our literature review: 1) Which nutrient pathways have received the most and the least research attention over the last ten years? 2) What are the dominant methods and spatial-temporal scales of data collection? 3) How prevalent is the use of integrative conceptual frameworks, such as landscape ecology or integrated land-sea approaches, in studying coastal nutrient connectivity? 4) How often do studies consider the ecological impacts of nutrient connectivity or the management implications of their results? Building on the results of the systematic literature review, we then identified 15 future research needs for nutrient connectivity research in tropical and subtropical coastal environments. Finally, to help advance a scientific framework to address these research needs, we propose an integrated, spatially explicit, and multiscale framework for nutrient connectivity studies that we refer to as nutrientscape ecology.

2 Methods

2.1 Key concepts and definitions

We define the key concepts used in this study to establish conceptual clarity. By *nutrient connectivity*, we refer to the flows of nutrients in space and time that connect food webs, habitats, and ecosystems. A *connection type* defines which realms (i.e., land, air, sea, sediment) are connected by nutrients. A *nutrient pathway* is a specific type of connection process, such as atmospheric deposition or seabird-vectored nutrients. A *nutrient flow* is the physical movement of nutrients in space and time. The flow rate can be quantified with units such as m^3/s or µg/h. By definition, a nutrient flow occurs between a source system and a recipient system. A *nutrient source* is the location from which a nutrient flow originates. For example, a sewage outfall is an anthropogenic nutrient source. Nutrient connectivity between two entities, such as a seagrass meadow and a coral reef, can consist of multiple nutrient pathways and may be unidirectional or reciprocal (Sitters et al., 2015).

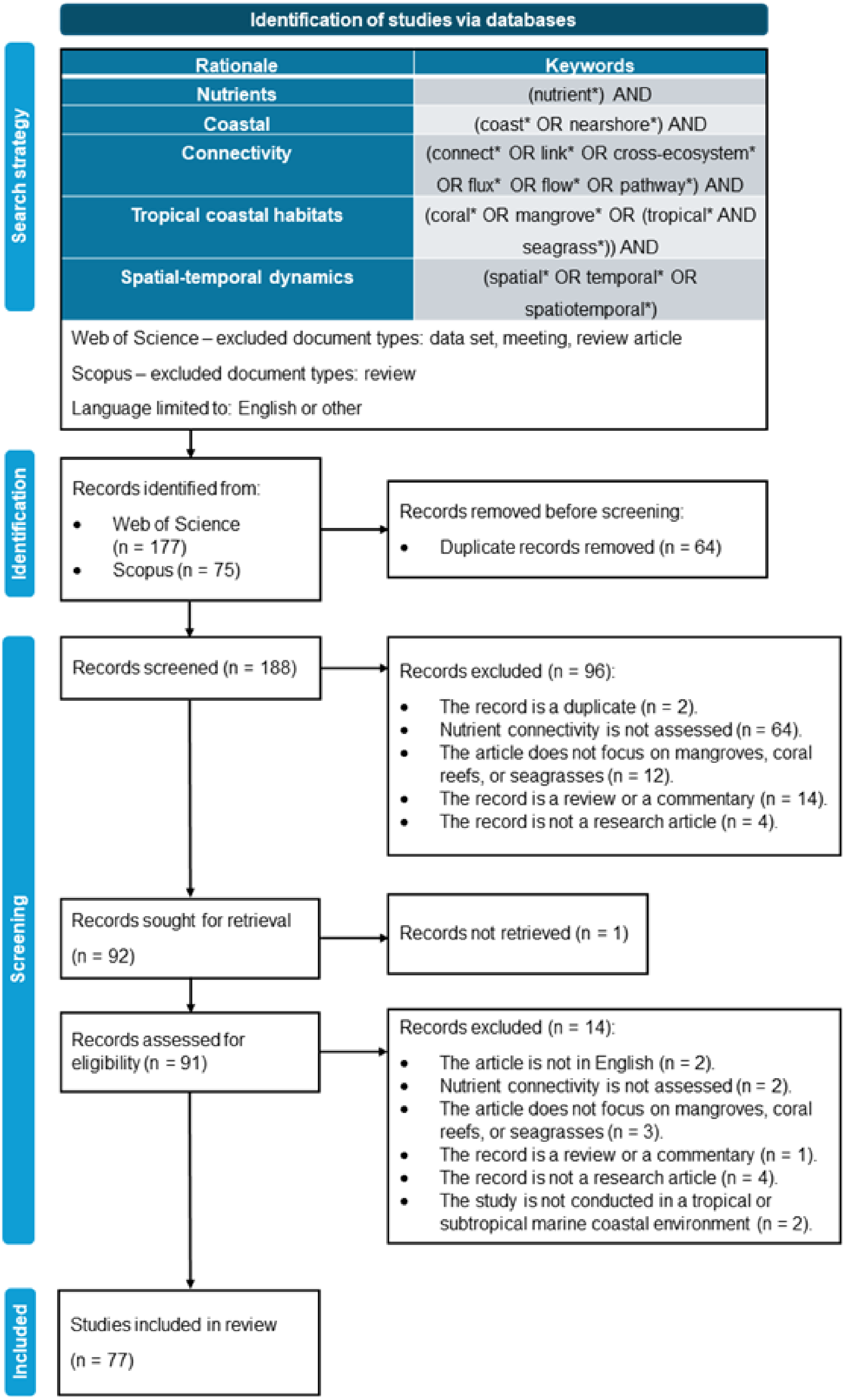
To understand the spatial-temporal dynamics of nutrient connectivity, it is essential to study spatial and temporal patterns (Risser, 1990). Landscape ecology focuses on pattern-process relationships by quantifying spatial and temporal patterns at a range of scales and investigating their ecological consequences (Turner, 1989; Wiens, 2002). Although a relatively young science, landscape ecology has made important contributions to our understanding and management of the linkages between nutrient pathways and landscape patterns in river catchments (Erős & Lowe, 2019; Hunsaker & Levine, 1995; Likens & Bormann, 1974; Torgersen et al., 2021). Here, we define key concepts applied in landscape ecology. A *spatial (temporal) pattern* refers to a structural feature of the landscape or seascape or a spatial (temporal) distribution (Turner, 1989; Wedding et al., 2011). Landscape and seascape spatial patterns can be quantified using *spatial pattern metrics* that measure the *composition* or *configuration* of the structural features studied (Pittman et al., 2021; Wedding et al., 2011). Composition metrics quantify the type, number, and proportion of the landscape and seascape structural features. Configuration metrics quantify the spatial arrangement of patches and mosaics, such as the juxtaposition of different habitat patches, fractal dimension, patch isolation or contagion (Fahrig et al., 2011; Turner & Gardner, 2015), and spatial gradients of structure, such as surface morphometry (Kedron & Frazier, 2019; Lausch et al., 2015). Importantly, the observation and measurement of the pattern depends on *scale*, i.e., the spatial or temporal dimension of the study, determined by both *resolution* and *extent*. *Resolution* is the precision of measurement (or *grain*), while *extent* refers to the area and duration of the study (Turner & Gardner, 2015; Wiens, 1989). Finally, *context* describes the social-ecological surroundings of a focal area in space and time (Fahrig et al., 2011; Turner & Gardner, 2015).

2.2 Systematic literature review

We conducted a systematic literature review of coastal nutrient connectivity studies in tropical and subtropical coastal environments over the past decade (01/01/2012-29/08/2022). We followed the guidelines of the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) extension in ecology and evolutionary biology (O'Dea et al., 2021). The literature search was conducted on the Web of Science and Scopus on 29/08/2022. All the databases available on these platforms were included in the search. The steps of the literature search and screening strategy are provided in the PRISMA 2020 flow diagram (Fig. 1).

The list of studies included in the review and the justifications for the exclusion of each article are provided in Appendix A (Tables A.1, A.2). The reporting items only relevant for quantitative meta-analyses were excluded (Appendix A, Table A.3). A list of data items recorded from each study is provided in Appendix A, Table A.4.

To address Research Question 3 “How prevalent is the use of integrative approaches, such as landscape ecology or integrated land-sea frameworks?”, the keywords used were: “integrated land-sea”, “ridge-to-reef”, “summit-to-sea”, and “catchment-to-sea”, spelled with or without hyphens. Additionally, we searched the studies for “landscape” or “seascape” ecology and the associated key concepts (see section 2.1).



Rationale	Keywords
Nutrients	(nutrient*) AND
Coastal	(coast* OR nearshore*) AND
Connectivity	(connect* OR link* OR cross-ecosystem* OR flux* OR flow* OR pathway*) AND
Tropical coastal habitats	(coral* OR mangrove* OR (tropical* AND seagrass*)) AND
Spatial-temporal dynamics	(spatial* OR temporal* OR spatiotemporal*)

Web of Science – excluded document types: data set, meeting, review article

Scopus – excluded document types: review

Language limited to: English or other

Records identified from:

- Web of Science (n = 177)
- Scopus (n = 75)

Records removed before screening:

- Duplicate records removed (n = 64)

Records screened (n = 188)

Records excluded (n = 96):

- The record is a duplicate (n = 2).
- Nutrient connectivity is not assessed (n = 64).
- The article does not focus on mangroves, coral reefs, or seagrasses (n = 12).
- The record is a review or a commentary (n = 14).
- The record is not a research article (n = 4).

Records sought for retrieval (n = 92)

Records not retrieved (n = 1)

Records assessed for eligibility (n = 91)

Records excluded (n = 14):

- The article is not in English (n = 2).
- Nutrient connectivity is not assessed (n = 2).
- The article does not focus on mangroves, coral reefs, or seagrasses (n = 3).
- The record is a review or a commentary (n = 1).
- The record is not a research article (n = 4).
- The study is not conducted in a tropical or subtropical marine coastal environment (n = 2).

Studies included in review (n = 77)

Fig. 1 The PRISMA 2020 flow diagram describing each stage of the literature search and screening process adapted from Page et al. (2021). The search strategy shows the rationale for the inclusion of keywords in the search string applied in this systematic literature review. The asterisk (*) at the end of the keyword broadens the search by representing any group of characters. This allows for capturing, for example, the plural forms of the keywords (http://www.prisma-statement.org/References).

2.3 Limitations

Although we focus on recent studies, we recognize that a large body of literature has evolved since the pioneering studies on coastal nutrient connectivity in the mid-twentieth century (Hutchinson, 1948; Odum, 1953, 1968). Our interest in recent scientific practice meant that we designed the search strategy to capture only studies published in the last ten years that examined 1) nutrients, 2) connectivity, 3) tropical and subtropical coastal marine ecosystems, and 4) spatial-temporal dynamics. Studies that could be relevant for coastal nutrient connectivity were excluded if they failed to explicitly mention relevant search terms in the abstract, keywords, or title. For example, studies that mapped the distribution of sediments or organic matter in coastal environments were not retrieved if they did not refer to nutrients and connectivity in the framing of their study. This might partly explain the low number of remote sensing studies captured in this review. Similarly, we examined the prevalence of integrative approaches by searching for concepts that we considered to be well-established in the study of land-sea connections in tropical and subtropical environments, such as “integrated land-sea” (Álvarez-Romero et al., 2011) and “ridge-to-reef” (Carlson et al., 2019) (see section 2.2). We acknowledge that this search may omit some studies that do not refer to this established terminology of land-sea studies. To partially address this limitation, we also quantified the number of studies that sampled both marine and terrestrial environments. It should also be noted that the literature review was limited to peer-reviewed journal articles in English, thereby excluding gray literature and articles published in other languages.

3 Results

3.1 Nutrient pathways and coastal habitat types

The majority of studies examined unidirectional nutrient pathways from land or oceanic sources to a single focal marine coastal habitat (Fig. 2). Seventy-eight percent of the reviewed studies focused on one of the three marine coastal habitat types (coral reefs, mangroves, and seagrasses), 15% included two habitat types, and 7% included three habitat types (Fig. 2A). Coral reefs were the most studied single habitat type (49%), followed by mangroves (29%) and seagrass meadows (1%).

Most studies (62%) focused on a single focal nutrient pathway (Fig. 2B). Land-sea runoff and submarine groundwater discharge received the most research attention (62% and 29%, respectively). A third of studies (33%) focused on anthropogenic nutrient sources, and 28% examined nutrient flows from non-anthropogenic sources. The remainder (39%) did not explicitly distinguish between anthropogenic and other sources of nutrients. Eighty-one percent of the studies that assessed nutrient flows from non-anthropogenic sources were focused on oceanic sources of nutrients, while the rest (19%) studied animal-derived nutrients.

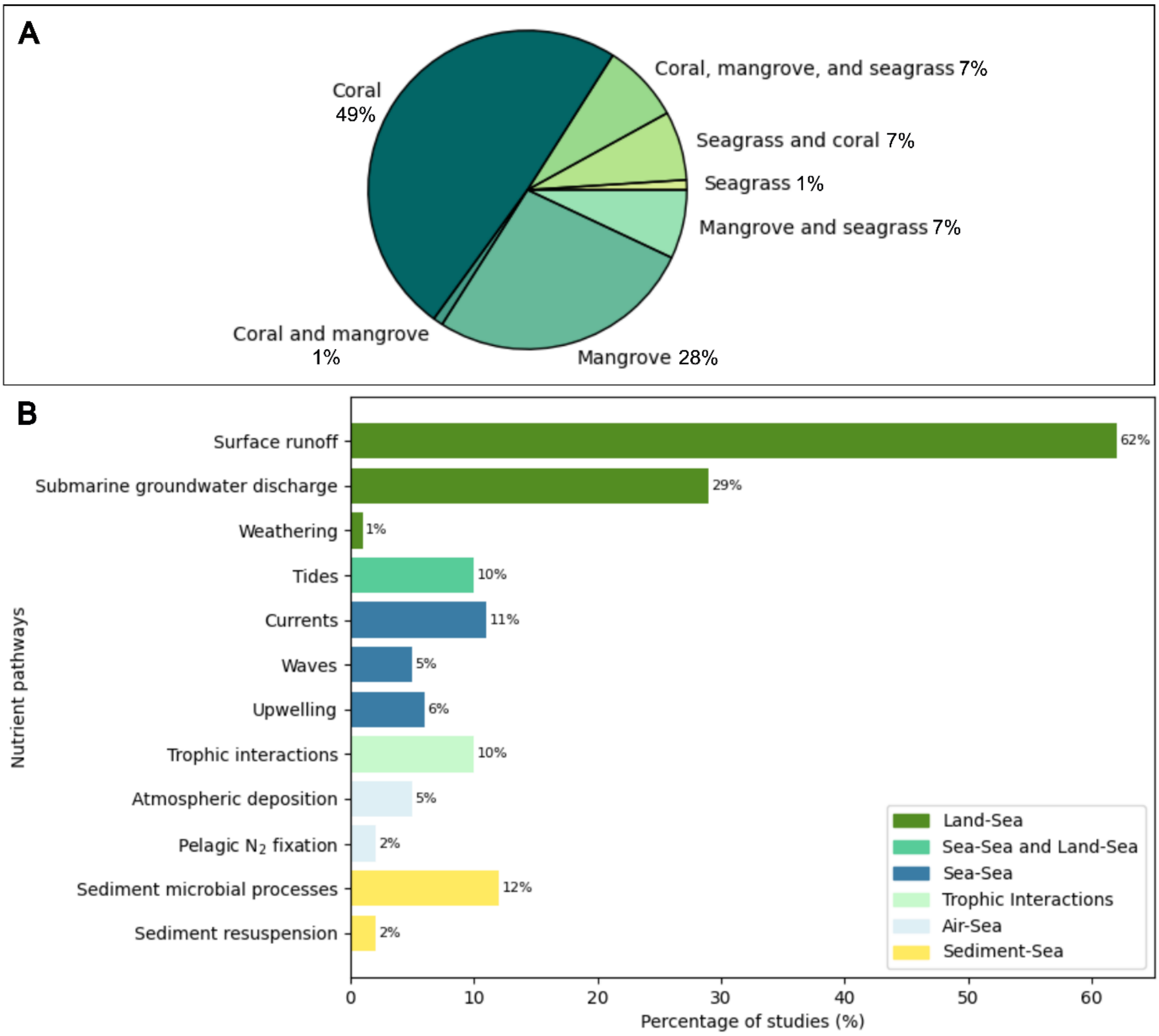


Fig. 2 The proportion of studies that focused on A) one or more coastal habitat types (coral, mangrove, and seagrass) and B) different nutrient pathways. As a single study could investigate multiple nutrient pathways, the sum of the percentages is more than 100%. Nutrient pathways of the same connection type are shown in the same color.

3.2 Conceptual frameworks

Amongst studies focused on connections between land and sea, 12% referred to integrative approaches for coastal studies, such as the “ridge-to-reef” (Amato et al., 2020; Delevaux et al., 2018, 2019; Shuler et al., 2020; Shuler & Comeros-Raynal, 2020) or the “integrated land-sea” frameworks (Comeros-Raynal et al., 2021; Rodgers et al., 2012; Sakamaki et al., 2022). Additionally, two studies referred to a “catchment-to-sea” approach (Comeros-Raynal et al., 2021; Quak et al., 2016).

One study explicitly employed the landscape ecology framework (Rodgers et al., 2012). Rodgers et al. (2012) quantified spatial patterns of coastal landcover and land use and modeled the relationship between a watershed health index and coral reef health. Additionally, some studies applied key concepts or metrics associated with landscape ecology (e.g. spatial pattern, context, and configuration - see section 2.1), without explicitly situating their study in the wider landscape ecology conceptual framework and scientific literature. Seventy-six percent of studies considered spatial patterns, for example by discussing the spatial distribution or identifying a spatial gradient of nutrient concentrations. However, as many as 16 of these studies did not use the concept of “spatial pattern” explicitly, indicating a limited take up of landscape ecology ideas within the coastal nutrient connectivity literature. Several studies quantified spatial patterns using landscape ecology spatial metrics such as “bottom roughness” (Amador et al., 2020), “habitat complexity” (Delevaux et al., 2018), “percent benthic cover” (Comeros-Raynal et al., 2021; Li et al., 2015; Yoshioka et al., 2016), without referring to landscape ecology as a conceptual framework. A small number of studies implicitly discussed the importance of landscape and seascape context and configuration (e.g. Cantarero et al., 2019; Delevaux et al., 2018; Quak et al., 2016; Signa et al., 2017). One study used the concept “configuration” (Comeros-Raynal et al., 2021) and none used the concept “context” in the spatially explicit sense defined in landscape ecology.

3.3 Scale

Spatial and temporal scales were frequently inadequately quantified and reported. In many cases, spatial resolution and extent had to be approximated from maps. Half of all studies provided a rationale for choosing the spatial or temporal scale(s). Where a rationale was provided, almost half of such justifications concerned temporal scale. For example, a common justification for the choice of temporal scale was the importance of capturing tidal and seasonal variability or short-term rainfall events (e.g. Smith et al., 2016; Tait et al., 2017; Wadnerkar et al., 2019).

Amongst studies that collected spatial data (67 of 77), 41% provided information on spatial resolution. The most reported spatial resolutions were between 100 m and 1,000 m (12 studies) (Fig. 3). For studies that collected discrete samples at multiple sites over the study area, spatial resolution was defined based on the distance between sample sites. For example, the spatial resolution of a study with twenty equally spaced sample sites within a study area of 50 m x 40 m (2 km^2) would be 10 m. Nine percent of the reviewed studies collected data at multiple spatial resolutions. In terms of spatial extent, the majority (64%) of studies were “local” (defined here as <50 km^2), while 27% were “regional” (defined here as >50-10,000 km^2). The remaining 9% of the reviewed studies covered study extents larger than 10,000 km^2.

Nineteen studies could not be assessed for their temporal resolution because they did not collect temporal data or because the authors did not report the resolution. Similarly, six studies could not be assessed for their temporal extent. Almost a third of the studies relied on a single field mission, while one-quarter of the studies conducted two to four field missions in a single year. Consequently, more than 50% of studies did not consider year-to-year variability in nutrient flows, and almost one third did not capture seasonal variability. Twelve percent of studies collected data at multiple temporal scales.

A trade-off between spatial and temporal resolutions was apparent, as the studies that relied on only one sample site tended to justify this by the need to collect high-resolution temporal data (Gleeson et al., 2013; Kaiser et al., 2015; Reithmaier et al., 2021; Starke et al., 2020; Terada, 2022). Similarly, there was a trade-off between resolution and extent. For example, studies with very high temporal resolutions (<1 hour) tended to have a limited temporal extent (1-7 days), and vice versa.

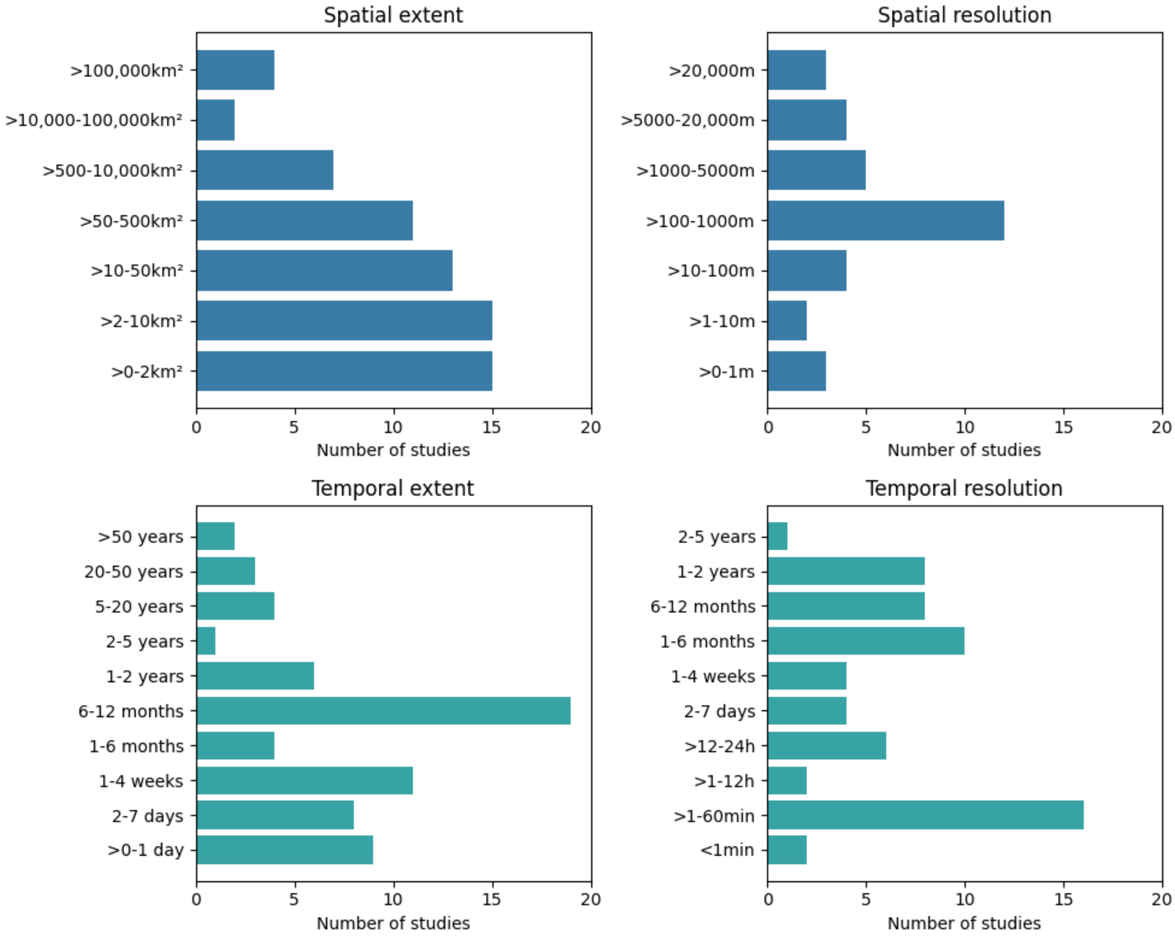
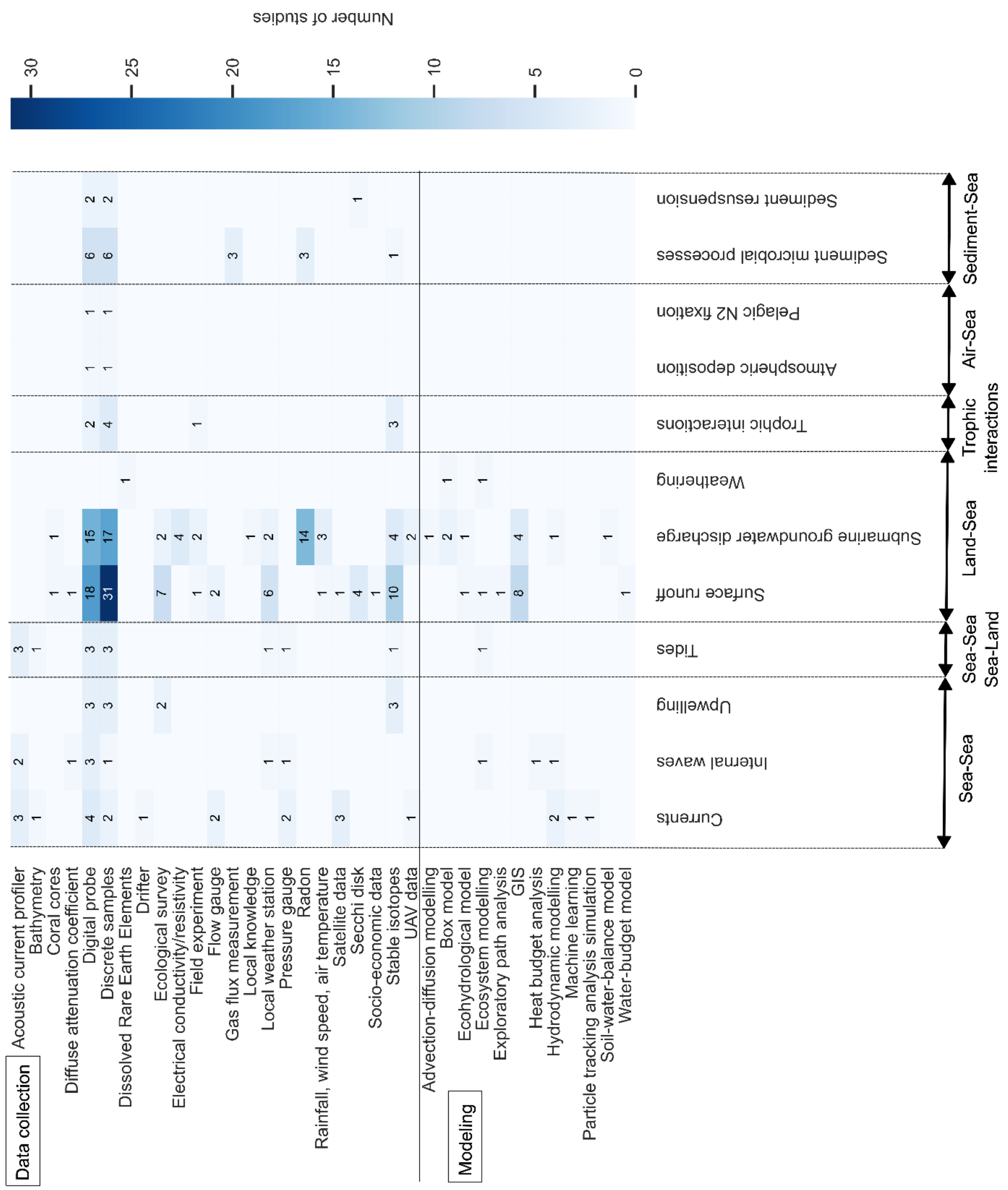


Fig. 3 The number of studies in the reviewed literature that collected data at the specified spatial/temporal extents and resolutions.

3.4 Methods

Most studies focused on mapping nutrient flows through in-situ sampling at point locations (Fig. 4). Not counting coastal groundwater, rainwater, and mangrove samples, only one study sampled both marine and terrestrial environments (Quak et al., 2016). Few studies used field experiments, social-economic data, local knowledge, remotely-sensed data, or machine learning (Fig. 4).

Stable isotope analysis was the most prevalent method for identifying the source of nutrients (anthropogenic vs non-anthropogenic). For example, several studies used the elevated ratio of the nitrogen isotope N15:N14 (δ15N) as an indicator of nutrient flows from wastewater discharge (Amato et al., 2020; Fong et al., 2020; Richardson et al., 2017; Sanchez et al., 2020), aquaculture (Li et al., 2015), and runoff from agricultural lands (Sakamaki et al., 2022). In addition to δ15N, some studies analyzed the carbon isotope δ13C to distinguish between terrestrial and oceanic nutrient sources (Perez et al., 2020; Sakamaki et al., 2022). Additionally, radon and radium isotopes were used to estimate submarine groundwater discharge (e.g. Amato et al., 2020; Gleeson et al., 2013; Richardson et al., 2017; Shuler et al., 2020; Smith et al., 2016). In addition to stable isotope analysis, spatial and/or temporal co-occurrence of likely nutrient sources and increased nutrient concentrations were commonly used as evidence of a causal connection. For example, Limates et al. (2016) mapped the spatial and temporal co-occurrence of poor water quality, mangroves, seagrass meadows, septic systems, storms, and tourist arrivals to determine the sources of coastal water pollution and nutrient loading in the Philippines.



	Currents	Internal waves	Upwelling	Tides	Surface runoff	Submarine groundwater discharge	Weathering	Trophic interactions	Atmospheric deposition	Pelagic N2 fixation	Sediment microbial processes	Sediment resuspension
Data collection												
Acoustic current profiler	3	2		3								
Bathymetry	1			1								
Coral cores					1	1						
Diffuse attenuation coefficient		1			1							
Digital probe	4	3	3	3	18	15		2	1	1	6	2
Discrete samples	2	1	3	3	31	17		4	1	1	6	2
Dissolved Rare Earth Elements							1					
Drifter	1											
Ecological survey			2		7	2						
Electrical conductivity/resistivity						4						
Field experiment					1	2		1				
Flow gauge	2				2							
Gas flux measurement											3	
Local knowledge						1						
Local weather station		1		1	6	2						
Pressure gauge	2	1		1								
Radon						14					3	
Rainfall, wind speed, air temperature					1	3						
Satellite data	3				1							
Secchi disk					4							1
Socio-economic data					1							
Stable isotopes			3	1	10	4		3			1	
UAV data	1					2						
Modeling												
Advection-diffusion modelling						1						
Box model						2	1					
Ecohydrological model					1	1						
Ecosystem modelling		1		1	1		1					
Exploratory path analysis					1							
GIS					8	4						
Heat budget analysis		1										
Hydrodynamic modelling	2	1				1						
Machine learning	1											
Particle tracking analysis simulation	1											
Soil-water-balance model						1						
Water-budget model					1							

Fig. 4 Data collection and modeling methods applied to the study of different nutrient pathways in the reviewed literature. The value in each cell indicates how many studies applied a specific method (listed on the y-axis) to the study of a specific nutrient pathway (listed on the x-axis). The different nutrient pathways are grouped together according to their corresponding connection type. Animal-vectored nutrient pathways

are included here as a separate category, as animals may connect different realms depending on the species in question.

3.5 Ecological impacts and management

Twenty-one percent of studies discussed the effects of climate change on nutrient connectivity. Most of these studies only briefly mentioned potential impacts, and none included “climate change” in their title. Twenty percent of studies assessed the ecological impacts of nutrient connectivity, including effects on coral trophic strategy and growth, coral-to-macroalgae regime shifts, phytoplankton production, and fish density (Table B.1, Appendix B). Most (73%) of these studies assessed the ecological impacts of anthropogenic nutrient sources and terrestrial runoff. Fifty-one percent of studies briefly mentioned the potential implications of their results for management applications, and 7% included management as a research focus and provided specific recommendations for managers. The ecological impacts and guidance for management identified in the reviewed studies are provided in Appendix B (Tables B.1 and B.2).

4 Discussion

The importance of land-to-sea nutrient flows for nearshore marine ecosystems has long been recognized (Fabricius, 2005; Odum, 1968). A large body of research has provided insights into the dynamics of nutrient flows in different coastal environments, from tide-driven mangrove estuaries (Gleeson et al., 2013; Smith et al., 2016) to wave-driven coral reef environments (Adam et al., 2020; Huang et al., 2012). The causal links between watershed land use change, increased nutrient loading to coastal waters, and decreased water quality are well-established (Fabricius, 2005; Kagalou et al., 2012; Oliver et al., 2011). Building on this previous work, this systematic literature review advances research on coastal nutrient connectivity by identifying 15 research needs that must be addressed to better integrate nutrient flows into coastal management strategies and spatial planning (Table 1). Following a brief discussion of the key findings of the literature review, we present a novel integrated approach for coastal nutrient connectivity studies that we call nutrientscape ecology, aimed at supporting future studies that address the identified research needs. We recognize that related science may have occurred before our decadal review period, however, our focus was on the most recent state of practice in studying coastal nutrient connectivity.

Table 1 Future research needs in nutrient connectivity studies in tropical and subtropical coastal environments.

Research needs	
Nutrient pathways and coastal habitat types	
1	Investigating the interactions between multiple nutrient pathways rather than focusing on a single pathway.
2	Studying nutrient flows and their ecological impacts across terrestrial and marine environments and multiple coastal habitat types.

3	Advancing the understanding of the different nutrient sources (anthropogenic and non-anthropogenic) contributing to the observed patterns of nutrient flows and hotspots.
4	Studying the dynamics and ecological significance of animal-vectored nutrient pathways.
Scale	
5	Developing an understanding of how the spatial-temporal patterns and ecological impacts of nutrient connectivity change across scales.
6	Collecting long-term datasets to differentiate between long-term trends and short-term variability.
Conceptual frameworks and methods	
7	Developing and applying a conceptual framework that supports whole-system research and cross-disciplinary study of coastal nutrient connectivity.
8	Recognizing the importance of local knowledge and collaboration.
9	Leveraging the potential of new technologies, such as networks of field-deployed instruments, remote sensing, and machine learning.
10	Developing predictive science and quantifying spatial linkages between landscape and seascape patterns and nutrient flows.
Human impacts and management	

11	Examining the cumulative impact of nutrient flows and multiple stressors on the ecosystem.
12	Advancing our understanding of the potentially contrasting ecological impacts of nutrients from different sources.
13	Investigating the impacts of climate change on coastal nutrient connectivity.
14	Investigating the feedback loops between the social-economic and ecological systems (social-ecological systems interactions).
15	Conducting research that specifically aims to inform local environmental management and restoration in practice.

The literature review revealed that many studies focused only on a single nutrient pathway. This tendency is likely due to the specialization of researchers in particular pathways and associated methods and the limited time and resources to carry out fieldwork. However, nutrient pathways do not occur in isolation. Instead, we propose that the coastal nutrientscape is formed through the interactions of multiple nutrient pathways that operate in complex ways over time across a geographical space (Adam et al., 2020; Graham et al., 2018; Leichter et al., 2012; Shantz et al., 2015). For example, Ziegler et al. (2019) showed that while tides can directly act as physical vectors of nutrients, tides can also interact with animal-mediated nutrient pathways through their impact on food web dynamics. Additionally, the relatively small number of cross-habitat nutrient studies in coastal ecosystems highlights a significant knowledge gap and also presents future opportunities to address our limited ecological understanding of interconnected coastal seascapes (Olds et al., 2018). Prioritizing a single habitat type for conservation action may reduce the success of conservation investments such as restoration and threat mitigation (McAfee et al., 2022; Vozzo et al., 2023).

Different nutrient pathways operate across different spatial and temporal scales (Shantz & Burkepile, 2014). Studies conducted at inadequate spatial-temporal scales will provide narrow, oversimplified and potentially misleading results (point samples, snapshots) that do not adequately capture the ecosystem reality (see e.g. Shuler & Comeros-Raynal, 2020). For example, Delevaux et al. (2019) found that their results were consistent with a previous regional-scale study that did not account for within-watershed spatial heterogeneity. However, quantifying finer scale (within-watershed, 60 m x 60 m) spatial patterns revealed ecologically meaningful insights that supported different recommendations for local management (Delevaux et al., 2019). Such careful consideration of scale was largely lacking in most reviewed studies. We encourage explicit quantitative reporting of the study scale and data resolutions to allow a scale-dependent operational understanding of the different nutrient pathways under study. Trade-offs between resolution and extent may be inevitable due to a range of practical limitations, such as limited funding and resources. Our proposed nutrientscape framework both encourages funders to consider the “more than the sum of the parts” knowledge benefits of a whole-system approach and also the potential for bringing together different studies across scales resulting in economies of scale. We recognize that no single discipline can address the whole-system knowledge gap and call for more transdisciplinary working (e.g. between biogeochemists, ecologists, hydrologists, social scientists, and management practitioners) in the design and implementation of research projects.

In addition to explicit consideration of scale and scaling, working within a clearly defined conceptual framework will help advance coastal nutrient connectivity research. The conceptual understanding of the coastal environment affects what research questions are being asked, and what methods are being used. For instance, in local knowledge systems across the Pacific Islands, land and sea are traditionally not understood as separate but as fundamentally interconnected (Hickey, 2007; Poepoe et al., 2007). This conceptual understanding of a land-sea continuum rather than a binary classification was reflected in the management practices. For example, Hawai'ians traditionally divided high islands into zones known as *ahupua'a* that generally extended from the mountain into the sea (Smith & Pai, 1992). This system allowed for the balanced management of the different terrestrial and marine resources along a so-called ‘ridge-to-reef continuum’ (Minerbi, 1999; Smith & Pai, 1992; Wilmot et al., 2022). In contrast, Western environmental research and management is conventionally siloed into studies of landscapes and studies of seascapes that are typically conducted by distinct and separate disciplines and managed by different institutional units (Álvarez-Romero et al., 2011; Collin et al., 2013, 2021; Stoms et al., 2005).

Although conceptual frameworks to support integrated land-sea management in the coastal zone have been proposed (Álvarez-Romero et al., 2011; Beger et al., 2010; Makino et al., 2013), the primary focus has been on risk management from land-based sources of pollution impacting aquatic ecosystems (Álvarez-Romero et al., 2011; Carlson et al., 2019). Furthermore, these frameworks place little emphasis on the role of landscape ecology and systems science where spatial pattern metrics, scale, and scaling relationships provide additional insights into the fundamental role of landscape and seascape structure and function and enable scenario modeling and spatial prediction to unobserved regions (Frazier, 2023; Wu, 2004). Here, we propose a new framework that builds on previous calls for integrated land-sea studies, specifically focusing on a whole-system, spatially explicit and cross-disciplinary approach to study nutrient connectivity.

A shared conceptual framework for coastal nutrient connectivity studies could support a broader application of a spatially explicit social-ecological systems approach and facilitate cross-disciplinary collaborations. Furthermore, building a coordinated evidence base would support greater comparability of results between studies and help identify and prioritize knowledge gaps within the research field (Dunham et al., 2018; Fausch et al., 2002; Ostrom, 2009; Pittman et al., 2018).

5 Nutrientscape ecology

To support research efforts that address the 15 research needs identified (Table 1), we present here a new framework for nutrient connectivity studies that we term “nutrientscape ecology” (Fig. 5). Nutrientscape ecology integrates social-ecological systems thinking with the spatial pattern-focused concepts and analytical tools of landscape ecology. We propose that the integrated, multiscale, and spatially explicit study of the coastal nutrientscape – nutrientscape ecology – could help inform the management of nutrient connectivity and thereby contribute to local efforts to manage human impacts and increase the resilience of tropical coastal environments to climate change. Indeed, due to the fundamental role of nutrient flows in determining coastal ecosystem dynamics, the management of nutrient connectivity ought to be a high priority in coastal conservation and restoration efforts (Howarth et al., 2005; Kostamo et al., 2018; Seitzinger et al., 2010). A key goal of our proposed nutrientscape ecology framework is to support solution-focused research that is informative and useful for local managers and stakeholders and helps bridge the science-policy gap.

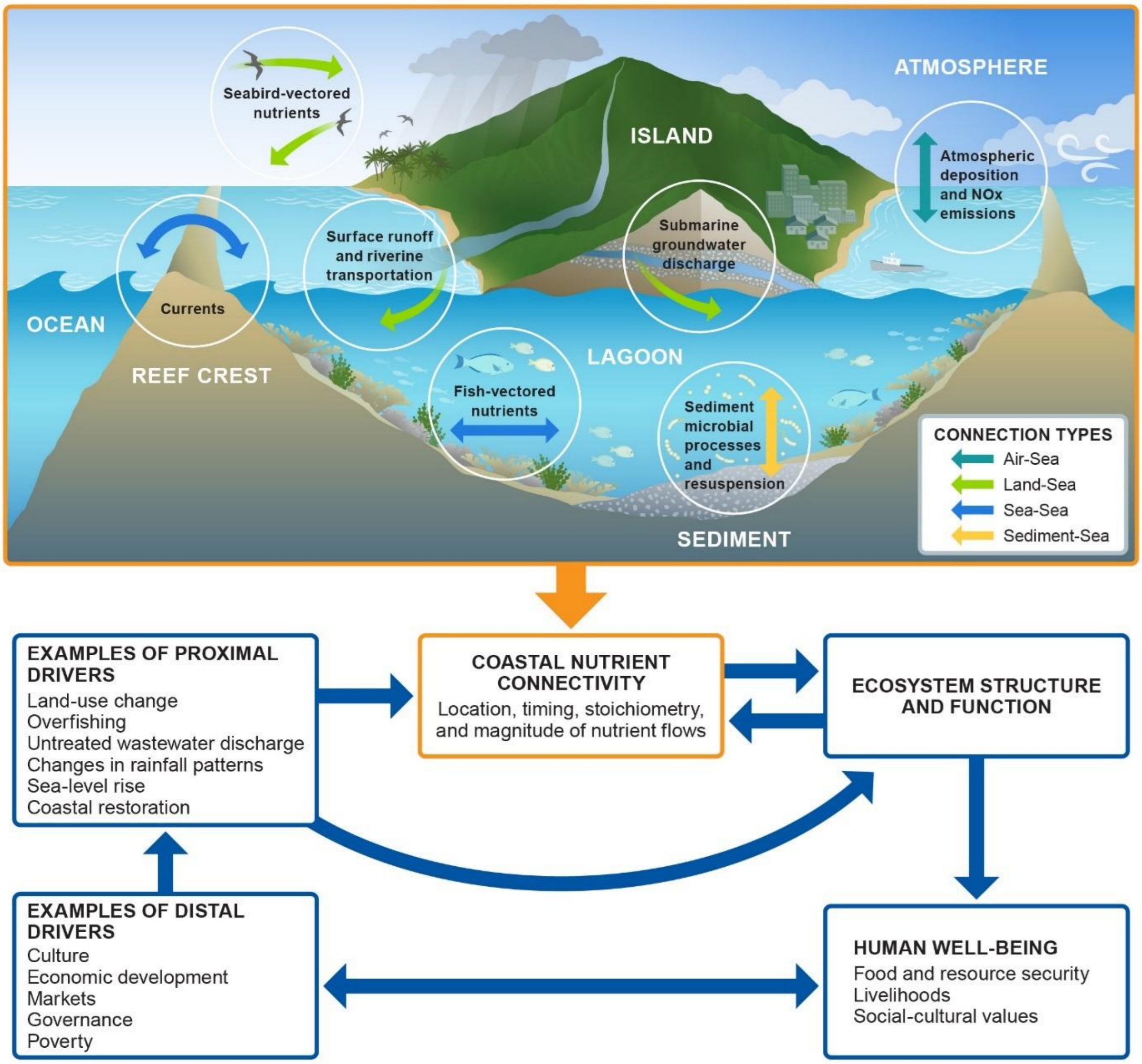


Fig. 5 Nutrientscape ecology: the integrated, spatially explicit, and multiscale framework for studying coastal nutrient connectivity. Social-ecological systems analysis can help us understand how distal and proximal anthropogenic drivers act together to alter coastal nutrient connectivity, and how the resulting ecological changes impact human well-being. The analytical and conceptual tools of landscape ecology enable the spatial study of pattern-process relationships associated with different

coastal nutrient pathways at a range of scales: for example, from the whole island to individual habitat patches and from decadal trends to diurnal cycles.

5.1 Nutrientscape ecology: theoretical foundations

We propose that leveraging Social-Ecological Systems (SES) thinking would benefit and increase the policy impact of coastal nutrient connectivity research in several ways. First, rather than studying parts of the system in isolation, the aim of SES thinking is to understand how system components interact to form the complex whole (Odum, 1977; Ostrom, 2009; Pittman et al., 2018). Thus, SES encourages the examination of the interlinkages between multiple habitat types and different nutrient pathways including linkages to human well-being and human impacts. Additionally, from a SES perspective, changes in nutrient connectivity are considered in the context of other drivers of change, such as climate change (Ban et al., 2014; Donovan et al., 2020; Zaneveld et al., 2016).

Second, taking a whole-system perspective and studying multiple nutrient pathways requires cross-disciplinary collaboration. However, when experts from different disciplines rely on different epistemologies, it may take considerable time and effort to build a shared understanding of the research problem statement and potential solutions. Consequently, an advance in nutrientscape ecology requires a shift in mindset from specialized single disciplinary and reductionist research into collaborative cross-disciplinary and holistic approaches (Odum, 1977; Pittman et al., 2018; Voigt, 2011). The SES approach was developed as a unifying framework that facilitates the integration of the different research approaches and methods used in different disciplines to study a complex system (Ostrom, 2009). Hence, SES could expedite the cross-disciplinary collaborations required for studying multiple nutrient pathways and habitat types.

Third, through its focus on interactions between components of a system, the SES approach allows for identifying feedback loops within and between the social-economic and ecological systems (Folke et al., 2005; Leslie et al., 2015; Levin et al., 2013; Scheffer et al., 2001). For example, diminishing fish stocks may lead to increased fishing effort by fishers that do not have access to an alternative livelihood. This, in turn, can result in an even greater reduction of the fish stocks (Cinner et al., 2009; Nyström et al., 2012). Overfishing can disrupt fish-vectored nutrient pathways (Layman et al., 2011) and risk deteriorating the food and nutritional security of coastal populations that depend on fish-derived micronutrients in their diet (Maire et al., 2021). Identifying and understanding feedback loops is critical for the success of environmental management strategies, both to avoid unintended consequences of management interventions and to find effective levers to increase systemic resilience to disturbances (Hughes et al., 2017). Positive feedback loops could also be harnessed to amplify the impacts of a management action (Farmer et al., 2019; Riechers et al., 2021).

Despite theoretical and methodological advancements in SES research, few studies have implemented a spatially explicit approach (Pittman et al., 2018). Yet, understanding spatial patterns is often key for understanding system dynamics (Bailey, 2010; Jenerette & Wu, 2004; Loreau et al., 2003; Polis et al., 1997). Spatial information is also essential for environmental management and spatial planning (Caldow et al., 2015; Van Kouwen et al., 2007). To bridge the conceptual analysis of complex systems and driver-impact-relationships with the spatial study of real ecosystems, the analytical tools of landscape ecology can be leveraged (Virah-Sawmy et al., 2009). We propose that integration of landscape ecology and SES will form a solid foundation for the whole-system science of coastal nutrient connectivity.

To support the operationalization of nutrientscape ecology, we provide a set of recommended questions to consider during the formulation of a research project (Table 2). Then, we discuss analytical tools from landscape ecology and SES and explore novel technologies that could be leveraged to develop nutrientscape ecology as a multiscale, integrated, and spatially explicit science.

Table 2. Questions and examples to consider before starting a nutrientscape ecology study. Funding considerations, although crucial, are not included here. To successfully carry out the project, the types of expertise required – across different disciplines – should be thoughtfully considered.

Social-ecological systems	**1. Identify components of the social-ecological system and their interactions**	
	1.1. Consider potential nonlinearities in the interactions.	Nutrients may have a positive fertilizing effect until a threshold is breached, after which the effect becomes negative (Stockbridge et al., 2020).
	1.2. What are the proximal and distal drivers of change?	Increased terrestrial nutrient loading to coastal waters may be associated with land use change (proximal driver) driven by economic development (distal driver) (Ramos-Scharrón et al., 2015).

	1.3. What are the relevant temporal scales, and are there trends or periodicities that should be considered?	Riverine transport of nutrients from land to sea may be impacted by long-term climate periodicities, such as El Niño and the Pacific Decadal Oscillation (Slater et al., 2019).
Landscape ecology	**2. Develop a spatial understanding of the system**	
	2.1. Is the consideration of spatial heterogeneity important for the research question at hand?	The influence of land cover spatial heterogeneity on nutrient connectivity depends on the relative abundance of different land cover types (Gergel, 2005).
	2.2. Does the nutrient flow undergo stoichiometric transformations as it moves through space or through the food web?	Benthic consumers may alter the stoichiometry of dissolved nutrient pools that are subsequently used by algae (Cross et al., 2005).
	2.3. How do the interactions between system components occur spatially?	Fish movement patterns determine the spatial distribution of fish-derived nutrients, creating nutrient hotspots within the coral reef environment (Shantz & Burkepile, 2014).
	2.4. What are the relevant spatial scales, and are local spatial interactions generating	Jenerette & Wu (2004) observed nitrogen limitation at a local scale but not at broader spatial scales. In other words,

	emergent phenomena at broader spatial scales?	they found nitrogen limitation to be scale dependent.

5.2 Nutrientscape ecology: analytical tools

5.2.1 Multiscale analysis

Understanding scale is a core component of landscape ecology research (Turner, 1989; Wiens, 2002), and the first key recommendation for any study in nutrientscape ecology is quantitatively reporting and justifying the spatial and temporal extent(s) and resolution(s) of the study. Avoiding ambiguous and inappropriate scale selection will address a key knowledge gap identified in this review. The second recommendation is to employ a multiscale approach to better understand how nutrient pathways operate and interact across scales and avoid limitations with scale-dependent results. For example, biogeochemical processes that impact the composition (i.e., stoichiometry) of a nutrient flow can occur at the level of individual organisms, ecosystems, and landscapes-seascapes (Cherif et al., 2017; Van de Waal et al., 2018). A multiscale nutrientscape ecology framework is enabled by integration of new and increasingly cost-effective data from drones, satellites, and in-situ sensor networks that would increase the study's spatial and temporal resolution and extent (Besson et al., 2022; Thomson et al., 2021).

Furthermore, a better understanding of long-term environmental change could be achieved through local knowledge and funding to enable location-specific long-term research programs such as the US National Science Foundation’s Long-Term Ecosystem Research (LTER). Important advances in watershed nutrient dynamics and connectivity have resulted from the LTER programs at Hubbard Brook Experimental

Forest (New Hampshire) since the 1960s (Likens & Bormann, 1974), Moorea Coral Reef LTER (Adam et al., 2020), and Florida Coastal Everglades LTER (Armitage et al., 2011). Much of this research has been influenced by landscape ecology and systems thinking and we encourage the continued cross-pollination of ideas and transferable technologies from these disciplines to advance our understanding of the nutrientscape.

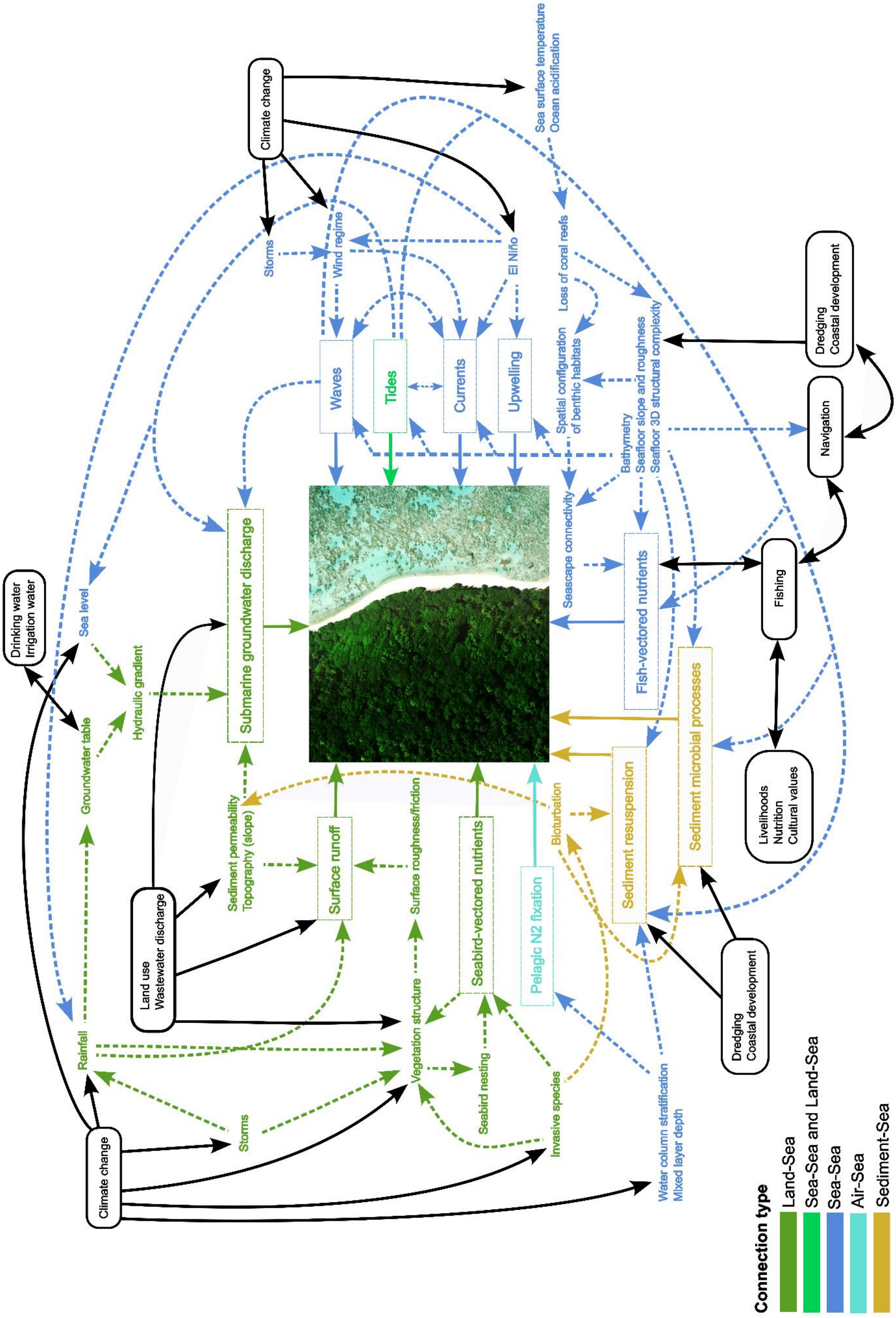
5.2.2 Integrated analysis

By "integrated nutrientscape ecology", we mean taking a whole-system perspective on the coastal nutrientscape: studying land and sea, the social and the ecological, multiple habitats, and multiple nutrient pathways and their interactions. Systems mapping can be used to identify the system's key components, their interactions and possible feedback loops, and proximal and distal drivers of change. This literature review revealed that many studies do not identify the proximal sources of nutrients (e.g. wastewater discharge), and even fewer studies identified the underlying social, political, or economic drivers (e.g. increase in unsustainable tourism). The systems map shown in Fig. 6 illustrates that climate change is expected to directly and indirectly affect many system components, highlighting the urgent need to address the knowledge gap about climate change impacts identified in this literature review.

Another tool for analyzing SES is the drivers–pressures–state–impact–responses (DPSIR) framework (EEA, 1999). This framework has been widely used to communicate chains of cause–effect relationships in coastal and marine environmental policy (Atkins et al., 2011a, 2011b; Gari et al., 2015; Patrício et al., 2016). In particular, DPSIR has often been applied to link drivers of land-based nutrient loading to eutrophication in coastal waters (Karageorgis et al., 2005; Pinto et al., 2013; Pirrone et al., 2005). Compared to a systems map, a disadvantage of this framework is that it proposes linear unidirectional causal chains and fails to capture complex system dynamics and interactions (Niemeijer & de Groot, 2008; Rekolainen et al., 2003). Nevertheless, coupled with a whole-system approach, the DPSIR framework can be useful for structuring problems by identifying and communicating the proximal and distal anthropogenic drivers of environmental change (Atkins et al., 2011a; Lewison et al., 2016).

Missing from both the systems map and the DPSIR framework are the spatial and temporal dynamics (Agramont et al., 2022; Cumming et al., 2017). For example, at relatively broad scales (10-100s km, seasons-years), there can be temporal variation in the circulation patterns of coastal waters caused by the monsoon season or El Niño (Craig et al., 2007; Wang et al., 2019). Similarly, surface runoff is often spatially and temporally focused, for example near agricultural lands during and after a large storm (Adam et al., 2020; Fong et al., 2020).

The whole-system study of coastal nutrientscapes will require integrating data collected across the land-sea continuum including social-economic data. When conducting research in the lands and seas of indigenous peoples, the conceptual framework should support pluralistic knowledge creation and the decolonization of research (Reynolds & Wheeler, 2022; Smith, 2021). A greater appreciation and application of local knowledge, in written form or through surveys and interviews, could help advance nutrientscape ecology by providing important historical and local contextual information. Participatory mapping can be a useful tool to summarize and visualize local knowledge in a spatially explicit way (Klonner et al., 2021).


Climate change
Sea surface temperature
Ocean acidification
Storms
Wind regime
El Niño
Loss of coral reefs
Waves
Tides
Currents
Upwelling
Spatial configuration of benthic habitats
Bathymetry
Seafloor slope and roughness
Seafloor 3D structural complexity
Dredging
Coastal development
Navigation
Drinking water
Irrigation water
Sea level
Hydraulic gradient
Groundwater table
Submarine groundwater discharge
Seascape connectivity
Fish-vectored nutrients
Fishing
Livelihoods
Nutrition
Cultural values
Sediment microbial processes
Sediment resuspension
Bioturbation
Pelagic N2 fixation
Seabird-vectored nutrients
Surface roughness/friction
Surface runoff
Sediment permeability
Topography (slope)
Land use
Wastewater discharge
Rainfall
Vegetation structure
Seabird nesting
Invasive species
Storms
Climate change
Water column stratification
Mixed layer depth
Dredging
Coastal development
Connection type
Land-Sea
Sea-Sea and Land-Sea
Sea-Sea
Air-Sea
Sediment-Sea

2014

Fig. 6 Systems map of the coastal nutrientscape. The key nutrient pathways are shown in dashed-lined boxes and solid arrows. Impacts and interactions between the different components of the system are shown in dashed arrows. The black boxes and black solid arrows show anthropogenic impacts on the system components.

5.2.3 Spatial analysis

Developing accurate spatial models of nutrient connectivity is challenging because a nutrient flow is affected by biogeochemical processes taking place at different scales (Smithwick, 2021; Turner & Gardner, 2015), and the stoichiometry of the flow changes as it moves through space and interacts with the surrounding biotic and abiotic features (Schade et al., 2001; Sitters et al., 2015). Thus, the quantity and composition of a nutrient flow is a function of the local conditions (i.e., the biogeochemical processes occurring within a habitat patch), the composition and configuration of the surrounding environment (e.g., distance to different habitat patches), and the resistance to movement to, and away, from that point (e.g., water flow velocity determined by terrain roughness) (Gergel, 2005; Turner & Gardner, 2015).

Landscape ecology provides powerful tools for connectivity modeling that leverage the physical attributes of the landscape or seascape (Calabrese & Fagan, 2004; Treml & Kool, 2017). Terrestrial landscape ecology studies have highlighted the importance of geomorphological metrics such as slope, curvature, and terrain roughness in determining nutrient connectivity (Chadwick & Asner, 2016; Moore et al., 1991). For instance, in agricultural lands, soil phosphorus tends to be deposited in flatter, downslope areas where runoff converges and slows due to local curvature (Evans et al., 2016). Quantifying slope, curvature, and terrain roughness is foundational in hydrology (Hendriks, 2010) and widely used in seascape ecology studies of fish distribution and movement (Borland et al., 2021). However, the link between these geomorphological metrics and nutrient connectivity in coastal seascapes remains largely unexplored (Hearn et al., 2001), presenting an exciting research avenue for the spatially explicit, predictive study of the coastal nutrientscape.

In addition to geomorphological metrics, spatial pattern metrics that quantify habitat composition and configuration could be leveraged to model and predict the stoichiometric transformation of nutrient flows across geographical space (Smithwick, 2021; Sitters et al., 2015). Several studies have leveraged terrestrial composition and configuration metrics to predict riverine water quality and nutrient concentrations (Uuemaa et al., 2005; Wu & Lu, 2019). In a pioneering surface-flow simulation study, Gergel (2005) found that the spatial configuration of land cover types is most important in the prediction of nutrient connectivity patterns in watersheds with intermediate relative abundance of different cover types. In an empirical study, Jones et al. (2001) found that while land cover spatial pattern metrics were able to explain 65-86% of the variation in nitrogen loading to streams, the predictive power varied depending on the biophysical characteristics of the watershed (e.g. the relative importance of atmospheric nitrate deposition). The findings of these pioneering studies suggest that developing spatial analysis in nutrientscape ecology could allow establishing heuristics for determining when simple composition metrics are sufficient and when more elaborate configuration metrics would be needed. We advocate building on these terrestrial case studies and developing predictive modeling of nutrient connectivity across land *and* sea.

5.3 Nutrientscape ecology: novel technologies

In addition to analytical developments, we identify recent technological advancements to support the operationalization of nutrientscape ecology in practice. We note that technological and theoretical advancements go hand in hand whereby novel approaches for data collection and computational modeling may be used to both inform and test nutrientscape ecology theory. We anticipate that future technological evolution and application of an integrated nutrientscape conceptual framework will enable the formulation of novel research questions and hypotheses.

5.3.1 Data collection

New remote sensing technologies provide unprecedented amounts of environmental data. Multiple satellite constellations now provide daily revisit times, and the spatial and spectral resolutions have been improving at each generation of satellites (Fig. 7). Additionally, drone-based mapping can achieve up to a sub-centimeter scale spatial resolution while also avoiding the issue of persistent cloud cover in many tropical coastal regions (Bennett et al., 2020; Collin et al., 2018). Marine and terrestrial habitat maps derived from satellite and drone data can be used to calculate composition, configuration, and geomorphological metrics, thereby supporting spatially explicit nutrient connectivity modeling (Lepczyk et al., 2021). Furthermore, while nutrients dissolved in water do not have a significant optical signal, their presence can be inferred through a number of proxies detectable from remotely-sensed data (Soto et al., 2009; Wang et al., 2018a). For example, increased nutrient loading can result in elevated phytoplankton biomass in coastal waters (i.e., greener surface waters), which can be detected from remotely-sensed imagery presenting opportunities for spatial indicators of change (Cael et al., 2023; Cillero Castro et al., 2020). Thermal infrared sensors mounted on drones or satellites can be used to map sea surface temperature and thereby identify potential groundwater discharge sites (Oberle et al., 2022; Oehler et al., 2018). Dye tracing experiments that leverage drones allow tracking coastal water flows at very high spatial resolutions (Johansen et al., 2022).

In addition to remote sensing, there is opportunity for developing networks of field-deployed sensors capable of data collection at high temporal resolutions (1 sec to 24 h) (Fig. 7B) (Bieroza et al., 2023). Field-deployed sensors can provide detailed time-series data that cannot be obtained from traditional field sampling and subsequent laboratory analyses (Reading et al. 2017). Nutrients such as ammonium, nitrate, and phosphate can be measured using wet-chemistry sensors and ion-selective electrodes (Pellerin et al., 2016). Additionally, optical sensors can be leveraged to estimate a range of key parameters associated with biogeochemical flows, such as turbidity and concentrations of phytoplankton and colored dissolved organic matter (Bieroza et al., 2023). The high-frequency data collection through sensor networks could reveal previously unobserved patterns in the flows and transformation processes of nutrients in space and time (Bieroza et al., 2014, 2023). The data from field-deployed sensor networks can also serve as calibration and validation data for remote sensing models (Lyu et al., 2022). However, the cost of setting up and maintaining a sensor network is still prohibitively high for many individual research groups. Creating a comprehensive sensor network may therefore require a coordinated effort between multiple research groups and universities, as well as collaborations with research institutions that develop new sensor technologies.

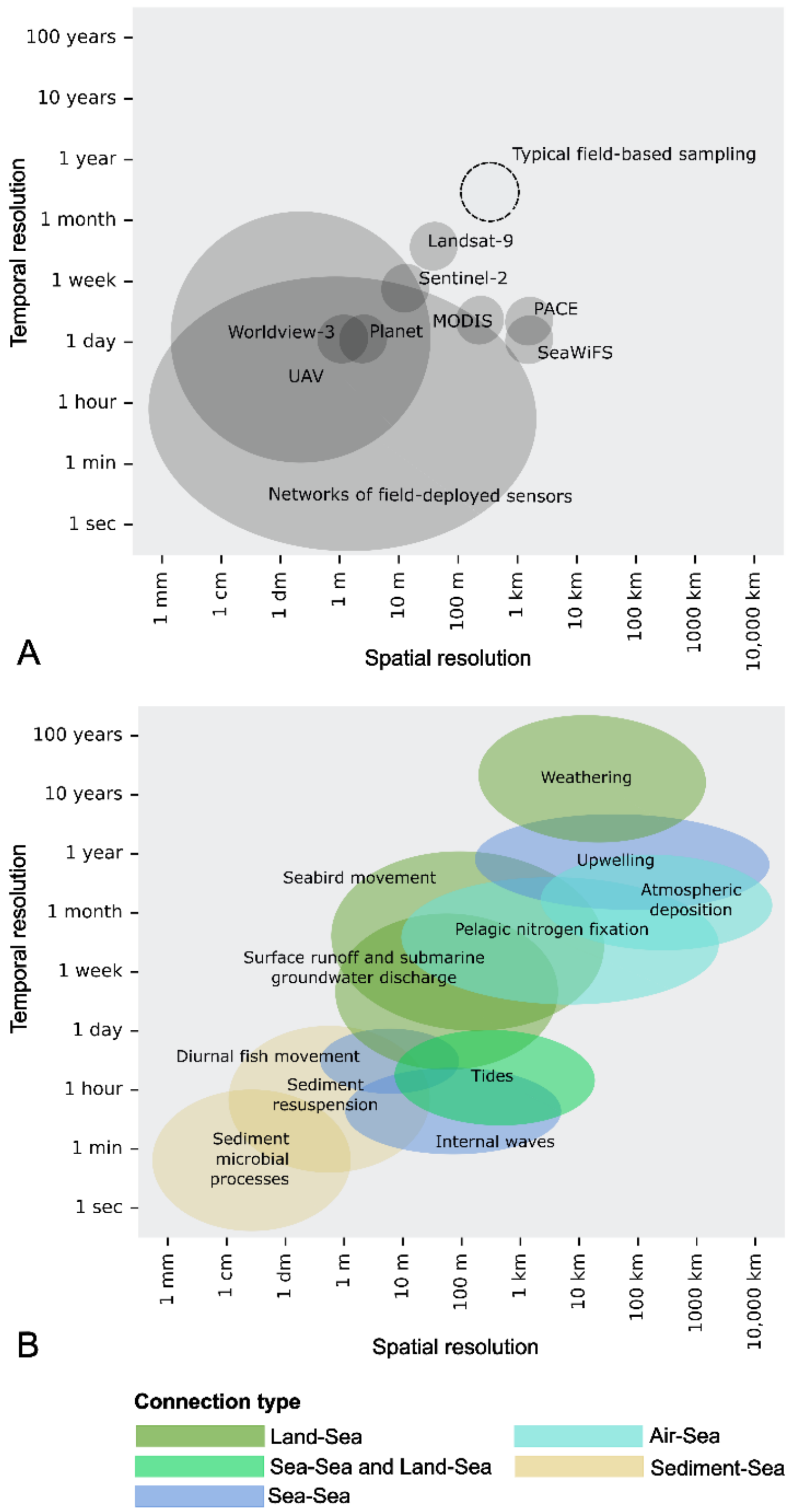


Fig. 7A The temporal and spatial resolutions of remote sensing technologies (satellites and UAVs) and field-deployed instruments. The typical temporal and spatial resolutions of traditional field campaigns are shown with the black dashed-line circle: many field studies collected data every 1-12 months to cover seasonal variability, at a spatial resolution of 100-1,000 m. 7B Temporal and spatial resolutions likely to be relevant for studying different coastal nutrient pathways. The selection of the temporal and spatial scale(s) will depend on the specific research questions of the study. Scale information integrated from Dickey (2020), Hedley et al. (2018), and Taniguchi et al. (2019).

The complementary use of field-deployed sensor networks, remote sensing, and traditional field experiments enables the multiscale study of environmental change (Shiklomanov et al., 2019). The integrated application of novel technologies could provide insights into how local and regional alterations might drive changes in global biosphere integrity (Nash et al., 2017). To fully realize the potential of novel technologies in coastal nutrient connectivity research, interdisciplinary collaborations between data scientists, remote sensing experts, ecologists, hydrologists, and biochemists should be encouraged (Shiklomanov et al., 2019; Ward et al., 2020). Innovative ways to combine multiple sources of data need to be explored (Trantas et al., 2023). In the following sections, we have summarized two promising modeling approaches for making full use of data from different sources in nutrientscape ecology: digital twins and physics-informed machine learning.

5.3.2 Computational modeling

The large quantities of environmental data provided by remote sensing and in-situ sensor networks is stimulating advances in computational modeling techniques, such as digital twins (Blair, 2021; Blair & Henrys, 2023). A digital twin is a virtual representation of a physical system (Jones et al., 2020) and provides a spatial template with which to integrate and model diverse cross-scale spatial data (Brocca et al., 2024). Digital twins differ from other computational modeling approaches primarily through their usage of evolving data in real-time so that the states of the virtual and physical systems are synchronized (Jones et al., 2020; Wright & Davidson, 2020). In contrast, a traditional computational model describes the behavior of the system according to set processes that do not evolve over time, thereby making the model potentially inaccurate over timescales within which significant alterations in the system and its behavior would occur (Wright & Davidson, 2020). Thus, digital twins could support timely environmental management interventions, as the model is built to continuously integrate new information moving towards near-real time models (Moghadam et al., 2020; Trantas et al., 2023). This makes digital twins a promising spatial modeling approach for supporting nutrient connectivity management in highly dynamic coastal environments. However, environmental digital twins research is still nascent, and more work is needed to explore and realize the full potential uses of this modeling approach (Blair & Henrys, 2023; Purcell et al., 2023; Purcell & Neubauer, 2023).

Another promising new technology to support nutrientscape ecology is physics-informed machine learning (Karniadakis et al., 2021). This novel research field integrates physical rules and domain knowledge with machine learning, providing three key advantages for the predictive modeling of social-ecological systems. First, while purely data-driven machine learning models may achieve good training and validation accuracies, their predictions may still be physically unrealistic (Karniadakis et al., 2021). For example, a model trained on existing environmental data may not be able to accurately extrapolate into the future when environmental and climate conditions change (Kashinath et al., 2021; Zhong et al., 2023). Second, many traditional machine learning models are black boxes – in other words, the model predictions are not explained in a meaningful way (Rudin, 2019). Integrating a physics-based understanding into the machine learning model supports the interpretability of the model (Kashinath et al., 2021; Rudin, 2019). For example, physical meaning can be incorporated into the intermediary nodes of a neural network, thus enabling an interpretable information flow through the network (Wu et al., 2024). Third, applying purely physics-based models is limited by the requirement of high-quality data, expert knowledge for accurate model parameterization, and a trade-off between computational cost and high spatial resolution (Soriano et al., 2021). A number of pioneering studies have already applied physics-informed machine learning to study issues relevant for coastal nutrientscape ecology, such as groundwater contamination (Soriano et al., 2021), terrestrial runoff (Zhong et al., 2023), surface water flows (Bertels & Willems, 2023), sea surface temperature (de Bézenac et al., 2019), and ocean vertical mixing (Zhu et al., 2022). However, similarly to digital twins research, applications of physics-informed machine learning for predictive environmental modeling are only just emerging with great opportunity for further developments and discoveries (Kashinath et al., 2021; Palola et al., 2025).

6 Conclusions

Nutrient flows within and across ecosystems are major drivers of ecosystem structure and functions. These flows operate across multiple scales and are characterized by complex interactions. The condition of the nutrientscape directly and indirectly influences human health and well-being through intimately interconnected social-ecological systems. A key research priority is a better understanding of the local and global human impacts on nutrient flows and the consequences of these flows on the functioning and resilience of coastal social-ecological systems. This study summarized the recent state-of-science in tropical and subtropical coastal nutrient connectivity studies with a systematic literature review. Our results show that research to date has largely focused on unidirectional flows of nutrients, with limited consideration of the reciprocal flows between spatially connected ecosystems. Furthermore, nutrient connectivity studies are typically based on traditional field-based surveys and sampling at a single spatial scale within a narrow temporal window, thereby forming a set of snapshots of the system's patterns and processes. To develop improved resilience-based environmental management and restoration strategies, new research approaches are needed that understand nutrient connectivity from a spatially explicit whole-system perspective. We suggest that great potential exists for a nutrientscape approach to advance and accelerate the scaling up of coastal restoration through site selection, functionally meaningful design of interventions, and effective cross-scale monitoring.

Building on the results of our review, we identified 15 future research needs and presented a novel research approach that we called "nutrientscape ecology". The framework of nutrientscape ecology serves three primary purposes. First, this framework can advance coastal nutrient connectivity research as a multiscale, spatially explicit study of pattern-process relationships across landscapes and seascapes by applying landscape ecology concepts and analytical methods. Second, this work can support the application of systems thinking that goes beyond the study of individual nutrient pathways in isolation and situates the nutrient flows and pathways in the wider context of the coastal social-ecological system. Third, the framework encourages the novel integration of advanced technologies in nutrient connectivity research that are capable of generating insights into nutrient connectivity at scales meaningful to environmental management, conservation, and spatial planning. These technologies include remote sensing, field-deployed sensor networks, machine learning, and digital twins. A likely barrier to the implementation of the nutrientscape ecology framework is securing sufficient funding to conduct multiscale, cross-disciplinary research. Thus, there is a need for novel funding programs that understand the critical importance of nutrient connectivity to coastal social-ecological systems and recognize the benefits of a whole-system approach, cross-disciplinary collaborations, and long-term environmental monitoring.

While this literature review focused on tropical and subtropical coastal environments, the nutrientscape ecology framework can be readily applied to the study of nutrient connectivity in other coastal environments. This work can serve as a foundation to develop a predictive and solution-oriented science of nutrient connectivity that supports local management efforts in the context of mitigating and adapting to accelerated global warming and other environmental changes.

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8 Statements

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and commented on previous versions of the manuscript. All authors read and approved the final manuscript. The datasets generated during the current study are available from the corresponding author on reasonable request.

Appendix A – Additional information on the systematic literature review

Please view the Excel file through this link.

Appendix B – Ecological impacts and management implications identified in the reviewed literature

Table B.1. Ecological impacts of nutrient connectivity assessed in the reviewed literature.

Ecosystem component / function impacted	Study	Ecological impacts	Nutrient pathway(s)	Attributed nutrient source(s)
Coral trophic strategy	Thibault et al. (2022)	Corals less exposed to seabird-vectored nutrients were dominated by heterotrophy, and vice versa.	Terrestrial runoff	Natural (seabirds)
Coral growth	Guo et al. (2017)	Nutrient concentrations were found to be lower than the estimated threshold for negative effects on coral physiology.	Terrestrial runoff	Not attributed
Macroalgal proliferation	Adam et al. (2021)	The consistent long-term nitrogen-enrichment of nearshore waters has likely contributed to patchy phase shifts from coral to macroalgae.	Terrestrial runoff; waves	Anthropogenic (sewage; land-use)
	Comeros-Raynal et al. (2021)	Hard coral cover had a positive correlation with surface runoff and nitrogen load. Turf algae was negatively related to phosphate load. No significant relationship was detected between	Terrestrial runoff	Anthropogenic (land-use)

		nutrient load and macroalgal cover.		
	Delevaux et al. (2018, 2019)	The ecological consequences of nutrient loading were modelled based on the results of previously published studies. Nitrogen: positive effects on macroalgae, turf algae; negative effects on CCA. Phosphorus: positive effects on turf algae.	Terrestrial runoff; submarine groundwater discharge	Anthropogenic (land-use)
	Fong et al. (2020)	Macroalgae were able to rapidly assimilate the nutrients pulsed by a rainfall event. Such nutrient subsidies potentially contribute to macroalgal proliferation on reefs.	Terrestrial runoff	Anthropogenic (sewage; land-use)
	Rodgers et al. (2012)	Healthy coral reef environments (assessed using the Reef Health Index that incorporates information on coral cover, coral richness, fish diversity, numerical abundance, and the biomass of fishes) tended to be associated with watersheds experiencing lower levels of anthropogenic impact.	Terrestrial runoff; waves	Anthropogenic (land-use)
	Li et al. (2015)	Live coral cover, species richness, and juvenile coral density were negatively	Terrestrial runoff; upwelling	Anthropogenic (aquaculture); Natural

		associated to nitrogen load. Macroalgal cover was positively correlated with nitrogen load.		(oceanic sources)
Plankton	Brocke et al. (2015)	Increased nutrient loading results in phototrophic blooms and increased organic matter concentrations in the water column. The degradation of organic matter that has settled onto the seabed leads to the formation of dense benthic cyanobacterial mats that negatively impact coral reef health.	Terrestrial runoff; currents; sediment microbial processes	Anthropogenic (land-use)
	Condie et al. (2012)	Phytoplankton and zooplankton were positively correlated with increased nutrient loading through river discharge	Terrestrial runoff; tides; trophic interactions	Anthropogenic (land-use)
	Pagano et al. (2017)	The tidally driven input of copepods from the ocean to the lagoon provides additional nutrients and can contribute to increased productivity in coral reef lagoons.	Tides	Natural (oceanic sources)
	Sevadjian et al. (2012)	Internal waves can lead to phytoplankton hotspots, which may in turn attract higher densities of mobile zooplankton and higher trophic levels.	Internal waves	Natural (oceanic sources)

	Schaffelke et al. (2012)	Seasonal nitrogen inputs to the coral reef environment caused increased phytoplankton production.	Terrestrial runoff; Sediment resuspension	Anthropogenic (land-use)
Fish	Delevaux et al. (2018a, 2018b)	The ecological consequences of nutrient loading were modelled based on the results of previously published studies. Nitrogen: negative effects on browsers and piscivores. Phosphorus: negative effects on browsers.	Terrestrial runoff; submarine groundwater discharge	Anthropogenic (sewage; land-use)
	Kamau et al. (2020)	Greater availability of nutrients was associated with increased primary productivity and pelagic fish density.	Terrestrial runoff; upwelling	Anthropogenic (sewage)

Table B.2. Management implications identified in the reviewed studies that included management as a research focus.

Study	**Nutrient pathway(s)**	**Management implications**
Condie et al. (2012)	Surface runoff; tides; trophic interactions	Different water quality management strategies should be designed for coastal lagoons and estuary channels
Delevaux et al. (2018)	Submarine groundwater discharge	Identification of priority areas on land to support coral reef conservation (e.g., upgrading cesspools; minimizing increase in phosphorus from the injection well discharge; applying best

		management practices for fertilizer use)
Delevaux et al. (2019)	Submarine groundwater discharge	Identification of priority areas on land and at sea to support coral reef conservation (reduction of anthropogenic nutrient load from land; marine closures)
Rodgers et al. (2012)	Surface runoff; groundwater discharge; waves	Quantitative evidence of the impact of land use on coral reef condition can support the development of stronger legislation
Shuler et al. (2012)	Surface runoff; groundwater discharge	Identification of priority areas (watersheds associated with the highest antropogenic nutrient loading); highlighting the importance of groundwater management in addition to surface runoff management

Appendix C – List of the 188 records retrieved and screened

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6 Chapter 3

Mapping and monitoring water constituents can inform us about key ecological and biogeochemical processes taking place in coral reef environments. For example, chlorophyll-a concentration can be used as a proxy for nutrient load (Marra et al., 2007). Colored dissolved organic matter protects corals from the harmful effects of UV radiation (Zepp et al., 2008) and can be leveraged to estimate dissolved organic carbon (Vantrepotte et al., 2015). Suspended sediments impact water clarity and thereby the photosynthetic energy available for coral growth (Tuttle & Donahue, 2022). However, little is known about spatial-temporal variability in chlorophyll-a and other key water constituents within and in close proximity to coral reef environments (Andréfouët et al., 2022; Hochberg et al., 2020; Morais et al., 2025; Russell et al., 2019). Reliably mapping water constituents in optically shallow waters, in which benthic reflectance makes a significant contribution to the total optical signal, remains one of the key unresolved challenges in marine remote sensing (Hedley et al., 2016; Werdell et al., 2018).

Bio-optical and radiative transfer models can be used to calculate the total optical signal resulting from a specific combination of benthic cover, water column depth, and concentrations of optically active water constituents (Mobley, 1994). Analytical remote sensing algorithms must therefore solve an inverse problem: the input parameters of the bio-optical and radiative transfer models must be inferred from the output of the model (i.e., remote-sensing reflectance) (Lee et al., 1999; Petit et al., 2017). This inverse problem of coastal marine remote sensing is mathematically ill-posed because the solutions are not unique (Defoin-Platel & Chami, 2007; Hadamard, 1902). In other words, multiple different combinations of benthic reflectance, depth, and water constituent concentrations may result in a similar remote-sensing reflectance (Lee et al., 2001; Mobley et al., 2005). In Chapter 3, I used a newly developed method in probabilistic machine learning called simulation-based inference (Cranmer et al., 2020; Tejero-Cantero et al., 2020) to address the inverse problem of marine remote sensing. The method has previously been applied in neuroscience (Gonçalves et al., 2020; Lueckmann et al., 2017), and Chapter 3 presents its first application to environmental remote sensing.

The algorithm was validated on field data collected on Tetiaroa atoll (South Pacific). Prior to this study, the only coral reef bio-optical surveys in the South Pacific (French Polynesia, Te Ao Māʼohi) were conducted in the Tuamotu atolls in the 1990s (Maritorena, 1996; Maritorena & Guillocheau, 1996). This is likely due to the great logistical challenges associated with collecting bio-optical data in remote locations with limited access to research facilities (e.g., freezers) and in reef environments so shallow that data collection must be conducted from a small vessel rather than an oceanographic cruise ship. Chapter 3 allowed me to gain valuable experience in funding acquisition, planning, and conducting a field campaign in a remote location. Additional details and results from the field campaign are provided in the Supplementary materials (section 11) of this thesis.

Simulation-based inference advances water quality mapping in shallow coral reef environments

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Keywords

Bayes; coral reef; inverse problem; machine learning; neural network; radiative transfer; remote sensing; statistical inference

Abstract

Human activities are altering coral reef ecosystems worldwide. Optical remote sensing via satellites and drones can offer novel insights into where and how coral reefs are changing. However, interpretation of the observed optical signal (remote-sensing reflectance) is an ill-posed inverse problem, as there may be multiple different combinations of water constituents, depth, and benthic reflectance that result in a similar optical signal. Here we apply a new approach, simulation-based inference, for addressing the inverse problem in marine remote sensing. The simulation-based inference algorithm combines physics-based analytical modelling with approximate Bayesian inference and machine learning. The input to the algorithm is remote-sensing reflectance, and the output is the likely range (posterior probability density) of phytoplankton and suspended minerals concentrations, coloured dissolved organic matter absorption, wind speed, and depth. We compare inference models trained with simulated hyperspectral or multispectral reflectance spectra characterised by different signal-to-noise ratios. We apply the inference model to in-situ radiometric data (n=4) and multispectral drone imagery collected on the Tetiaroa atoll (South Pacific). We show that water constituent concentrations can be estimated from hyperspectral and multispectral remote-sensing reflectance in optically shallow environments, assuming a single benthic cover. Future developments should consider spectral mixing of multiple benthic cover types.

1 Introduction

Coral reefs support unique biodiversity and hold immense cultural and economic significance for coastal communities around the world (1,2). Alarmingly, coral reef ecosystems are undergoing rapid changes in community composition and ecological functions due to a combination of global and local drivers of change (3,4). Water quality is one of the most important determinants of coral health and resilience at a local scale (5–7). Concentrations of phytoplankton, minerals, and coloured dissolved organic matter (CDOM) are essential optically active water quality parameters that can inform us about ecological and biogeochemical processes taking place in the reef system (8). However, little is known about the spatial distribution and temporal variability of these water quality parameters within and across different coral reef systems (1,9,10). Indeed, understanding the spatial-temporal dynamics of water quality is a key knowledge gap in coral reef science and management (10–12). Field-based water quality surveys tend to have limited spatial coverage, and long-term monitoring studies are rare (9,13,14).

Remote sensing via satellites, airplanes, or drones is a powerful tool for mapping and monitoring coral reef environments over large geographical regions (11,15). Marine remote sensing is based on estimating ecological parameters of interest from remote-sensing reflectance R_{rs} (16). However, estimating water constituent concentrations from remotely sensed data is challenging in optically shallow coastal environments, where benthic reflectance makes a major contribution to the total optical signal (17,18). Indeed, reliably mapping water constituents in optically shallow waters remains one of the major unresolved challenges of marine remote sensing (8,19).

Shallow water remote sensing methods can be divided into empirical and analytical approaches (17). Traditional empirical methods use statistical regression analysis to define the relationship between R_{rs} and in-situ measurements (20,21). Empirical methods are computationally simple and thereby generally easy to implement (20). However, empirical methods usually suffer from limited transferability (17,22), i.e., a decreased performance beyond the local study site and in changing environmental conditions (19,23,24). Analytical methods, in contrast, offer greater potential for transferability to different locations and applicability in environments characterised by variable water constituent concentrations (17,25). Analytical methods leverage the radiative transfer equation that mathematically describes the transfer of electromagnetic radiation in the aquatic medium (16,26). In practice, solving the radiative transfer equation requires the use of empirical approximations, and hence these methods are commonly known as *semi*-analytical methods (27–30). Semi-analytical methods require high-quality bio-optical data for model calibration and are relatively computationally expensive (17,24,25,31).

To find a solution, semi-analytical methods must solve an inverse problem: the input parameters of the radiative transfer and bio-optical models must be inferred from the output of the model (Figure 1) (32). Spectral optimisation methods iteratively minimise the distance between modelled $\hat{R}_{rs}$ and observed R_{rs}. The distance between the two spectra is estimated by minimising a cost function, such as least squares error (28,33). Semi-analytical inversion methods leveraging hyperspectral data can be used to simultaneously estimate bathymetry, benthic cover, and water column optical properties (34). However, the inversion problem of coastal marine remote sensing is mathematically ill-posed because the solution is not unique (35,36). In other words, there may be multiple different combinations of water constituents, depth, and benthic reflectance that result in a similar optical signal (34,37). Yet, traditional semi-analytical inversion methods only provide a single solution without an estimate of uncertainty in the result (28,38). Spectral optimisation methods may fail to retrieve the global minimum and instead provide the local minimum near a given initial guess as the “best” solution (33,38). Furthermore, the performance of spectral optimisation methods is highly dependent upon the quality of the input spectra, as well as the choice of starting values (39,40).

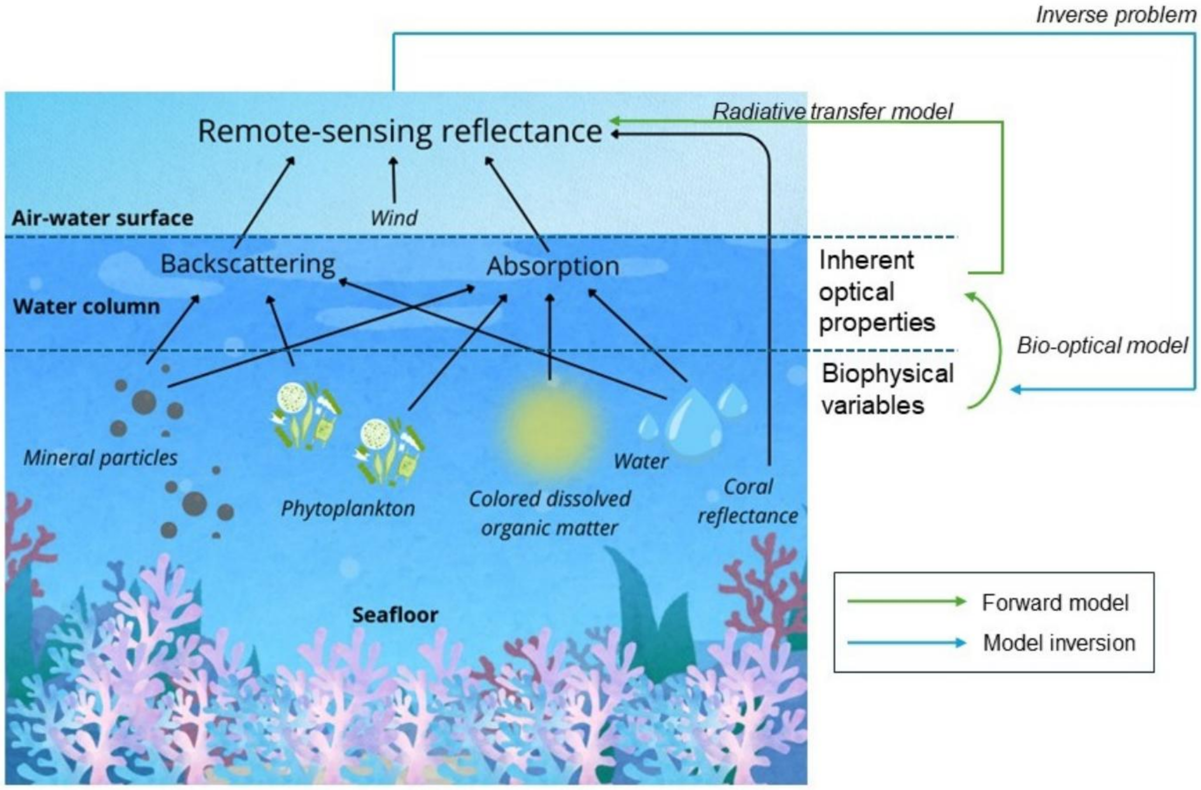

Figure 1. The inverse problem of marine remote sensing. Light travelling through the water column is absorbed and scattered by optically active water constituents, such as suspended minerals, phytoplankton, and coloured dissolved organic matter (CDOM). The impacts of these biophysical variables on light transfer can be described through the bio-optical modelling of inherent optical properties, i.e. the backscattering

and absorption coefficients associated with the water constituents. Additionally, in optically shallow environments, the signal measured by the optical sensor (remote-sensing reflectance) is affected by reflectance from the seafloor. Remote-sensing reflectance just above the water column can be modelled from the inherent optical properties and benthic reflectance using radiative transfer modelling.

In this study, we investigate the extent to which probabilistic machine learning can be leveraged to map water constituent concentrations in coral reef environments from hyperspectral and multispectral data. We apply a Simulation-Based Inference (SBI) algorithm that tackles the inverse problem of marine remote sensing in optically shallow coral reef waters. Rather than providing an estimate of a single “best” solution to the inverse problem, the SBI algorithm produces a distribution of plausible solutions (a posterior probability density) of the water quality parameters, wind speed, and depth. Additionally, we examine how the performance of the SBI algorithm depends on 1) the spectral resolution (hyper- vs multispectral); and 2) the signal-to-noise ratio of the spectral data.

2 Methods

We apply SBI, which combines physics-based analytical modelling with approximate Bayesian statistics and machine learning. We design the algorithm specifically for optically shallow reef environments (brown coral, <20-metre depth). The input to the algorithm is R_{rs}, and the output consists of posterior probabilities for phytoplankton and minerals concentrations, absorption by CDOM, wind speed, and depth. In the following sections, we summarise the principles of SBI and describe the key steps of algorithm development.

2.1 Simulation-based Inference

Radiative transfer modelling software can be used to simulate remote-sensing reflectance R_{rs} and other radiometric quantities of interest under different environmental conditions (41,42). However, an analytical expression for the likelihood function is typically not available for these computationally expensive simulators, and conventional Bayesian inference methods cannot therefore be applied (43,44). SBI is an approximate Bayesian inference method that circumvents the problem of likelihood intractability and only requires the ability of sampling from the likelihood, which corresponds to a forward evaluation of the simulator. Different variants of SBI exist, which either target the likelihood function, a likelihood ratio, or the posterior distribution directly (45). In the presented work we conduct neural-posterior estimation, which uses neural networks for conditional density estimation to approximate the posterior distribution (43,46).

The simulator, in this case a marine radiative transfer model (EcoLight, version 5.3, Numerical Optics Ltd.), takes a vector of input parameters θ (phytoplankton and minerals concentrations, absorption by CDOM, wind speed, and depth) and produces an output $x \sim p(x|\theta)$ ($\hat{R}_{rs}$) (Figure 2). A simulated dataset is generated by drawing samples from the priors $\pi(\theta)$ defined independently for each parameter following a literature review (see section 2.3.). The simulated dataset is used to train a conditional density estimator $q_{\Phi}(\theta)$ to approximate the true posterior distribution $p(\theta|x)$. The density estimator can then be applied to real measured data x_o to estimate the posterior distribution $p(\theta|x_o) \propto p(x_o|\theta)\pi(\theta)$.

The density estimator applied was a Mixture Density Network with 3 layers with 90 nodes each, and 6 mixture components (47). The density estimator is amortised, allowing for inference without having to repeat the computationally expensive simulations or to run additional Markov Chain Monte Carlo sampling (43,45,46).

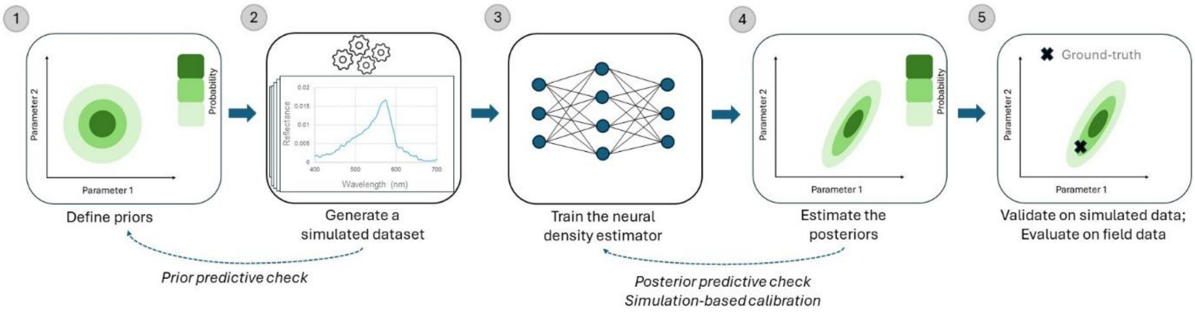

Figure 2. Illustration of the simulation-based inference workflow. After defining the prior distribution (1), we generate a simulated dataset (2), which is used to train a conditional density estimator (3). Once the neural network is trained, we can evaluate it at different observations to get the posterior distribution (4). Finally, the result is validated on different data modalities (5). To control the workflow, we additionally perform prior and posterior predictive checks.

The inference scheme, hereafter the SBI algorithm, was coded in Python 3.10 and leverages the sbi toolbox for simulation-based inference (48). All data and code are freely available via the Open Science Framework data repository (49). All SBI models were trained on a High-End CPU (see Appendix A for details).

2.2 Simulator

EcoLight, the state-of-the-art model for solving radiative transfer equations, was used to create a large, simulated dataset (50). The $\hat{R}_{rs}$ spectra were simulated between 400-700 nm at a spectral resolution of 5 nm (61 bands). EcoLight couples a water column bio-optical model with models of bottom reflection, air-water surface, and atmosphere. The bottom reflectance was specified as brown coral. The brown coral reflectance was the average spectrum calculated from a global benthic reflectance dataset (51). Wind speed was included in the model as it affects sea surface roughness and thereby the transfer of light across the air–sea interface (Appendix B) (16,52).

In the ocean optics literature, different terms and notations are sometimes used to refer to the same bio-optical variables (16,53–55). To avoid confusion, it is important to make the distinction between biophysical variables (e.g., concentrations of phytoplankton and minerals) and inherent optical properties (e.g., absorption and scattering by phytoplankton and minerals). In this study, we follow the terms used in the EcoLight technical documentation (Table 1) (50) and by (54). Phytoplankton concentration (mg/m^3) refers to the concentration of chlorophyll-bearing particles, approximated by chlorophyll-a concentration (50). The minerals concentration is the concentration of inorganic particles, such as suspended mineral sediments, measured in g/m^3 (50). CDOM absorption is measured in m^{-1} at 440 nm (50). Full details of the parameterisation of the bio-optical model in EcoLight are provided in Appendix B.

Table 1. Input parameters to the EcoLight bio-optical model: definitions and units.

Parameter	**Definition or synonym**	**Unit**
Phytoplankton concentration	Concentration of chlorophyll-bearing particles, approximated by chlorophyll-a concentration	mg/m^3
CDOM absorption	Yellow matter; gelbstoff	m^{-1} at 440nm
Minerals concentration	Concentration of inorganic particles, such as suspended mineral sediments	g/m^3
Wind speed	Speed of wind affecting sea surface roughness	m/s
Depth	Depth of the water column	m

2.3 Priors and training data

Prior distributions were defined independently for each of the five input parameters to EcoLight: wind speed, depth, absorption by CDOM, and concentrations of phytoplankton and minerals (Figure 3A). Lognormal distributions were used for CDOM, phytoplankton, and minerals (35,56,57). Coral reef environments are in general characterised by low concentrations of optically active water constituents (Appendix C). Occasionally, however, short-term events such as sediment plumes induced by heavy rainfall may increase the concentrations by several orders of magnitude (58). While the mean concentration of suspended minerals is typically less than or close to 1 g/m^3 (10,53), storm-driven increases in sediment runoff and resuspension can lead to suspended minerals concentrations of 5-30 g/m^3 (59). A lognormal probability distribution captures this variability by assigning a high probability to low concentrations, while also accommodating for the possibility of high concentrations (57). The distributions were truncated to exclude unrealistically high values. The thresholds for truncation were 7 mg/m^3 for phytoplankton concentration, 2.5 m^{-1} at 440 nm for CDOM absorption, and 30 g/m^3 for minerals concentration. The thresholds were based on a literature review (Appendix C).

The prior for wind speed was defined as a lognormal distribution based on the Copernicus global wind dataset (60) (Appendix B, Figure B.1). Lastly, a uniform distribution was assigned for the depth variable, indicating that any depth in the specified range is equally probable. As the detectability of the bottom in coral reef waters has been estimated to be up to 20 metres (51), the depth range was limited to 0.10-20.00 metres (Figure 3A). To validate the specified prior distributions, we conducted a prior predictive check. First, we sampled from the prior and ran the simulator 1,000 times. We then compared the simulated data with field observations (see section 2.5) and found that all observations were within the support of the simulated data (Figure 3B).

We then created a large dataset of simulated $\hat{R}_{rs}$ spectra and corresponding input parameters θ using EcoLight. 30,000 samples were drawn from the prior distribution and used to produce 30,000 different parameterisations of EcoLight. 29,000 simulated data points were used as training data, while 1,000 simulated data points were set aside as a test dataset to conduct inference diagnostics (see section 2.4). We assumed no correlation between the different variables, as such correlations may vary from system to system and with changing environmental and climate conditions (10,61).

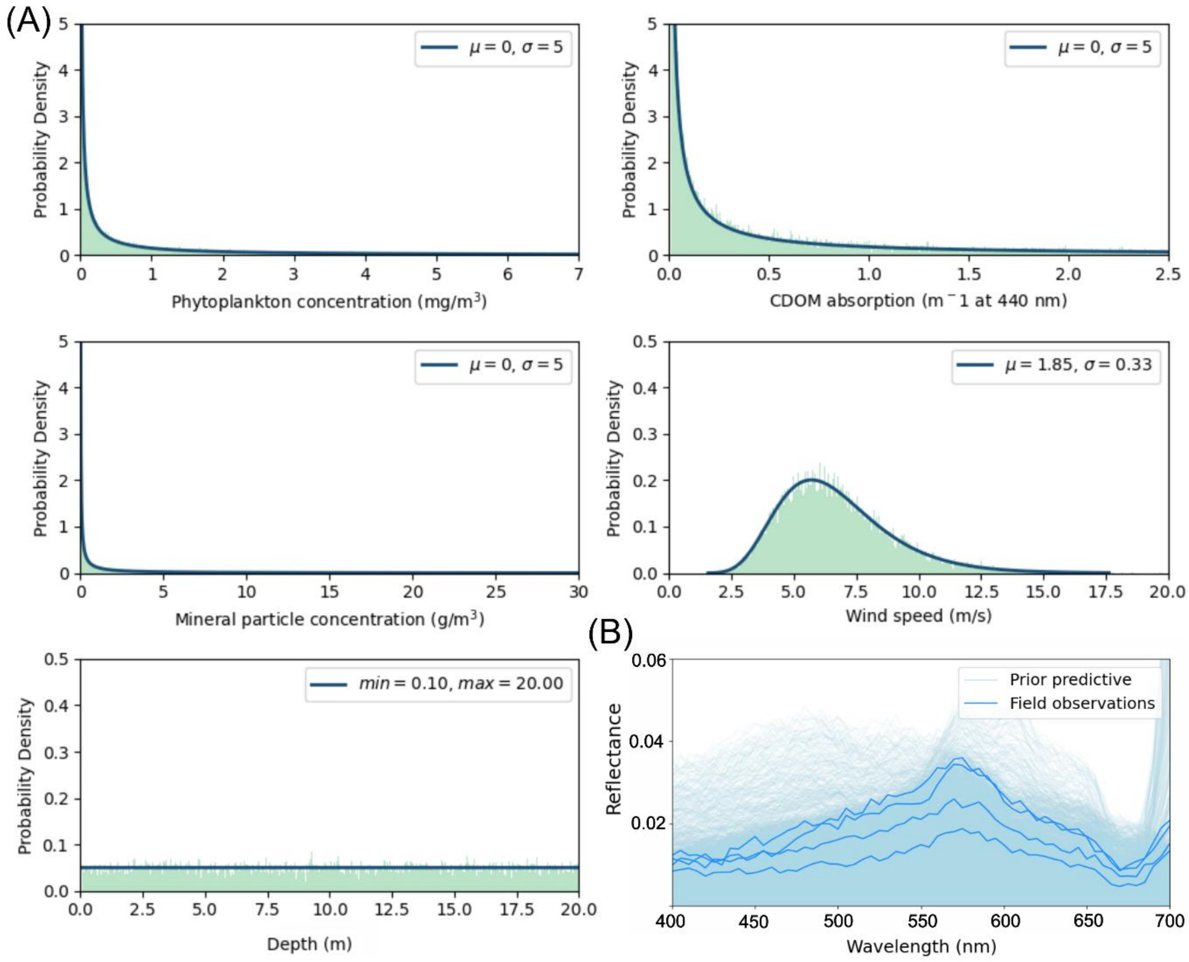

Figure 3. (A) Prior distributions for each of the EcoLight input parameters. A probability density function (in blue) is shown in addition to a histogram (in green) of the 30,000 samples drawn. The parameters of the lognormal distribution are the mean μ and standard deviation σ. CDOM = coloured dissolved organic matter. (B) Prior predictive check. The four R_{rs} spectra observed in the field (dark blue) lie within the support of the simulated $\hat{R}_{rs}$ spectra (light blue).

2.3.1 Signal-to-noise ratio

Stochasticity was introduced into the simulations by adding noise to the spectral data (40). Optical remote sensing is affected by noise from multiple sources, including transmission errors, thermal effects, and photon noise (62–64). The combination of noise from different sources can be represented by a Gaussian noise term (64). The variance of the Gaussian is calculated from a signal-to-noise ratio: $SNR = E[signal_\lambda^2]/E[noise_\lambda^2]$ and $\sigma^2 = (\sum_\lambda signal_\lambda^2/N)/SNR$, where N is the number of wavelengths λ. We tested three levels of signal-to-noise ratio (50, 100, and 500) and assumed an additive noise model (64,65): $signal_{observed,\lambda} = signal_{true,\lambda} + noise_\lambda$.

Signal-to-noise ratios are wavelength-dependent and vary from sensor to sensor (62,63,66). The aim of this study is to demonstrate a new general solution to the inverse problem of marine remote sensing. A detailed, sensor-specific characterisation of the noise model was beyond the scope of this study.

2.3.2 Spectral resolution

To examine the impact of spectral resolution on inference performance, we downsampled the simulated reflectance data to correspond to the bands of a multispectral drone sensor (MicaSense RedEdge-MX Dual Camera System). This camera system has seven narrow bands in the visible region: coastal blue (444 nm), blue (475 nm), green 1 (531 nm), green 2 (560 nm), red 1 (650 nm), red 2 (668 nm), and red edge (705 nm). Remote sensing via airborne drones enables a very high spatial resolution (<10 cm) and the possibility to capture and monitor rapidly changing water quality conditions (67). This makes it well-suited for water quality monitoring in coral reef environments (68).

2.4 Inference diagnostics

A test dataset of 1,000 simulated data points (simulated $\hat{R}_{rs}$ and the corresponding input parameters θ) was used to conduct three types of inference diagnostics before applying the SBI algorithm to field-collected data. First, in a posterior predictive check, we drew a single simulated "ground-truth" $\hat{R}_{rs}$ spectrum from the test dataset. We then created a new simulated dataset (hereafter, PPC dataset) using parameters $\theta_{posterior}$ (n = 1,000) which were sampled from a posterior distribution estimated for the simulated ground-truth spectrum $\hat{R}_{rs}$ (69,70). We then checked that the ground-truth spectrum lies within the support of the simulated $\hat{R}_{rs}$ spectra in the PPC dataset. Second, we conducted simulation-based calibration using the entire test dataset to assess if the variances of the posterior are balanced, in other words neither over-confident nor under-confident (71,72). Simulation-based calibration is based on calculating a rank statistic from the marginal posterior estimates. If the posteriors have well-calibrated uncertainties, the rank statistics should be uniformly distributed (72). An empirical cumulative distribution function of the rank statistics with respect to the 95% confidence interval of a uniform distribution can be used to visualise the simulation-based calibration (72). Third, we quantified inference performance on the simulated test dataset by calculating coverage probability. The coverage probability measures how often the true parameter value falls within the credible intervals (between the 5th and 95th percentiles) of the posterior distributions.

2.5 Field data

Field data for the evaluation of the SBI algorithm performance was collected from the coral reef atoll of Tetiaroa in the South Pacific (Te Ao Mā'ohi, French Polynesia) in July and August 2022 (Figure 4A). Only sampling sites from brown coral patches (*Porites lobata*) not covered in turf, sand, or algae were included, leaving a dataset of four samples for the algorithm application. Additionally, SBI was applied to drone data, for which ground-truth data from one sampling site was available (Figure 4B).

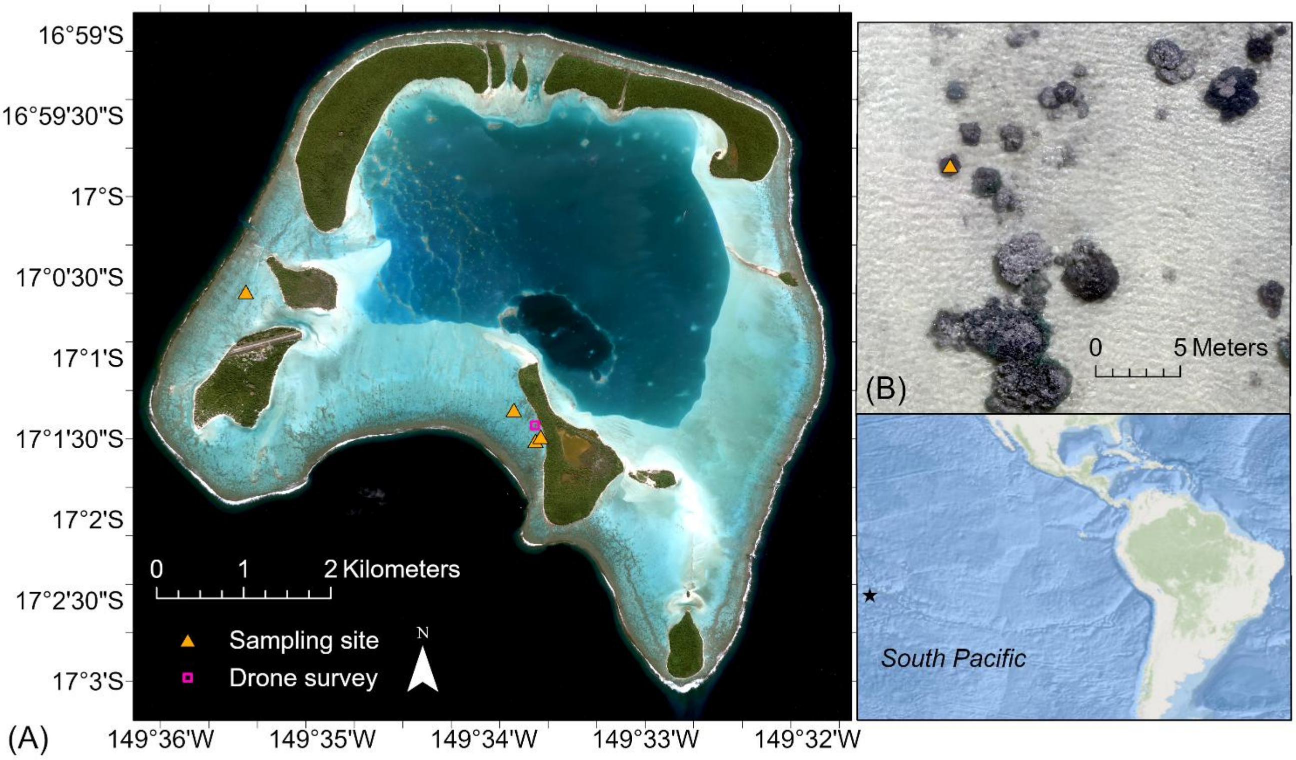

Figure 4. (A) Field sampling sites and drone survey location in Tetiaroa, a coral reef atoll in the South Pacific. (B) Imagery from the drone survey. Satellite imagery: Pléiades ©CNES 2022, Distribution AIRBUS DS, tous droits réservés. Usage commercial interdit. Basemap credit: Esri, Garmin, GEBCO, NOAA NGDC, and other contributors.

2.5.1 Hyperspectral measurements

Just below surface (0⁻) hyperspectral measurements were conducted at each sampling site using a pair of TriOS RAMSES irradiance and radiance radiometers mounted on a frame (Kutser et al., 2013). The TriOS RAMSES radiometers cover the wavelength range of 320-920 nm at a spectral resolution of 3.3 nm. The irradiance sensor was pointed straight up to measure downwelling irradiance $E_d(0^-,\lambda)$, and the radiance sensor was pointed straight down to measure upwelling radiance $L_u(0^-,\lambda)$. The irradiance and radiance measurements were repeated 3-5 times over a 2-minute time interval (55). The mean of these repeated measurements was used in the subsequent calculations. Sub-surface remote-sensing reflectance $r_{rs}(0^-,\lambda)$ was then calculated from these measurements $r_{rs}(0^-,\lambda) = L_u(0^-,\lambda)/E_d(0^-,\lambda)$ (sr^{-1}). Sub-surface remote-sensing reflectance was converted to remote-sensing reflectance just above the water surface $R_{rs}(0^+,\lambda)$ applying $R_{rs} = 0.5r_{rs}/1 - 1.5\, r_{rs}$ (28).

Cubic spline interpolation was used to convert the data from 3.3 nm resolution to 5 nm so as to match the spectral resolution of the simulated dataset. Additionally, to evaluate the versions of the SBI model trained on multispectral reflectance data (corresponding to the bands of the MicaSense RedEdge-MX SDual Camera System), a downsampled field reflectance dataset was created.

2.5.2 Drone survey

A drone survey was conducted over a shallow reef in Tetiaroa on 3 August 2022. The data was acquired using a DJI Inspire 2 drone equipped with a MicaSense RedEdge-MX Dual Camera System. The drone was flown at an altitude of 20 m, producing <5 cm resolution imagery. Radiometric calibration of the imagery was performed using a MicaSense reflectance panel as the calibration target. Images of the panel were recorded before and after the flight, by holding the drone above the panel. The calibration was performed in Agisoft Metashape (version 1.8.4), using the reflectance values given on the panel, lighting conditions recorded by the downwelling light sensor and the standard Agisoft radiometric calibration workflow. Ground-control points for georeferencing were taken using a differential GNSS (Emlid Reach RS+). The imagery was processed in Agisoft to generate a single orthomosaic. Water sampling was conducted at a single sampling site on top of a patch of brown coral immediately after the drone survey. The surface reflectance at the sampling site was extracted from the orthomosaic using the 'extract' function in the Raster package in R (version 3.6-26) (73). The value returned by the extraction method was interpolated from the values of the four nearest pixels.

2.5.3 Water sampling and ancillary data

Discrete water samples were collected using dark 1L HDPE bottles at each sampling site and transported to the United Kingdom (UK) for laboratory analysis of chlorophyll-a concentration and CDOM absorption. The samples were collected from surface water (<50 cm below surface). Before sample collection, the bottles were flushed twice with water from the sampling site. Immediately after sample collection, the bottles were placed in a cool and dark box. The samples were filtered and frozen within 2-3 hours. At the local research station and during transportation to the UK, the samples were kept frozen at -20^{o}C. Upon arrival in the UK, the samples were stored in a -80^{o}C freezer until analysis.

We followed the protocol published by the International Ocean Colour Coordinating Group for the spectrophotometric measurement of CDOM absorption (74). Chlorophyll-a concentration was fluorometrically measured following the EPA Method 445.0 (75). Additionally, turbidity measurements were conducted in-situ using a multiparameter water quality sonde (EasyProbe 30). Suspended particulate matter (SPM) concentration was estimated from turbidity using an empirical relationship (76): $[SPM] = m \times Turbidity$, where m is an empirically estimated conversion factor (76). The relationship between turbidity and SPM concentration may vary in space and time, for example due to changes in grain size of the suspended particles (76). According to a study focused on the Great Barrier Reef, the conversion factor may vary between 1 and 5 (76). The estimated SPM concentrations are therefore highly uncertain. To take this into account, we report the estimated range of SPM concentrations (defined by the lower (1) and upper (5) limit of conversion factors) rather than a single value. SPM consists of both organic and inorganic particles, and therefore only provides an upper boundary for mineral concentration.

Depth was measured using a weighted transect line and benthic cover was recorded using a digital camera. The site location was recorded at an accuracy of at least 50 cm using a Bad Elf Flex GNSS receiver. Wind speed was approximated by the same researcher every day.

3 Results

We start by presenting the inference diagnostics results. We then provide results of SBI applications to field-collected data and discuss how SBI performance is affected by signal-to-noise ratio and spectral resolution. We highlight novel insights that can be drawn from applying a probabilistic machine learning approach in marine remote sensing.

3.1 Inference diagnostics

The inference diagnostics indicated that the SBI algorithm is well calibrated and does not have a systematic bias in posterior estimation. First, the posterior predictive check confirmed that the ground-truth $\hat{R}_{rs}$ spectrum is within the 5 to 95 percentiles of the posterior predictive (Figure 5A). Second, simulation-based calibration showed that all the estimated parameters fall within or near the 95% confidence interval of the uniform distribution, evidencing that the posterior mean is well calibrated and is neither systematically under- or overestimating the parameters, nor is it under- or over dispersed (Figure 5B). Finally, the evaluation of algorithm performance on independently generated simulated data (n = 1,000) indicated good correspondence between the estimated posterior and the true parameter values. A minimum of 91% coverage probability was achieved for all the inferred parameters, regardless of the signal-to-noise ratio or whether the inference model was trained with hyper- or multispectral data (see Appendix D for additional results).

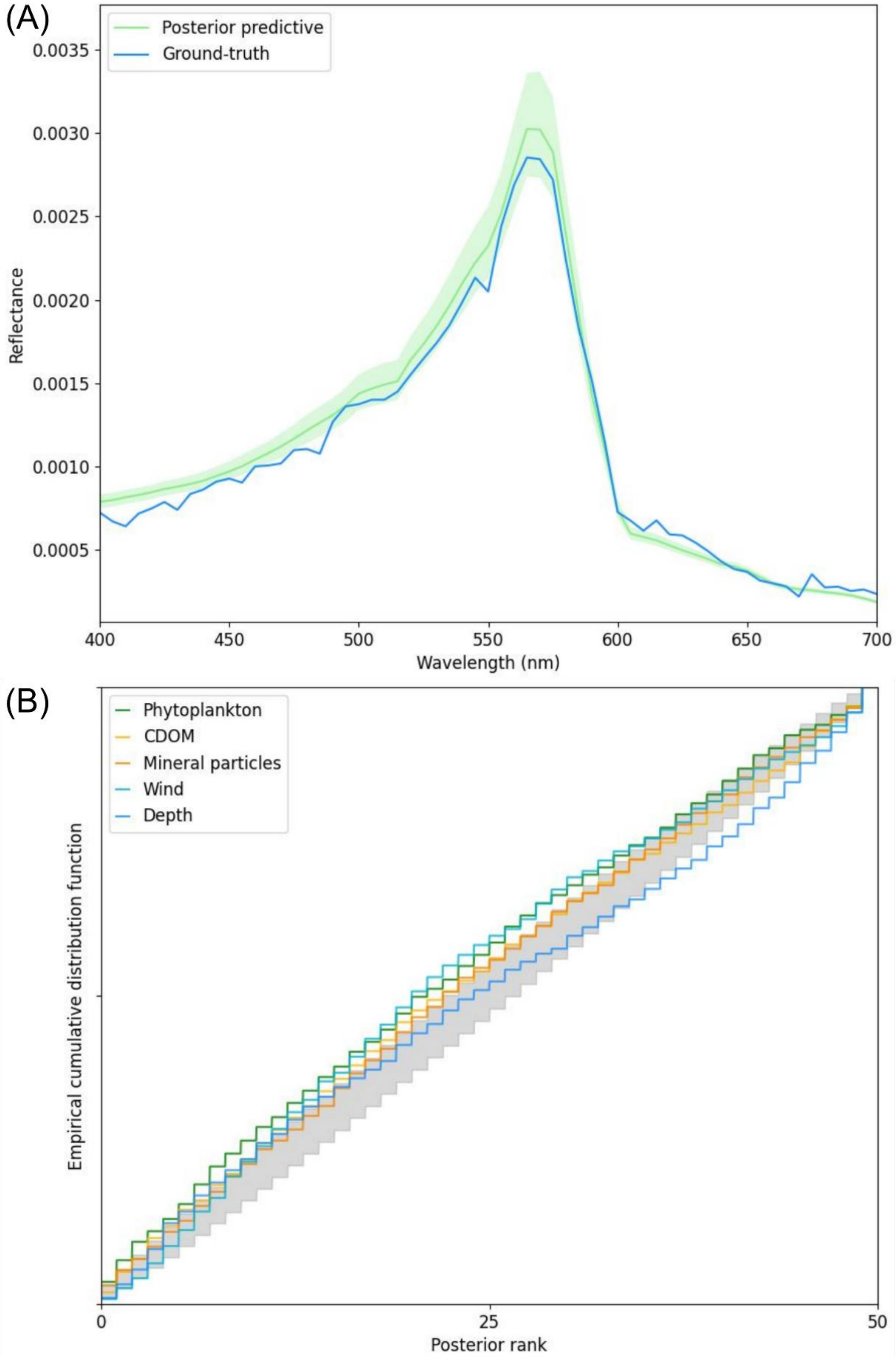

Figure 5. (A) Posterior predictive check. The ground-truth simulated spectrum (blue line) lies within the 5 to 95 percentiles of the posterior predictive (light green area). The mean of the posterior predictive is shown with the dark green line. (B) The Cumulative

Distribution Functions (CDFs) of simulation-based calibration ranks for each of the five θ parameters (each shown with a line of a different colour) with respect to the 95% confidence interval of a uniform distribution (shown in light grey). The plots shown here represent applications of the SBI model trained with hyperspectral spectra characterised by a medium-level signal-to-noise ratio of 100 SNR. CDOM = coloured dissolved organic matter.

3.2 Application to field data

Plots of univariate and pairwise marginalised posterior distributions can be used to visualise the results of statistical inference (Figure 6). If the posterior is well-calibrated, the true (field-measured) parameter value should lie at a random location (weighted by the posterior mass) within the posterior. The application of the SBI algorithm on the field dataset (n = 4) showed that the θ parameters were generally well retrieved (Figure 6). Phytoplankton concentration was overestimated at one of the sampling sites (Site 1, Figure 6A, B, C). At Sites 3 and 4, the field-measured values for phytoplankton and wind speed laid at the lower end of the posterior (Figure 6E, F).

Out of all inference models (trained with data characterised by different spectral resolutions and noise levels), the inference model trained with hyperspectral data characterised by a medium level of signal-to-noise ratio (100) had the best overall inference performance. Inference performance was assessed based on both coverage probability and the width of the 95% confidence interval calculated from the one-dimensional marginal posterior distribution (Appendix D). Coverage probability measures how often the field-measured parameter value falls between the 5th and 95th percentiles of the posterior. The confidence interval width can be used to quantify how confidently each of the parameters is retrieved.

The inference model trained with noisier data (signal-to-noise ratio of 50) produced, in general, slightly wider posterior distributions. In other words, the inference model tended to be less confident about the inferred parameters (Figure 6B). The inference model trained with data characterised by the lowest level of noise (signal-to-noise ratio of 500) performed worse, producing posteriors that were not always overlapping with the ground-truth values (Figure 6C).

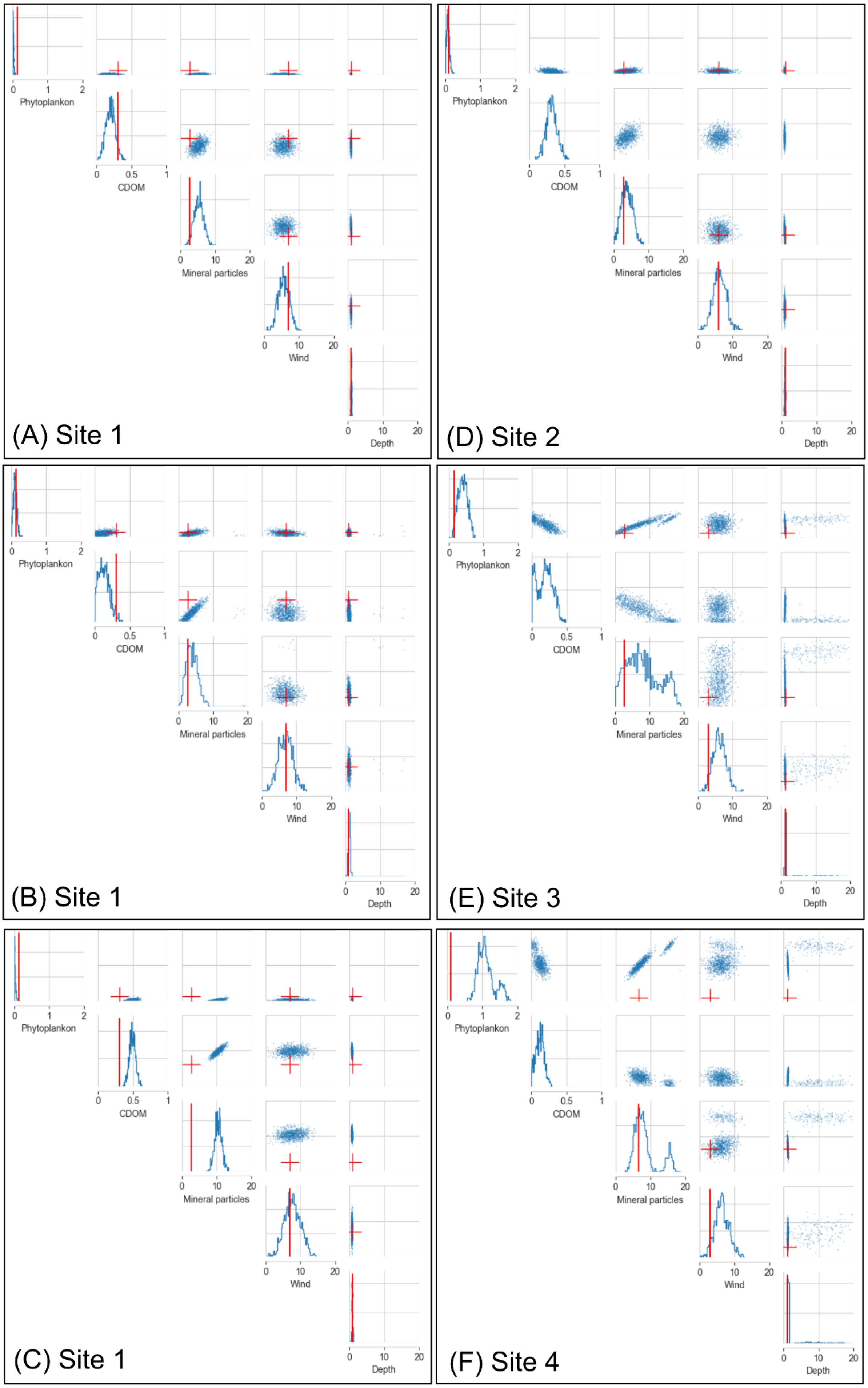
(A) Site 1
(D) Site 2
(B) Site 1
(E) Site 3
(C) Site 1
(F) Site 4
Phytoplankon
0
1
2
CDOM
0
0.5
1
Mineral particles
0
10
20
Wind
0
10
20
Depth
0
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Figure 6. Inference performance on real observations: univariate and pairwise marginalised posterior distributions for the five parameters. (A), (D), (E), and (F) show the results for Sites 1, 2, 3, and 4. These plots were generated with the SBI model trained with hyperspectral data characterised by a signal-to-noise ratio of 100. (B) and (C) show results for Site 1 for the SBI model trained with hyperspectral data characterised by different signal-to-noise ratios (50 and 500, respectively). Coloured dissolved organic matter (CDOM) absorption was only measured at one of the sites (Site 1). The field-measured (ground-truth) values are shown in red, and the posterior distributions are shown in blue. The ground-truth values for minerals concentration are an estimate of suspended particulate matter derived from turbidity data. The suspended particulate matter values shown are the means of the possible ranges (see section 2.5.3.).

Considering the impact of spectral resolution on inference performance, we found the SBI algorithm to be relatively robust to decreased spectral resolution, with little difference in coverage probability between the hyperspectral and multispectral applications with medium and high levels of noise (Figure 7, Appendix D). However, decreasing the spectral resolution did make the algorithm somewhat less confident about water constituent estimates, producing slightly wider 95% confidence intervals at most sampling sites (Figure 7). Phytoplankton concentration was consistently retrieved with the least uncertainty (narrow posterior distributions) (Figure 7). The parameters were accurately retrieved from the drone-measured multispectral remote-sensing reflectance (Figure 8).

Note that plotting the 95% confidence interval (Figure 7) does not show the distribution of posterior mass within that interval, nor are the potentially multimodal posterior structures visualised. The most meaningful interpretation of the results is obtained by combining insights from Figures 6 and 7. For example, when the inference indicated large uncertainty about minerals concentrations (e.g., Sites 3 and 4, inference using hyperspectral data), there was also more uncertainty about depth (Figure 7), even though the majority of the posterior mass was still located in a single, narrow peak (Figure 6).

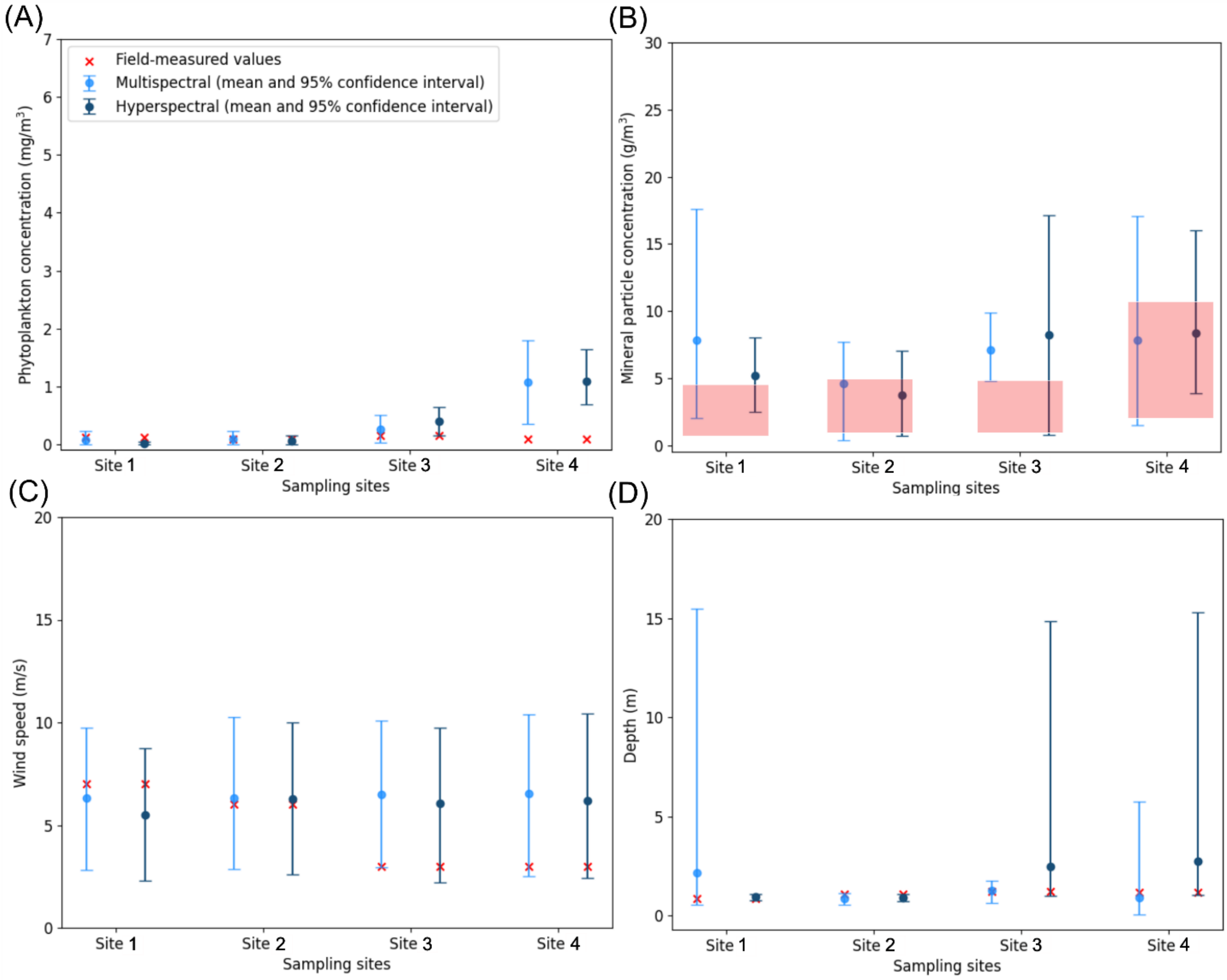

Figure 7. Inference performance on real observations at four sampling sites. The plots shown here apply the SBI model trained with hyperspectral or multispectral data characterised by a medium level of noise (signal-to-noise ratio of 100 SNR). (A)

phytoplankton concentration, (B) minerals concentration, (C) wind speed, and (D) depth. The blue dot corresponds to the posterior mean, while the red cross corresponds to the field-measured (ground-truth) value. The blue bars show the range of the 95% confidence interval associated with the posterior distribution. For minerals concentration (B), the ground-truth values are an estimate of suspended particulate matter derived from turbidity data. To represent the uncertainty associated with the suspended particulate matter estimate, a value range is shown instead of a point estimate (see section 2.5.3.). Note that the 95% confidence interval does not capture the distribution of the posterior mass within that interval.

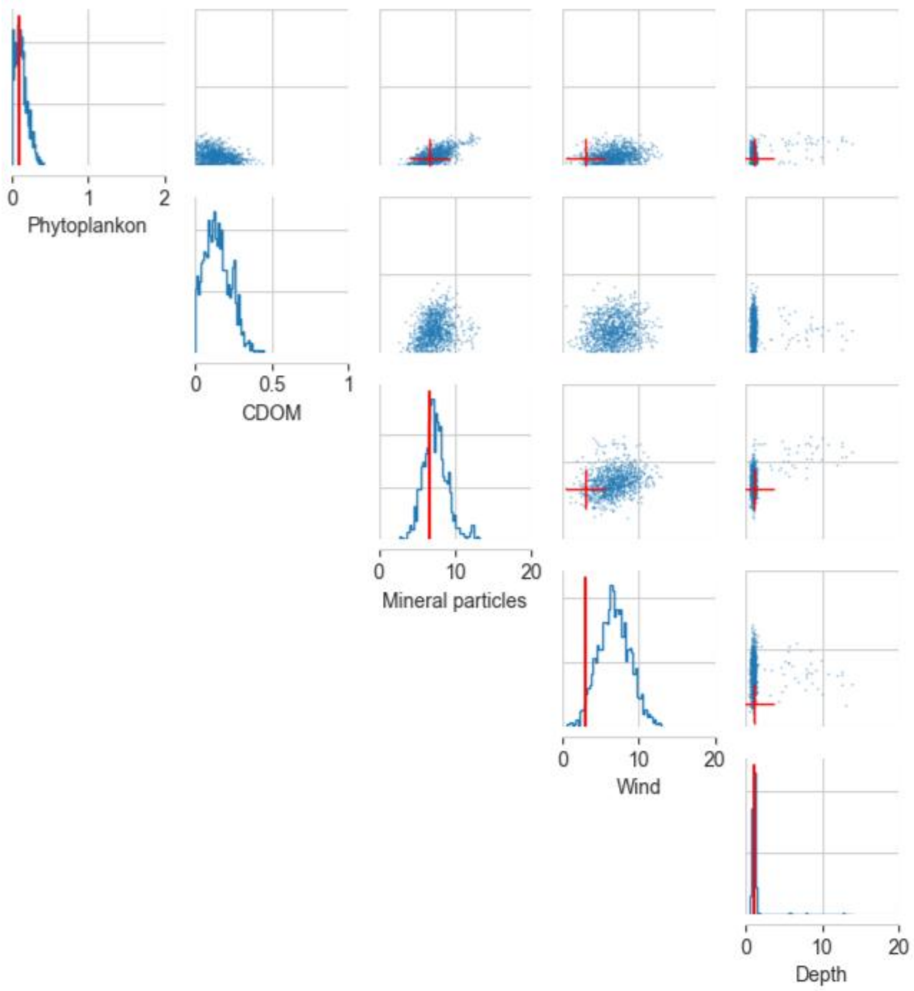

Figure 8. Inference on drone-measured remote-sensing reflectance: univariate and pairwise marginalised posterior distributions for the five parameters. The field-

measured (ground-truth) values are shown in red, and the posterior distributions are shown in blue. The ground-truth value for minerals concentration is an estimate of suspended particulate matter derived from turbidity data. The suspended particulate matter value shown is the mean of the possible range (see section 2.5.3.). No ground-truth measurement of coloured dissolved organic matter (CDOM) is available at this sampling site.

4 Discussion

The majority of marine remote sensing algorithms have been developed for optically deep waters (8). The satellite-based mapping of water constituents in optically shallow environments has received less research attention (25,77,78). While great advancements have been made in the retrieval of bathymetry and benthic cover type from satellite and drone data (79–82), few studies have focused specifically on developing algorithms for the accurate retrieval of water constituent concentrations in optically shallow environments (77,83). Importantly, improved inference of optically active water constituents would also help enhance the accuracy of benthic mapping (41,55,84,85).

Here we have presented an innovative probabilistic machine learning algorithm for the inference of phytoplankton and minerals concentrations, and CDOM absorption from hyperspectral or multispectral data. We found that the likely ranges of water constituent concentrations can be estimated from remote-sensing reflectance in shallow coral reef environments, assuming a single benthic cover. A key advantage of the SBI probabilistic machine learning approach is that the algorithm can be amortised: once trained, it can be applied, under the same assumptions, to new observations without any additional retraining. Applying the amortised algorithm is fast even without GPU or cloud computing, making SBI a promising approach for large-scale analysis of remotely sensed data. A future water quality mapping workflow could include the delineation of optically shallow/deep waters as a first step (86), and the application of the SBI algorithm tuned for shallow waters as a second step.

Plotting the posterior distributions – the pairwise marginalised posterior distributions in particular – provides useful insights into the likely parameter space corresponding to the observed remote-sensing reflectance. Thereby, the SBI approach provides a new way to address the ill-posed inverse problem of marine remote sensing. Instead of providing a single point estimate as a solution, without knowledge about whether the solution is a global or a local maximum, the SBI approach captures the range of plausible solutions, shown by elongated ellipses in the pairwise marginalised posterior.

Correlation structures in the pairwise marginalised posterior distributions can provide useful insights into the combinatory parameter space that solves the inverse problem. For example, in the field application results of the SBI models trained with datasets characterised by different signal-to-noise ratios, there was a consistent positive relationship in the pairwise marginalised posterior distribution for phytoplankton and minerals. This would suggest that the optical signal (remote-sensing reflectance) would be similar if phytoplankton and mineral concentrations were both either low or high. In this small field dataset, the observed, unintuitive correlation structure may result from small differences in benthic reflectance between sampling sites that the SBI algorithm cannot correctly interpret, as it was trained on a simulated dataset that assumed no variation in benthic reflectance. Nevertheless, the results demonstrate the potential of the SBI approach to offer novel insights into the structure of the parameter space that solves the ill-posed inverse problem. A larger field dataset and the development of approaches to account for the variation in benthic reflectance are required to fully realise the potential of the SBI approach.

Quantifying the widths of the posterior distributions can provide additional insights into the solution of the inverse problem. For example, the SBI algorithm was consistently more confident about phytoplankton concentration compared to the other inferred parameters. This suggests that the signal of phytoplankton pigments can be detected from the spectra even in the presence of the confounding impacts from other optically active constituents, such as suspended minerals. In contrast, the estimation of mineral concentration was often associated with large uncertainty, potentially due to the confounding effect of bottom reflectance.

4.1 Limitations and future developments

We evaluated inference performance on a small field dataset. For two out of four sites, field-measured values fell at the lower end of the posterior. Inference performance should be further evaluated on a larger field dataset to confirm whether this results from a small bias in the inference: for a well-calibrated posterior, the field-measured value should lie at a random location within the posterior, weighted by the posterior mass.

Phytoplankton concentration was slightly overestimated at one site. This could be explained by uncertainty associated with the field data due to potential sample degradation before analysis. The International Ocean Colour Coordinating Group (IOCCG) recommends sample storage in -80°C, however our field samples were stored at -20°C during transportation to the laboratory (87). Indeed, field measurements of phytoplankton, suspended minerals, and CDOM are characterised by large uncertainties (88,89), with reported average absolute percent differences of 6-13% between duplicate samples (90,91).

Another source of uncertainty in this first remote sensing application of the SBI algorithm comes from assuming fixed relations between water constituent concentrations and inherent optical properties (32). In other words, the inversion is conducted from remote-sensing reflectance directly to biophysical variables (e.g., concentrations of phytoplankton and minerals) rather than inherent optical properties (e.g., absorption and scattering by phytoplankton and minerals) (39,92). The uncertainty in the bio-optical model is particularly high in shallow coral reef waters, where measurements of water column biophysical variables and their bio-optical counterparts are widely lacking (1,10,93). The resulting bio-optical model misspecification (i.e., the inability to accurately reproduce the field data) for coral reef waters is a likely explanation for the worse performance of the SBI model when trained on less noisy simulated data. Future work could test implementing the SBI approach to infer inherent optical properties and investigate the uncertainties associated with the bio-optical model conversion between biophysical and optical variables. Additionally, novel approaches for dealing with model misspecification in SBI could be explored (94).

Another interesting avenue for future research would be the investigation of dimensionality reduction of hyperspectral data before inputting it to the conditional density estimator. Reducing the dimensionality of the input data from hyperspectral (61 spectral bands) to multispectral (7 spectral bands) did not drastically decrease inference performance. This suggests that lower-dimensional spectral data may be sufficient for water quality mapping applications. Future work could explore dimensionality reduction, for example using a convolutional neural network that could learn additional informative features from the hyperspectral data, such as spectral shape. Such an approach might be one way to better leverage the wealth of information provided by hyperspectral remote sensing sensors.

Further field data collection will be needed to thoroughly assess the performance of the SBI algorithm in different environmental conditions, especially in more turbid coral reef waters. Future developments should include variability in benthic reflectance in the simulations and consider the spectral mixing of multiple benthic cover types. Finally, future work could fine-tune the SBI algorithm to specific satellite and drone sensors through the application of sensor-specific, wavelength-dependent noise models.

5 Conclusions

The SBI algorithm performance was relatively robust to lower levels of signal-to-noise ratio, although the uncertainty associated with the inferred water constituent concentrations tended to be slightly higher with increased noise. In fact, including too little noise in the simulated dataset resulted in less accurate inference on field data. Uncertainty associated with the bio-optical model may explain why the SBI model trained with the least noisy dataset performed less well; the inference model likely became overly confident about the relations between the biophysical and optical variables.

We identify two research priorities for future work. First, there is a need for further bio-optical data collection to characterise spatial-temporal variability in the optical properties of shallow coral reef waters. A larger field dataset covering a range of environmental conditions is essential for future algorithm development and evaluation. Indeed, we call for a coordinated effort to produce a curated dataset consisting of *in situ* hyperspectral reflectance and water quality measurements from shallow coral reef waters around the world. Second, this first application of SBI to marine remote sensing assumes a single benthic cover (brown coral). Future developments should focus on adapting the algorithm so that it can be applied to satellite pixels that include a mix of different benthic cover types. Establishing a freely available, curated spectral library covering a range of coral species and benthic substrates would help tackle the issue of spectral mixing.

This study advances the mapping of water quality in shallow coral reef environments and applies an innovative probabilistic machine learning approach to address the inverse problem of marine remote sensing. Mapping and monitoring the spatial-temporal dynamics of water constituent concentrations using remote sensing would provide new insights to key ecological and biogeochemical processes taking place in coral reef ecosystems. Ultimately, a better understanding of the variability in water constituent concentrations in coral reef environments could help identify priority sites for local management and restoration action. The SBI algorithm can be used to estimate the likely ranges of phytoplankton and mineral concentrations, absorption by CDOM, wind speed, and depth from hyperspectral or multispectral remote-sensing reflectance. This is a significant advantage over traditional spectral optimisation methods that only provide a single solution without an estimate of confidence in the result. Another important advantage of our approach is that the SBI algorithm is amortised: once it has been trained on simulated data, it can be applied to new observations without retraining. This makes SBI a promising approach for computationally efficient analysis of large amounts of satellite and drone data.

6 Data accessibility

All data and code used in the study are open source and freely available via the Open Science Framework data repository (49) and the associated GitHub repository (https://github.com/pirtapalola/SIMA).

7 Conflict of interest declaration

We declare we have no competing interests.

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Appendix A – Computational resources

Full details of the computational resources required for running the simulations and for training and applying the SBI algorithm.

A single run of EcoLight (version 5.3, Numerical Optics Ltd.) took 36 seconds. Running the 30,000 simulations took 300 hours. Running simulations can be easily parallelised, reducing the simulation time to a few hours for multithreading on multiple CPUs.

All inference networks were trained on a High-End CPU (Intel Core i9-12900H, 32 GB RAM), and training time was around 15 and 25 minutes for the hyperspectral and multispectral setting, respectively. Inference time was in both cases less than 0.5 seconds for a single observation. This highlights the benefit of the amortised setup, where the upfront training cost quickly pays off for multiple observations.

Appendix B – Parameterisation of the bio-optical model

Full details of the parameterisation of the bio-optical model in EcoLight and estimation of prior distribution for wind speed.

Contents

1 Bio-optical model

The transfer of light through water is mathematically described with radiative transfer equations (Equation B.1) (Mobley, 1994).

Equation B.1. $cos\theta \frac{dL(z,\theta,\phi,\lambda)}{dz} = -c(z,\lambda)L(z,\theta,\phi,\lambda) + L^{*}(z,\theta,\phi,\lambda) + S(z,\theta,\phi,\lambda)$

where $cos\theta$ is the vertical projection of radiance L in the direction specified by the polar coordinates, the zenith angle θ and azimuthal angle ϕ. The beam attenuation coefficient $c(z,\lambda)$ captures the attenuation of light (i.e., the *decrease* in radiance) as light travels through the water column. Light attenuation is caused by absorption $a(\mathrm{z},\lambda)$ and scattering $b(\mathrm{z},\lambda)$ by particulate and dissolved constituents and by water itself (Equation B.2) (Morel, 2009).

Equation B.2. $c(z,\lambda) = a(\mathrm{z},\lambda) + b(\mathrm{z},\lambda)$

The term $L^{*}(z,\theta,\phi,\lambda)$ captures the *increase* in radiance with depth resulting from scattering from adjacent paths. Finally, $S(z,\theta,\phi,\lambda)$ accounts for any additional in-water light sources, such as fluorescence (Mobley, 1994, 2001). Total absorption (a) can be expressed as the sum of the absorptions of pure seawater (a_w), phytoplankton (a_{phy}), colored dissolved organic matter (a_{CDOM}), and mineral particles (a_{SS}) as a function of wavelength (λ) (Equation B.3).

Equation B.3. $a(\lambda) = a_w(\lambda) + a_{phy}(\lambda) + a_{CDOM}(\lambda) + a_{SS}(\lambda)$

Similarly, total scattering (b) can be modelled as a sum of the scattering of water (b_w), phytoplankton (b_{phy}), and mineral particles (b_{SS}), assuming no scattering from $CDOM$ (Equation B.4).

Equation B.4. $b(\lambda) = b_w(\lambda) + b_{phy}(\lambda) + b_{SS}(\lambda)$

The light environment in coral reef waters is significantly affected by each of the three optically active water constituents (Russell et al., 2019).

1.1 Implementation in EcoLight

EcoLight couples a water column bio-optical model with models of bottom reflection, the air-water surface, and the atmosphere. The bottom reflectance model assumes a Lambertian reflecting surface. The air-water surface model uses Cox-Munk wind speed and wave slope statistics, temperature- and salinity-dependent Fresnel reflectance, and Monte Carlo simulations of rays interacting with the sea surface (Mobley, 1994). The parameterisation of the bio-optical model (Case-II bio-optical model) in EcoLight is described in Table B.1 and the following sections. In the atmospheric model, we assumed a solar zenith angle of 30°, which corresponds closely to the solar zenith angle at the time of field data collection.

Table B.1. EcoLight parameterisation. Very long equations (Raman scattering and the Fournier-Forand phase function) were not included for brevity.

Parameter		**Units**	**Values, equations, and notes**	**References**
Case-II bio-optical model				
Seawater	Absorption	m^{-1}	-	(Pope & Fry, 1997)
	Phase function	sr^{-1}	$\tilde{\beta}_w(\psi) = 0.06225 \times (1 + 0.835 cos^2\psi)$, where $\tilde{\beta}_w$ is the scattering phase function and ψ is the angle of the scattering	(Mobley, 1994)
	Elastic scattering	m^{-1}	$b_w(\lambda) = 16.06 \times 1.80 \times 10^{-4} \times (500/\lambda)^{4.32}$, where b_w is the scattering of seawater and λ is the wavelength	(Morel, 1974)
	Inelastic (Raman) scattering	m^{-1}	-	Appendix in (Mobley et al., 1993)
Phyto-Plankton	Specific absorption coefficient	$m^2 mg^{-1}$	-	(Prieur & Sathyendranath, 1981)
	Scattering	m^{-1}	$b_p(\lambda) = b_0(\lambda)[Chl]^{\beta}$, where β is the slope, λ is the wavelength, $[Chl]$ is chlorophyll concentration, and B_0 is a constant	(Boss et al., 2013; Morel, 2009; Voss, 1992)
	Phase function	sr^{-1}	Fournier-Forand	(Fournier & Forand, 1994; Mobley et al., 2002)
CDOM	Absorption	m^{-1}	$a_{CDOM}(\lambda) = a_{CDOM}(\lambda_0)e^{-\gamma(\lambda-\lambda_0)}$	(Russell et al., 2019)
Mineral particle	Specific absorption coefficient	$m^2 g^{-1}$	-	(Ahn, 1990)

Specific scattering coefficient	$m^2\ g^{-1}$	-	(Ahn, 1990)
Air-water surface boundary model			
Wind speed	$m\ s^{-1}$	Range: 0-20	-
Real index of refraction of water	-	Wavelength independent	-
Atmospheric model (RADTRAN-X)			
Solar zenith angle	°	30	
Cloud cover	%	0	
Sea-level pressure	mm Hg	760.0	
24-h averaged wind speed	$m\ s^{-1}$	5.0	(Dutheil et al., 2020)
Horizontal visibility	km	15	
Relative humidity	%	80	
Precipitable water content	cm	2.5	
Total ozone	Dobson	300	
Airmass type	-	1 (marine)	
Earth-sun distance	-	Annual average	
Bottom reflection model			
Benthic reflectance		Finite depth; dependent on wavelength	

1.1.1 Pure seawater

The description of the optical properties of pure seawater is well-established. We employed the absorption coefficients of Pope & Fry (1997). Elastic scattering was defined following Mobley (1994). Additionally, Raman (inelastic) scattering was included as it can be important in clear ocean waters at short wavelengths (400-500 nm) (Marshall & Smith, 1990). Fluorescence was assumed to be non-significant in oligotrophic waters (Marshall & Smith, 1990).

1.1.2 Phytoplankton

Phytoplankton absorption was calculated as the product of the specific absorption coefficient (a^*_{phy}) and its respective biomass (chlorophyll-*a* concentration) (Equation B.5). We employed the phytoplankton specific absorption coefficient values estimated by Prieur & Sathyendranath (1981).

Equation B.5. $a_{phy}(\lambda) = (a^*_{phy}(\lambda)[Chl])$

Scattering by phytoplankton was specified using an empirically derived power law between the particulate backscattering coefficient and chlorophyll concentration (Equation B.6) (Morel, 2009).

Equation B.6. $b_p(\lambda) = b_0(\lambda)[Chl]^{\beta}$

We used values from (Boss et al., 2013), where $\beta = 0.53$ is the slope, $\lambda = 550$ is the wavelength, $[Chl]$ is chlorophyll concentration, and B_0 = 0.30 is a constant. This global dataset (n = 55,883) is larger and has a better representation of oligotrophic waters than the previously published datasets (Gordon & Morel, 1983; Loisel & Morel, 1998; Morel, 1980; Voss, 1992). This is reflected by the smaller spectral slope compared to the estimates of previous studies (e.g., Gordon & Morel, 1983: $\beta = 0.62$).

1.1.3 Coloured dissolved organic matter

Russell et al. (2019) collected bio-optical data in a range of different coral reef environments in the Pacific Ocean and showed that $CDOM$ makes a significant contribution to total absorption in the water column in shallow coral reef environments. To estimate absorption by $CDOM$, we applied exponential decay function (Equation B.7).

Equation B.7. $a_{CDOM}(\lambda) = a_{CDOM}(\lambda_0)e^{-\gamma(\lambda-\lambda_0)}$

The spectral slope was set to the median value observed by Russell et al. (2019) in shallow reef systems in the Pacific ($\gamma = 0.014$).

1.1.4 Mineral particles

Mineral particle absorption was calculated as the product of the specific absorption coefficient (a_{SS}^{*}) and its respective concentration (Equation B.8). Mineral particle scattering was calculated in an analogous manner (Equation B.9). We employed the specific absorption and scattering coefficient values estimated by Ahn (1990).

Equation B.8. $a_{SS}(\lambda) = (a_{SS}^{*}(\lambda)[SS])$

Equation B.9. $b_{SS}(\lambda) = (b_{SS}^{*}(\lambda)[SS])$

2 Wind speed data

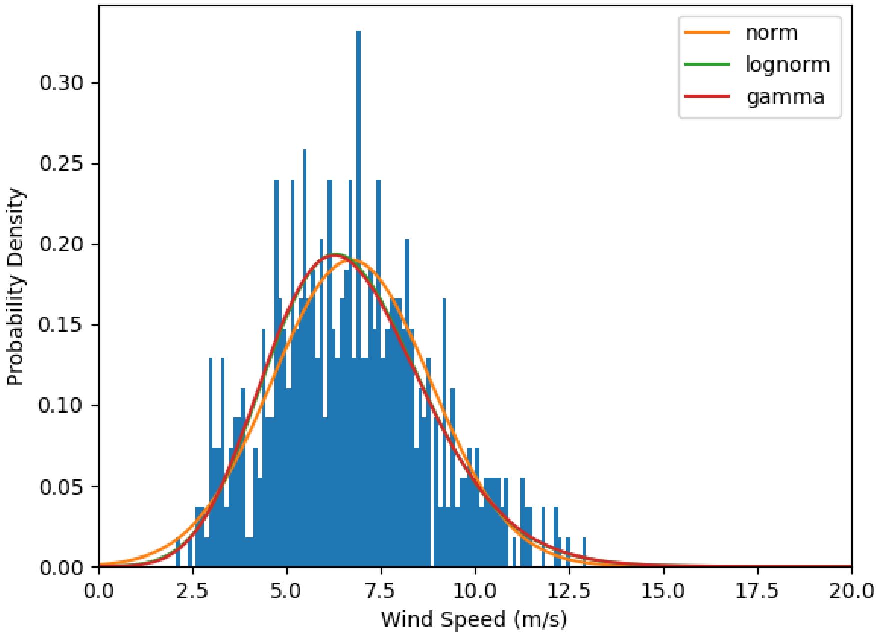

Figure B.1. Fitting distributions to the daily wind speed data (E.U. Copernicus Marine Service Information, 2023). The daily windspeed was extracted for a period of five years (2017-2022) in the study region (between longitudes -150° and -149° and latitudes -18° and -17°). Test results: Normal Distribution: KS = 0.0346, p-value = 0.5781. Lognormal Distribution: KS = 0.0258, p-value = 0.8866. Gamma Distribution: KS = 0.0262, p-value = 0.8739.

3 References

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Appendix C – Optically active water constituents in coral reef environments

Please view the Excel file through this link.

Appendix D – Additional results

Additional results for the SBI models trained with data characterised by different signal-to-noise ratios and spectral resolutions.

Contents

1 Test on simulated data

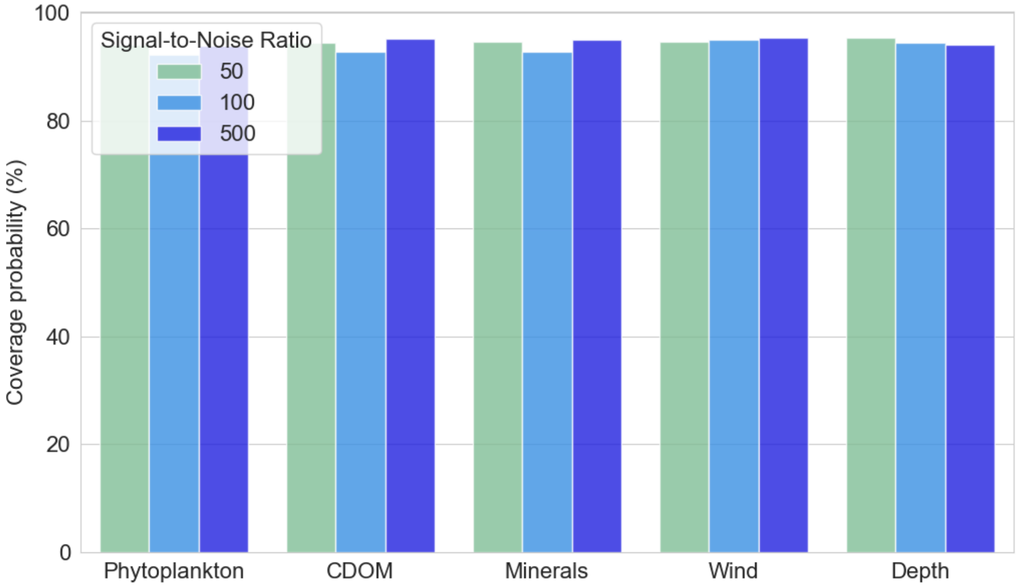

Figure D.1 Inference performance on simulated test data (n = 1,000): coverage probabilities acquired using the inference model trained with hyperspectral data.

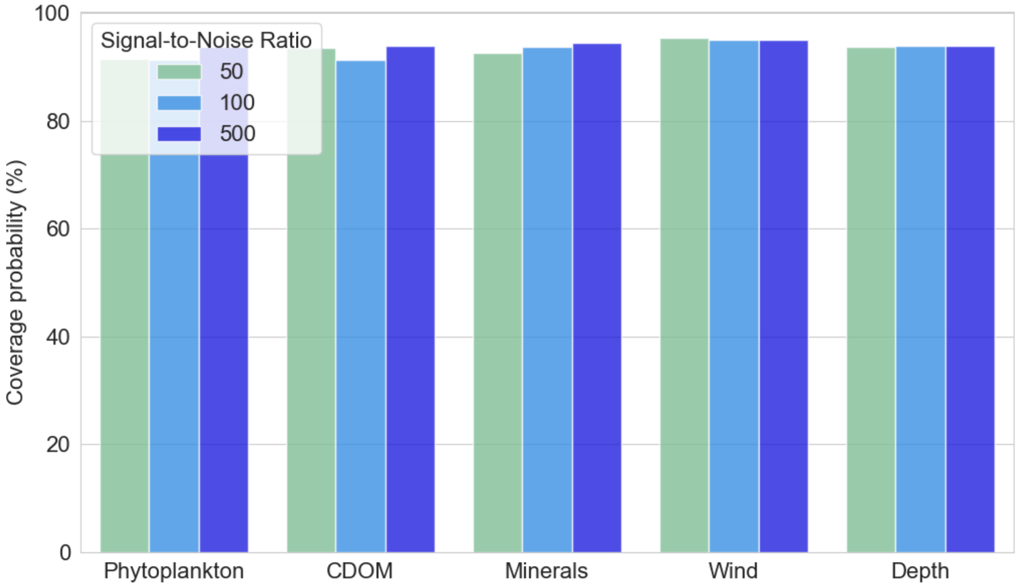

Figure D.2 Inference performance on simulated test data (n = 1,000): coverage probabilities acquired using the inference model trained with multispectral data.

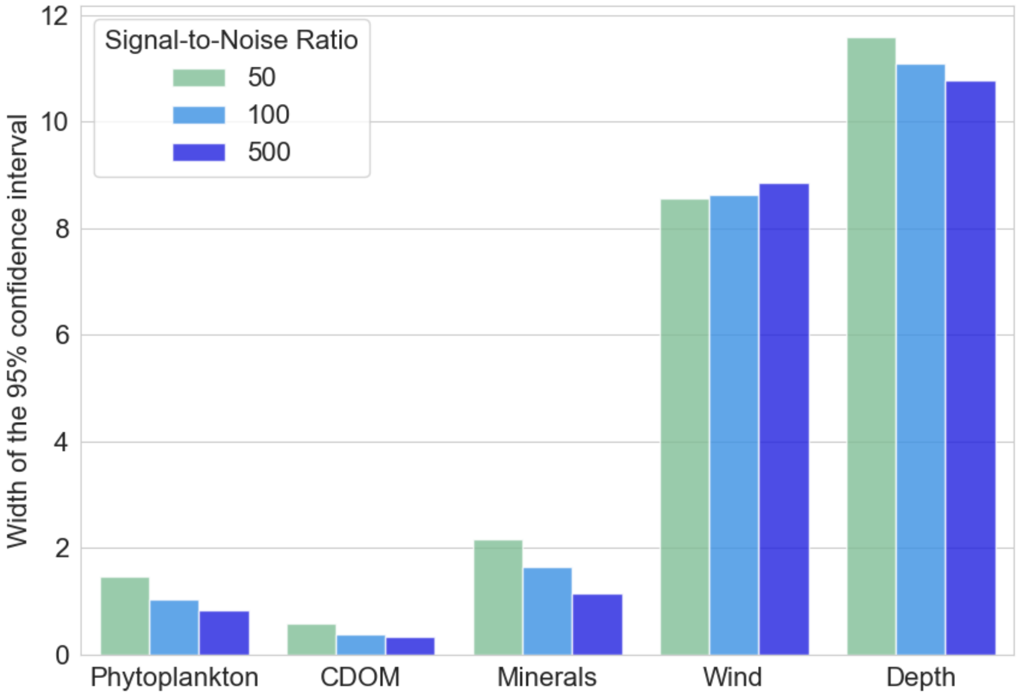

Figure D.3 Inference performance on simulated test data (n = 1,000): widths of the 95% confidence intervals acquired using the inference model trained with hyperspectral data. Note that the 95% confidence interval does not capture the distribution of the posterior mass within that interval. Thus, further analyses are needed to accurately describe the uncertainty associated with the inference of each parameter on simulated data.

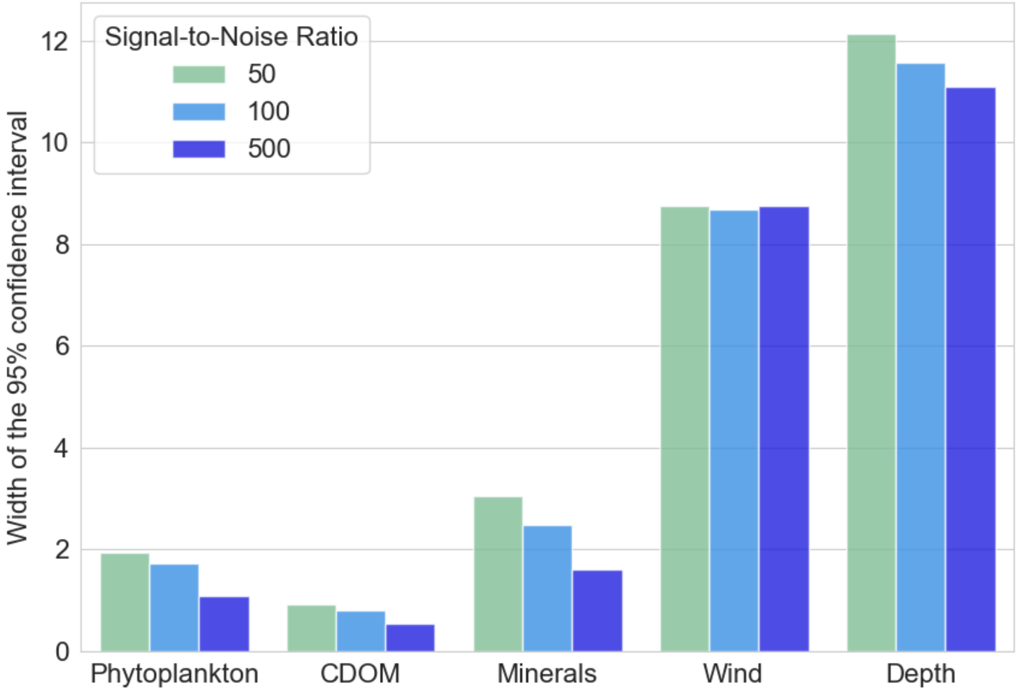

Figure D.4 Inference performance on simulated test data (n = 1,000): widths of the 95% confidence intervals acquired using the inference model trained with multispectral data. Note that the 95% confidence interval does not capture the distribution of the posterior mass within that interval. Thus, further analyses are needed to accurately describe the uncertainty associated with the inference of each parameter on simulated data.

2 Field data application

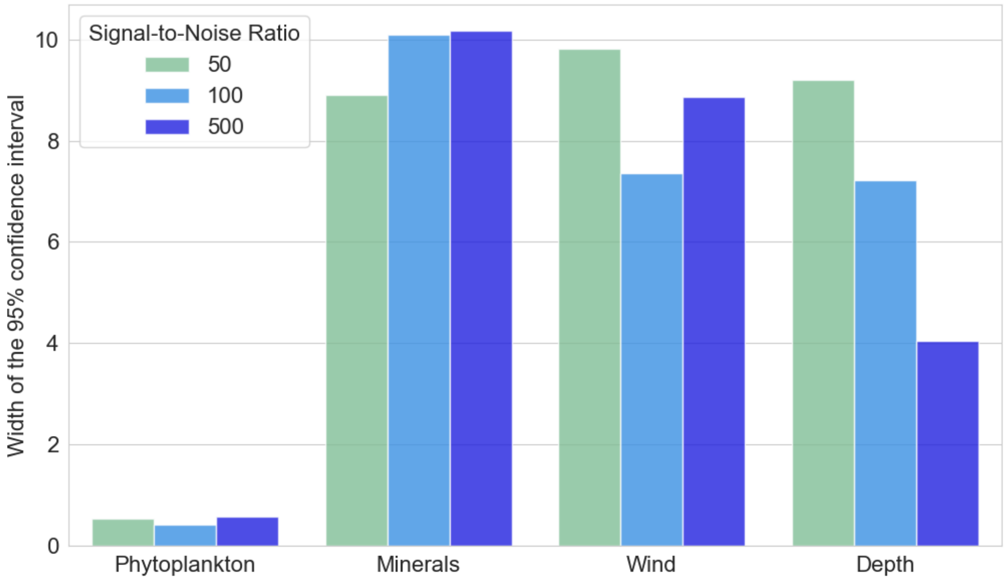

Figure D.5 Inference performance on real observations (n = 4): widths of the 95% confidence intervals acquired using the inference model trained with hyperspectral data. Note that the 95% confidence interval does not capture the distribution of the posterior mass within that interval.

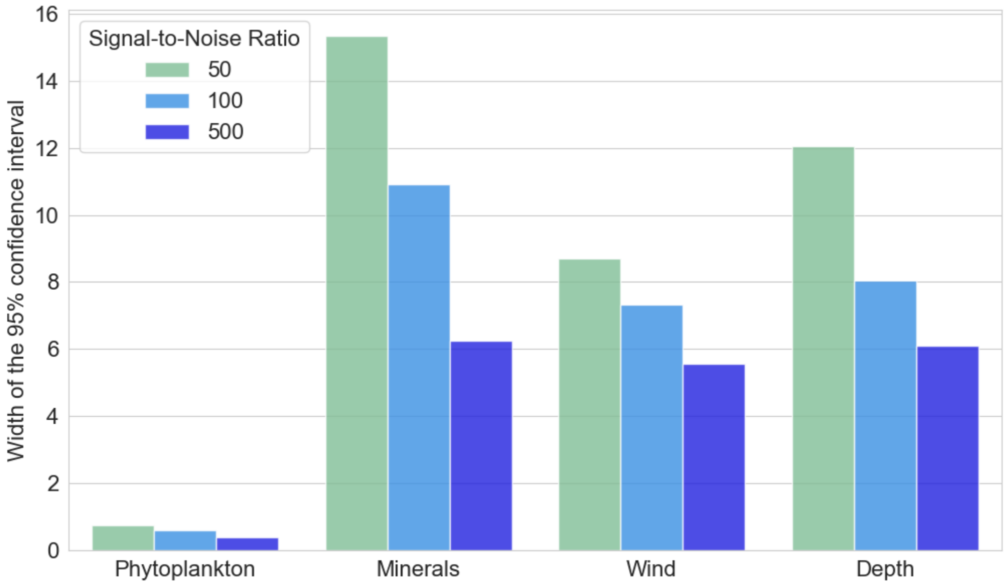

Figure D.6 Inference performance on real observations (n = 4): widths of the 95% confidence intervals acquired using the inference model trained with multispectral data. Note that the 95% confidence interval does not capture the distribution of the posterior mass within that interval.

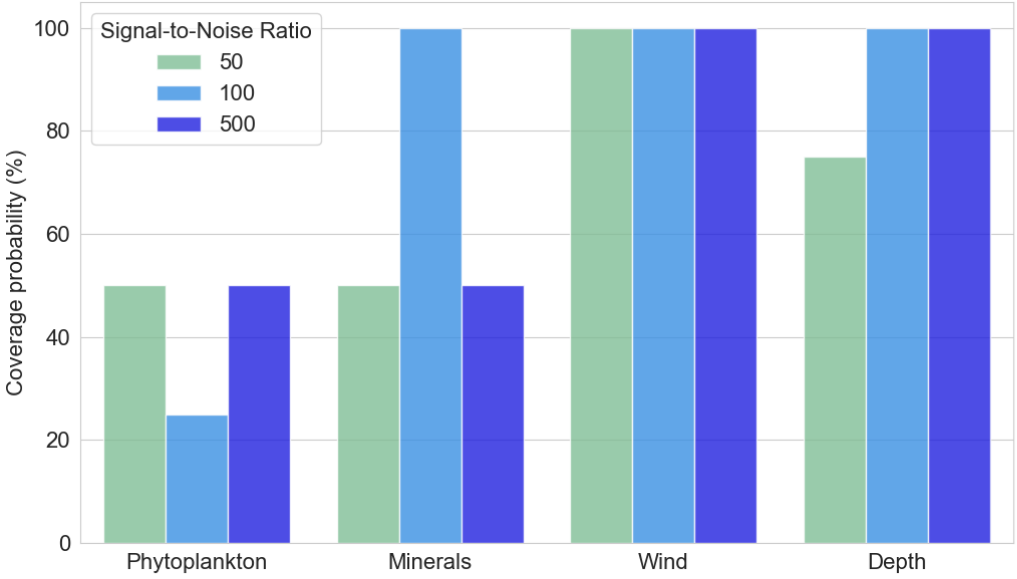

Figure D.7 Inference performance on real observations (n = 4): coverage probabilities acquired using the inference model trained with hyperspectral data.

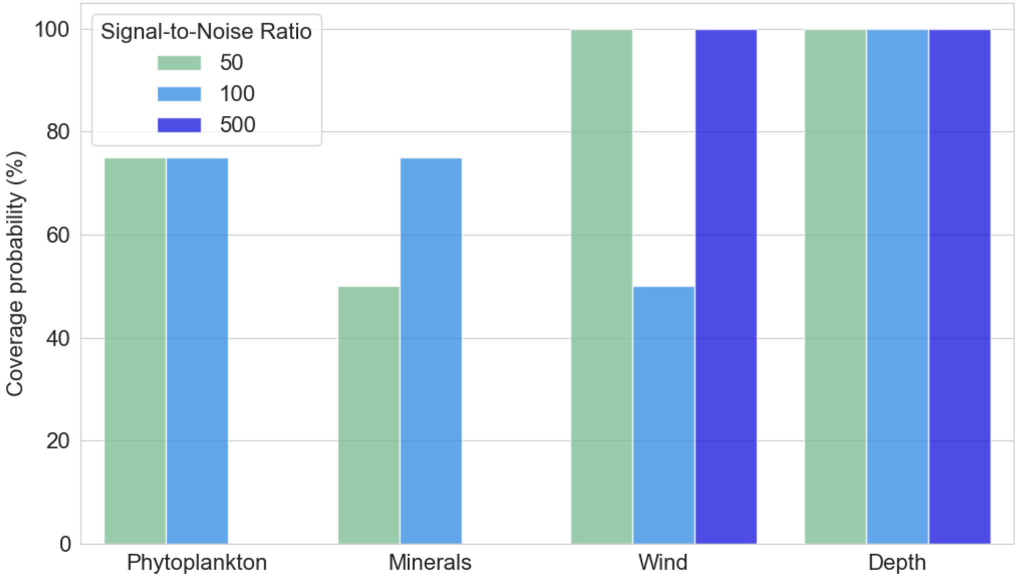

Figure D.8 Inference performance on real observations (n = 4): coverage probabilities acquired using the inference model trained with multispectral data. Coverage probability for phytoplankton and minerals using the model trained with a signal-to-noise ratio of 500 was zero.

7 Chapter 4

Atolls are threatened by sea level rise, increased cyclone and storm frequencies and intensities, and a degradation of coral reefs that supply the island-building sediments (Lincoln et al., 2022; Storlazzi et al., 2018). Indeed, atoll islands have been portrayed as islands in peril, heading towards unavoidable disappearance (Storlazzi et al., 2015; Weatherill, 2023). However, mounting empirical evidence shows a long history of atoll adaptation to changing climate conditions (Kench et al., 2018; Perry et al., 2011; Steibl, Kench, et al., 2024). The impacts of climate change on atolls are not uniform but depend on the unique geomorphological and ecological characteristics of each atoll system, as well as their exposure to oceanic and atmospheric processes (Fox et al., 2023; Khen et al., 2022; Sengupta et al., 2023). To inform atoll restoration action, there is a need to better understand heterogeneity in the enabling conditions of atoll resilience (Duvat & Magnan, 2019; Fox et al., 2023; Steibl et al., 2024).

Chapter 4 builds on the understanding of the importance of cross-ecosystem connectivity developed in the second chapter. Atolls are transboundary and interconnected land-sea systems, the landforms of which emerge as a result of the vertical accumulation of biogenic sediment generated in the coral reef system (i.e., reef accretion) (Ford et al., 2020; Perry et al., 2023). Interactions between the atoll and the ocean create what is known as the “island mass effect”, i.e., enhanced primary production in the nearshore waters surrounding an island (Gove et al., 2016; Vollbrecht et al., 2021). These productive nearshore waters provide important nutritional subsidies into the atoll system (Radice et al., 2019; Skinner et al., 2021), and can support atoll reef resilience to marine heatwaves by supplying food to corals during bleaching events (Fox et al., 2023). However, we have a limited understanding about variability in island mass effect magnitude around atolls, the drivers of that variability, and the extent to which the island mass effect occurs during marine heatwaves (Fox et al., 2023; Vollbrecht et al., 2021).

Many major atoll archipelagos, such as the Tuamotus, are located in the South Pacific, where patterns of marine heatwave occurrence are associated with the El Niño Southern Oscillation (ENSO) (Capotondi et al., 2024; Chapman et al., 2022; Pagli et al., 2025). Previous studies have documented reduced primary production in the open ocean during extreme El Niño in the tropical Pacific (Radenac et al., 2012), however patterns in nearshore primary production around Pacific islands during extreme El Niño have not been studied. This is an important knowledge gap given the importance of ENSO as a driver of geographic patterns in atoll exposure to marine heatwaves in the Pacific.

My aim in Chapter 4 was to contribute towards a better understanding of variability in the enabling conditions of atoll resilience to climate change. I leveraged satellite data to describe, for the first time, variability in island mass effect magnitude during marine heatwaves across South Pacific atolls. To understand drivers of the observed variability, I used Bayesian regression modeling and examined the extent to which atoll geomorphology could be used to explain island mass effect magnitude. Finally, I assessed patterns of change in island mass effect magnitude during extreme El Niño events, compared to neutral ENSO conditions.

Variability in the island mass effect and vulnerability to marine heatwaves across South Pacific atolls

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Keywords

atoll; chlorophyll-a; climate change; coral reef; El Niño Southern Oscillation; island mass effect; marine heatwave

Abstract

Atolls are at the forefront of global change impacts: marine heatwaves threaten atoll coral reefs and undermine atoll island resilience to sea-level rise. Nearshore waters surrounding islands are characterized by enhanced primary production relative to offshore waters, known as the “island mass effect” (IME). Productive nearshore waters around atolls can provide important nutritional subsidies to atoll reefs during marine heatwaves, thereby buffering the effects of thermal stress on corals. However, little is known about variability in IME across atolls and the extent to which it persists during heatwaves. We used satellite data from the Ocean Colour Climate Change Initiative and Copernicus to examine variability in IME magnitude and vulnerability to marine heatwaves across 71 South Pacific atolls. We found that atolls typically experiencing a higher annual IME relative to other atolls had more persistent IME during marine heatwaves, also retaining a higher IME magnitude during the heatwave periods. The most intense marine heatwaves were associated with two extreme El Niño events (2015/2016 and 2023/2024), and the two events were characterized by different patterns of change in heatwave intensity and IME magnitude across atolls. The observed differences between the two extreme El Niño events highlight the need to better understand heterogeneity in local-scale El Niño impacts. Future field studies are required to examine patterns in subsurface nearshore primary production during

heatwaves. Our approach allows identifying atolls that may be more buffered from marine heatwave impacts due to the persistence of IME during the heatwaves.

1 Introduction

Atolls are hotspots of biodiversity and biological productivity in some of the world’s most oligotrophic marine environments (Gove et al., 2016; Morais et al., 2025; Myers et al., 2000; Steibl et al., 2024b). However, low-lying atoll islands are at the forefront of climate change impacts, such as sea-level rise and more frequent storms (Lincoln et al., 2022; Storlazzi et al., 2018). Rather than static landforms, atoll islands are highly dynamic systems that emerge as a result of the vertical and lateral accumulation of biogenic sediment generated in the coral reef system (i.e., reef accretion) (Ford et al., 2020; Perry et al., 2023). The future of atoll land-sea systems relies on preserving and restoring healthy coral reefs that maintain an island-building capacity at a rate that matches sea-level rise (Steibl et al., 2024a). Reefs also play a critical role in protecting atoll islands from storm impacts, such as wave damage and wave-driven flooding (Beetham et al., 2017; Kench et al., 2022).

Atoll coral reefs are, however, increasingly threatened by extreme marine heatwaves (Goreau & Hayes, 2024; Lincoln et al., 2022). The thermal stress associated with marine heatwaves causes the symbiotic relationship between corals and their algal symbionts to break down, a phenomenon known as coral bleaching (Hughes et al., 2017; Spalding & Brown, 2015). Bleached corals are nutritionally compromised, and prolonged bleaching events can ultimately lead to coral mass mortality (Claar et al., 2018; Hughes et al., 2018). While coral die-offs from bleaching events can contribute to island-building in the short term (Kayanne et al., 2016), the loss of reef accretion and continuous sediment supply is an existential threat for atoll landforms in the long term (Kench, 2025).

Pelagic subsidies can support atoll reef resilience to marine heatwaves by providing a food supply to corals during bleaching events (Benkwitt et al., 2023; Fox et al., 2023). Nearshore waters surrounding islands are typically characterized by enhanced primary production relative to offshore waters, known as the “island mass effect” (hereafter, IME) (Gove et al., 2016; Messié et al., 2022). Around atolls, these productive nearshore waters can provide important energy and nutrient subsidies into the atoll system (Benkwitt et al., 2021; Skinner et al., 2019, 2021), that can critically buffer against marine heatwaves (Fox et al., 2023). Importantly, patterns of change in pelagic primary production nearshore may be different from the open ocean (De Falco et al., 2022; van Oostende et al., 2023). Atoll-induced localized upwelling can support elevated primary production near the atoll even when pelagic primary production is reduced at the regional scale, and this enhancement may occur at different depths of the water column (Fox et al., 2023; Vollbrecht et al., 2021).

Despite the importance of IME to atoll systems, we have a limited understanding about variability in IME magnitude around atolls, the extent to which it occurs during marine heatwaves, and the drivers of that variability (Fox et al., 2023; Vollbrecht et al., 2021). Atolls vary in geomorphological characteristics, such as size and lagoon openness to the ocean (Andréfouët et al., 2001; Johnson & Ortiz, 2023). Such variation in atoll geomorphology can drive variation in atoll IME (De Falco et al., 2022). Examining whether atoll size and openness can explain IME variability would improve our understanding of heterogeneity in the enabling conditions of atoll land-sea system resilience to climate change impacts.

Many major atoll archipelagos, such as the Tuamotus, are located in the South Pacific, where patterns of marine heatwave occurrence are associated with the El Niño Southern Oscillation (ENSO) (Capotondi et al., 2024; Chapman et al., 2022; Pagli et al., 2025). Previous studies have documented reduced primary production in the open ocean during extreme El Niño in the tropical Pacific (Radenac et al., 2012), however little is known about the patterns in nearshore primary production around Pacific islands during extreme El Niño (Vollbrecht et al., 2021). This is a significant knowledge gap given the importance of ENSO as a driver of geographic patterns in atoll exposure to marine heatwaves in the Pacific.

In this study, we examined variability in IME across atolls in the South Pacific using satellite data. Although satellite remote sensing does not capture subsurface patterns in primary production, it provides a powerful means to map atoll IME in surface waters across a large geographic extent, encompassing atolls characterized by a range of geomorphologies. The aims of this study were threefold. First, we characterized variability in IME magnitude around atolls, in particular during marine heatwaves. Our interest was understanding whether or not IME was present around atolls during marine heatwave months – not asserting causality between sea surface temperature and IME magnitude. The causal processes that can support IME during marine heatwaves may not be detectable from satellite data or broad-scale physics reanalysis data (Fox et al., 2023). Relevant processes, such as internal waves, often occur below the detectable surface layer of the water column or are highly localized, necessitating data at a high spatial resolution (Fox et al., 2023). Second, we examined whether IME magnitude scales with atoll size and lagoon openness. Our hypothesis was that larger atolls may be associated with greater IME magnitude due to the enhanced generation of turbulent eddy currents that bring more nutrients into the euphotic layer (De Falco et al., 2022). Additionally, the flushing of highly productive lagoonal waters out of the atoll could be a key mechanism that fuels the IME around atolls (Gove et al., 2016; Vollbrecht et al., 2021). We therefore expected more open atolls to be characterized by greater IME. Our third and final aim was to assess patterns of change in IME magnitude during extreme El Niño events, compared to neutral ENSO conditions.

2 Methods

Our study region (155°–130°W, 14°– 24°S) encompassed atolls across the South Pacific (Figure 1). Satellite data analyses were conducted in Python v3.13 and regression modeling was implemented in R v4.5.0. The data and code are freely available in a GitHub repository (https://github.com/pirtapalola/atoll_IME).

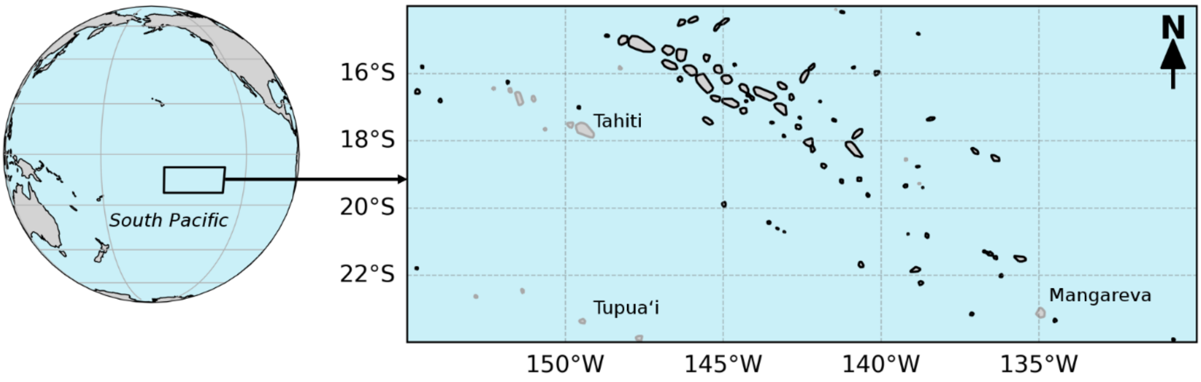

Figure 1. Location of the study region in the South Pacific. Atolls are shown with black contour lines, while high islands are shown with grey contour lines. To help the reader's orientation, major high islands of the archipelagos (Tahiti, Tupua‘i, and Mangareva) are named on the map.

2.1 Chlorophyll-a data

We used satellite-derived surface water chlorophyll-a as a proxy for phytoplankton biomass (Gove et al., 2016; Morais et al., 2025). We acquired monthly 1-km resolution chlorophyll-a data between 2003 and 2024 (European Space Agency Ocean Colour Climate Change Initiative, OC-CCI v.6.0) from NEODAAS (NERC Earth Observation Data Analysis and Artificial-Intelligence Service) (Sathyendranath et al., 2019). We did not include OC-CCI data from 1997-2002 due to data quality concerns associated with the SeaWiFS satellite mission that operated during this time (van Oostende et al., 2022). We removed low-quality and cloudy data by masking pixels flagged as invalid in the OC-CCI dataset (Sathyendranath et al., 2019). To avoid contamination by bottom reflectance, we excluded pixels shallower than 30 m (Gove et al., 2013, 2016; Maina et al., 2011; Messié et al., 2022). The shallow water mask was created using GEBCO global bathymetry data (GEBCO Compilation Group, 2024). The mask was extended by 4 km to the offshore direction to ensure any confounding impacts from shallow water pixels were fully removed (Gove et al., 2016; Messié et al., 2022) and to minimize issues with inter-mission inconsistencies within the OC-CCI dataset that are most prevalent in nearshore waters (van Oostende et al., 2022). We also masked pixels inside contour lines (i.e., deep lagoons). We excluded eight atolls for which gaps in the chlorophyll-a time series were found, leaving 71 atolls for subsequent analyses (see Supplementary materials).

2.2 Island mass effect detection

We quantified the magnitude of monthly IME for each atoll by identifying extreme chlorophyll-a values relative to regional oceanic conditions (Gove et al., 2016; Jena, 2016). Specifically, we identified pixels in a 30-km zone around each atoll (Gove et al., 2016) that exceeded a threshold of regional oceanic mean chlorophyll-a plus two standard deviations (SD), computed monthly (Figure 2). The monthly regional oceanic threshold value (mean + 2 SD) was computed in a 300x300-km region around each atoll, with a mask of 30 km extending from any shallow water mask to avoid confounding impacts from other atolls or high islands. We focused here on near-atoll chlorophyll-a enhancement, as our interest was in the local conditions around the atoll. We therefore did not consider the so-called "dynamic" or "delayed" IME, i.e., patches that are transported far from their island of origin via ocean currents (Bourdin et al., 2024; Messié et al., 2020). Our definition of IME as near-atoll extreme values *relative* to regional oceanic conditions allowed us to avoid confusing potential regionally elevated pelagic chlorophyll-a, for example during cold ENSO anomalies (La Niña events), with the IME (Figure 2).

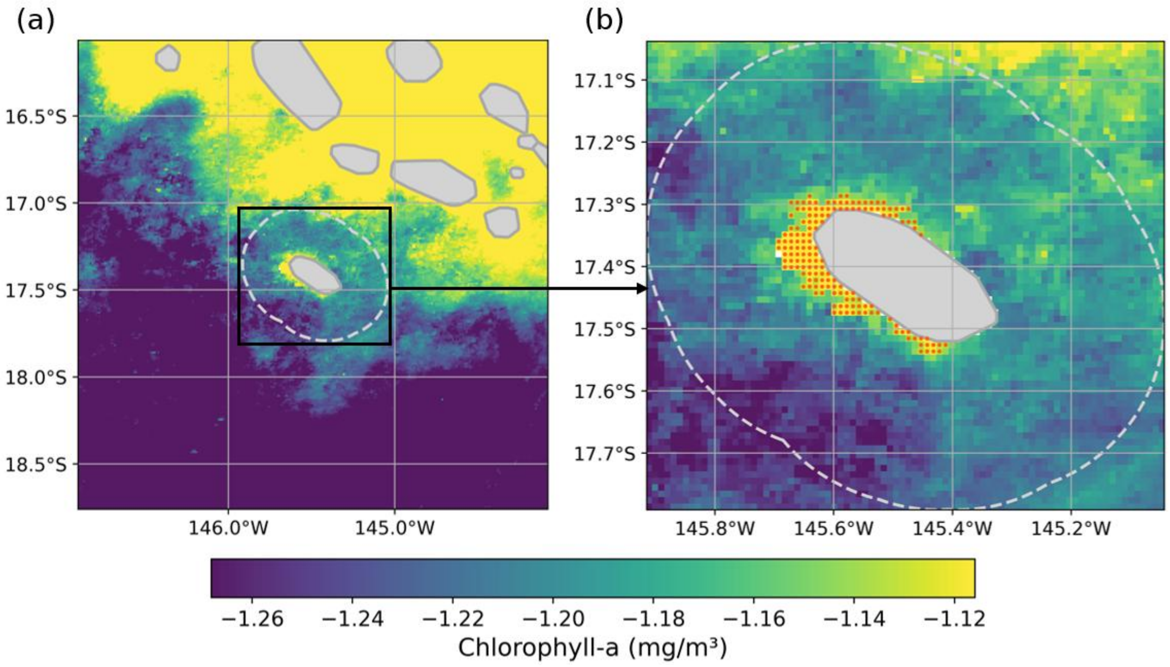

Figure 2. Example of monthly island mass effect detection: Anaa atoll in April 2011. (a) 300 x 300 km regional scope for background regional oceanic condition calculation. (b) Zooming in to the 30-km zone of interest (dashed light grey line) around the 30-m contour of the atoll (dark grey line). The pixels identified as island mass effect are highlighted with orange dots.

Two additional pre-processing steps were then applied: first, from the IME-attributed pixels identified for each atoll, we only included pixels that were closer to the atoll of interest than any other nearby island. Second, noise pixels (i.e. single pixels not forming clusters) were removed using DBSCAN clustering (Ester et al., 1996). Finally, we calculated nearshore chlorophyll-a enhancement relative to offshore waters by subtracting the regional mean oceanic value from each identified pixel (Gove et al., 2016). Total monthly magnitude of chlorophyll-a enhancement was calculated as the sum of the per-pixel magnitudes.

2.3 Marine heatwave detection

We focused our study on prolonged marine heatwaves, lasting a month or more, as it is these long-lasting thermal stress events that lead to widespread coral starvation and mortality in the absence of an external food supply (Baum et al., 2023; Hughes et al., 2017). We acquired monthly sea surface temperature (SST) data from the Global Ocean Physics Reanalysis dataset provided by E.U. Copernicus Marine Service Information (1/12° spatial resolution, corresponding to approximatively 8 km) (E.U. Copernicus Marine Service, 2025). We extracted the SST data in the same 30-km zone around each atoll that was used for IME detection (Gove et al., 2013). While monthly SST data does not capture ephemeral warm extremes that only last days or weeks, it is well-suited for detecting prolonged marine heatwave events (Jacox et al., 2022; Oliver et al., 2018) and matches the temporal resolution of the chlorophyll-a data.

We defined a prolonged marine heatwave as an event during which the monthly SST exceeded its 90th percentile, computed over the time period available (1993-2024) (Cheung et al., 2025; Le Grix et al., 2021). We quantified marine heatwave severity in terms of duration and intensity. We identified the duration of the longest-lasting marine heatwave detected over the entire study period for each atoll. We quantified marine heatwave intensity with a dimensionless index $I_{i,m}$, computed as follows: $I_{i,m} = (SST_{i,t} - SST_{i,m}^{clim}) / (SST_{i,m}^{PC90} - SST_{i,m}^{clim})$ (Hobday et al., 2018; Sen Gupta et al., 2020). $SST_{i,t}$ is the sea surface temperature observed in location i at time t. $SST_{i,m}^{clim}$ and $SST_{i,m}^{PC90}$ are the long-term mean and 90th percentile of the corresponding month (m) in the same location i. The index captures the local thermal impact of the heatwave by quantifying the magnitude of the anomaly relative to the typical climatology of the location (Hobday et al., 2018; Sen Gupta et al., 2020). For example, an index value of 1.2 means $SST_{i,t}$ is 20% more extreme than the 90th percentile threshold for a marine heatwave.

2.4 El Niño events

An extreme El Niño event was defined by the relevant climate index, Niño 3.4, exceeding a threshold of +2°C (Bamston et al., 1997; Bunge & Clarke, 2009; Tensubam et al., 2024; Trenberth, 1997). We quantified differences in IME magnitude and marine heatwave intensity between extreme El Niño events and “neutral” ENSO events (Niño 3.4 < |0.5°C|) (Deser et al., 2010; Pérez-Rosales et al., 2021). Additionally, we quantified differences in regional oceanic chlorophyll-a (see section 2.2) between extreme and neutral ENSO events. This allowed us to examine whether the patterns of change in IME magnitude during El Niño diverged from oceanic chlorophyll-a. To account for the typical seasonal evolution of ENSO events, we analyzed "seasonal years" (July to June) rather than calendar years (January to December) (Deser et al., 2010).

2.5 Statistical analysis

We assessed correlations using the Pearson (r) or the Spearman (ρ) correlation coefficient, as appropriate, using the 'scipy' package in Python (Virtanen et al., 2020). To test the effect of atoll geomorphology on IME magnitude, we performed Bayesian regression modeling using the 'brms' package in R (Bürkner, 2018). Average annual IME magnitude was used as the response. The predictors were atoll area (km^2) and lagoon openness to the ocean (Steibl et al., 2024a). Lagoon openness was modelled using the presence of channels cutting through the reef rim as a binary categorical predictor (closed / open lagoon). Both long-term average annual IME magnitude and atoll area were log-transformed to reduce skewness. We modeled spatial autocorrelation among atolls using a Gaussian Process over longitude and latitude values (Claessens et al., 2023). The Gaussian Process term introduces a smooth, distance-based spatial random effect (McElreath, 2020).

Bayesian regression modeling is based on estimating posterior distributions of model parameters, rather than point estimates. These posterior distributions are approximated by drawing samples from them using the Markov Chain Monte Carlo

(MCMC) algorithm (Bürkner, 2018). We ran four independent Markov chains to ensure robustness, each with 10,000 iterations and a warmup of 5,000 iterations. Reliable MCMC sampling was confirmed with the relevant diagnostics ($\hat{R}$, Effective Sample Size, and Bayesian Fraction of Missing Information) (Betancourt, 2016; Vehtari et al., 2019). We conducted standard Bayesian model validation steps, including prior predictive checks, computation of Gelman and Geweke diagnostics, and checking for model convergence. Additionally, we conducted leave-one-out cross-validation and a posterior predictive check. The full details of the validation diagnostics are provided in Table S1 and Figure S1, Supplementary materials.

3 Results

3.1 Island mass effect

We found that average annual IME magnitude ranged between +1 and +497 mg/m^3 per atoll, with a median of +24 mg/m^3 chlorophyll-a concentration enhancement over regional oceanic background conditions across our sample of n = 71 atolls (Figure 3a; Table S2; Figures S2–S4). In relative terms, the average annual chlorophyll-a enhancement ranged between +31% and +456%, with a median of +62% over regional (300 x 300 km) oceanic conditions.

IME was observed almost year-round (at least 10 months), on average over the study period, for 50% of the atolls (Figure 3b). For 17% of atolls, IME was observed for less than 6 months a year, on average. Only two atolls experienced an IME for less than 4 months annually, on average. Atolls with greater average annual IME magnitude also experienced more consistent year-round IME throughout the study period ($\rho = 0.91$, $p < 0.001$) (Figure 3c).

We found that atoll size had a positive effect on annual IME magnitude ($\beta_{\log(\text{area})} = 0.48$ [95% credible interval of the posterior: 0.34 – 0.62], posterior probability PP ($\beta_{\log(\text{area})} > 0$) = 100%) (Figure 3d). The effect of lagoon openness on annual IME magnitude was not significant ($\beta_{\text{openness}} = 0.09$ [-0.33 – 0.51], PP ($\beta_{\text{openness}} > 0$) = 64%) (Figure 3d).

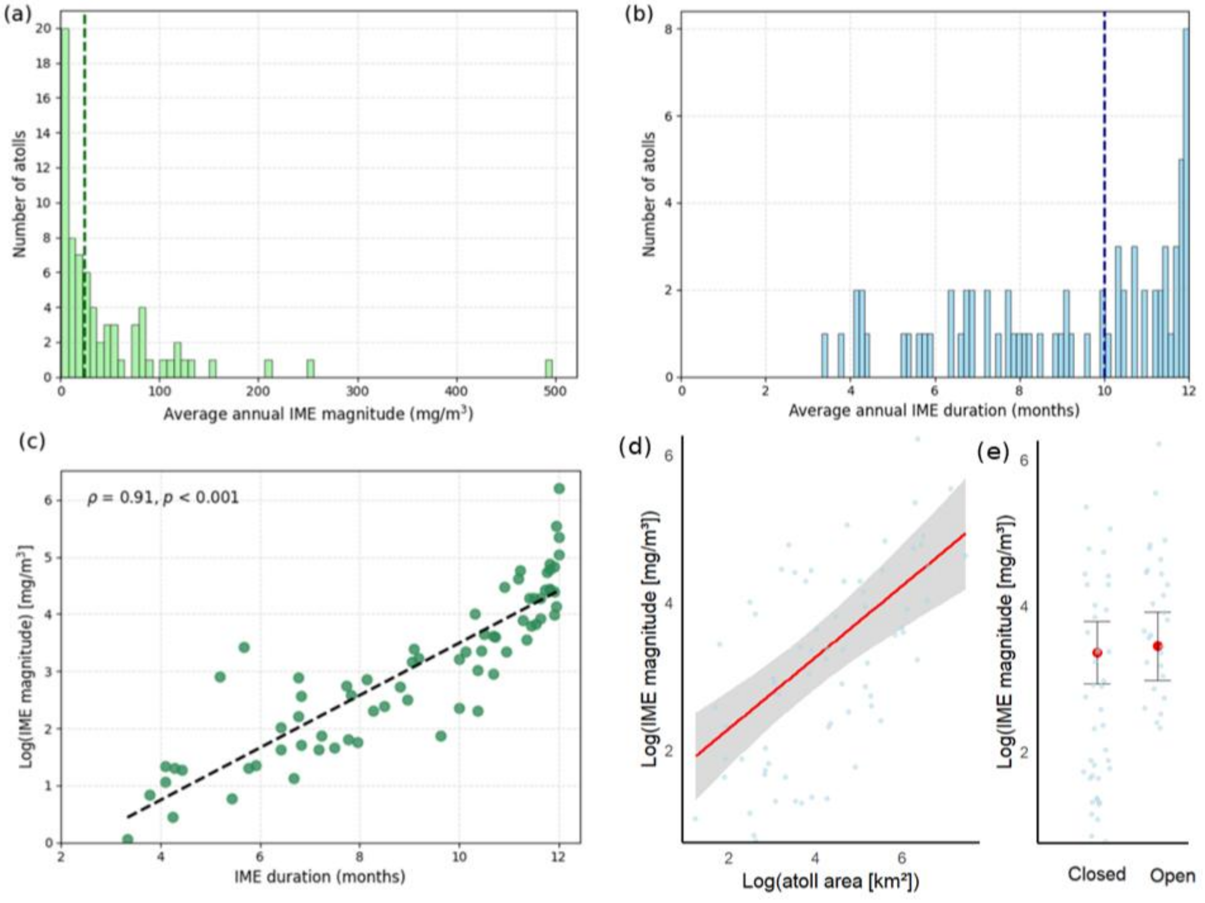

Figure 3. (a) Average annual island mass effect (IME) magnitude: annual chlorophyll-a enhancement (mg/m^3) relative to oceanic conditions (average over 2003-2024) across atolls in the South Pacific. (b) Average annual IME duration: number of months during which IME was observed a year (average over 2003-2024). The dashed vertical lines indicate the median value in both histograms. (c) Correlation between average

annual IME magnitude and duration, showing the Spearman correlation coefficient ρ and the p-value. (d-e) Conditional effects of atoll area (km^2) and lagoon openness (closed/open) on average annual IME magnitude. The red line (point) indicates the mean posterior conditional effect, and grey ribbon (error bar) the 95% credible intervals of the slope. Observed data are shown in light blue.

3.2 Atoll island mass effect during marine heatwaves

Higher average annual IME magnitude was correlated with higher IME magnitude during marine heatwave months ($r = 0.98$, $p < 0.001$) (Figure 4a) and a higher frequency (%) of marine heatwave months during which IME was observed ($\rho = 0.90$, p-value < 0.001) (Figure 4b).

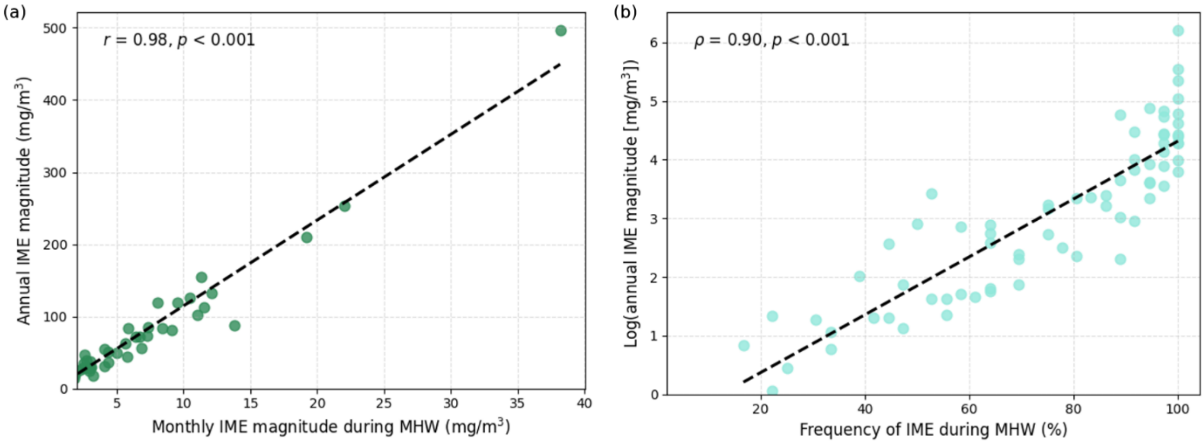

Figure 4. (a) Correlation between the long-term average annual island mass effect (IME) magnitude and average IME magnitude during marine heatwave (MHW) months. (b) Correlation between the long-term average annual IME magnitude and frequency (%) of MHW months during which IME was observed. The Pearson and Spearman correlation coefficients (r and ρ, respectively) and p-values are shown for both correlations.

3.3 Extreme El Niño events in 2015-2016 and 2023-2024

Two extreme El Niño events, during which the Niño 3.4 index exceeded +2°C, occurred over our study period: in 2015/2016 and 2023/2024. These events were associated with the highest average maximum marine heatwave intensities observed during our study period (2003-2024) (average across atolls: 2.14 and 1.85 in 2015/2016 and 2023/2024, respectively). These two extreme El Niño events were characterized by different geographic patterns: for atolls in the northeast, maximum heatwave intensities were lower in 2023/2024 compared to 2015/2016. The opposite was true for atolls in the southwest (Figure 5a). The difference in heatwave intensity between the 2023/2024 to 2015/2016 events ranged between -2.47 and +1.63 across atolls (Figure 5a). Mean regional oceanic chlorophyll-a was lower during extreme El Niño compared to a neutral ENSO year (2013/2014) for 97% of atolls in 2015/2016 and 93% of atolls in 2023/2024 (Figure 5b and S5). The difference in oceanic chlorophyll-a during extreme El Niño relative to neutral ENSO conditions ranged between -0.042 mg/m^3 and + 0.003 mg/m^3 in 2015/2016, and -0.040 mg/m^3 and +0.013 mg/m^3 in 2023/2024 (Figures 5b and S5). The magnitude of the reduction followed a northeast-southwest gradient, with the lowest reduction occurring in the southwest (Figures 5b and S5). The atolls for which regional oceanic chlorophyll-a increased during the extreme El Niño events relative to 2013/2014 were located in the southwest (Figures 5b and S5). No monthly marine heatwaves were observed around any atoll during the neutral ENSO year (2013/2014).

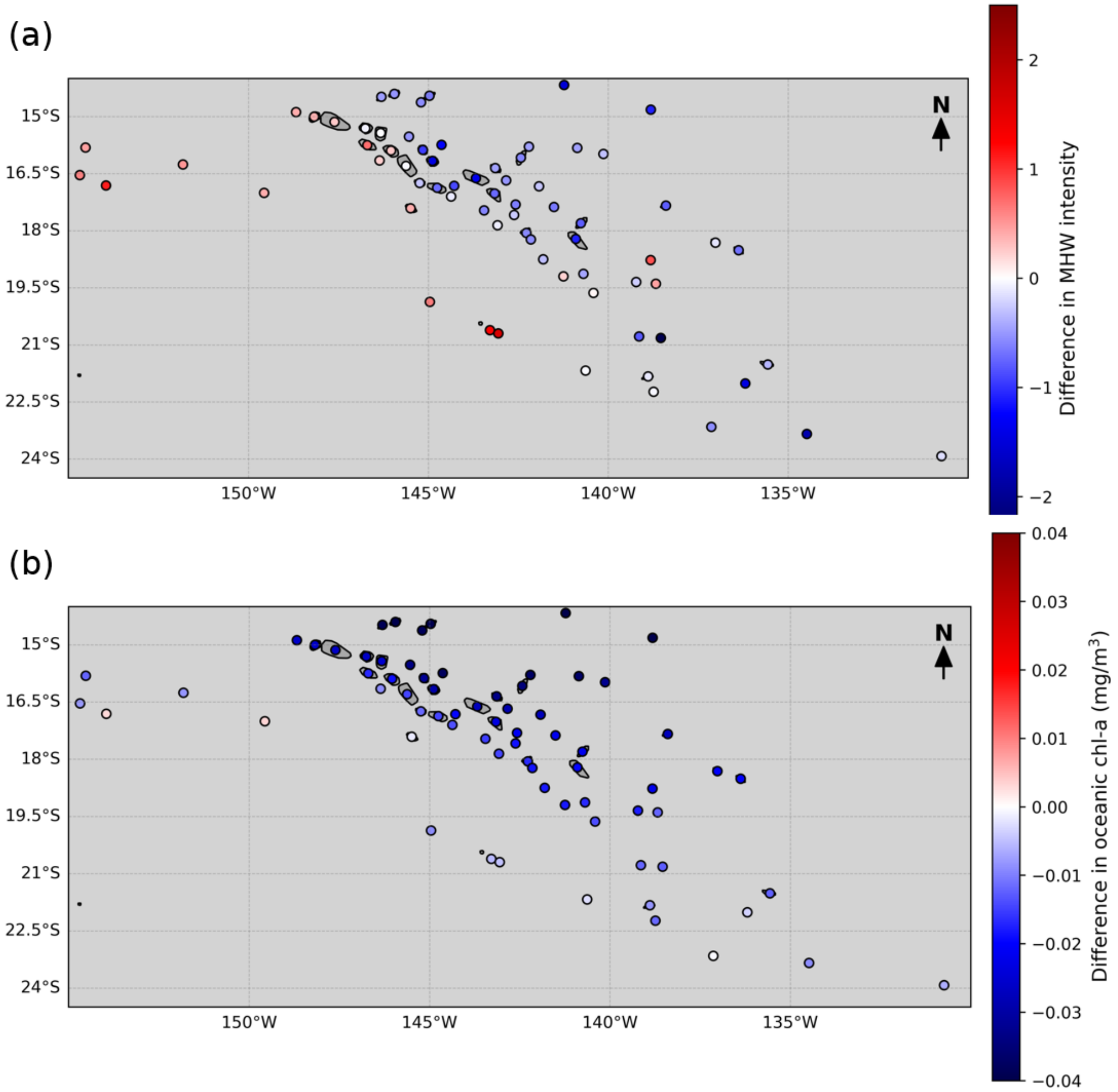

Figure 5. (a) Comparing maximum marine heatwave (MHW) intensity across atolls during the two extreme El Niño events: 2015/2016 and 2023/2024. Positive values indicate that MHW intensity was greater in 2023/2024, and vice versa. (b) Comparing regional oceanic mean chlorophyll-a across atolls during the extreme El Niño year (2015/2016) to the neutral ENSO year (2013/2014). Negative values indicate that oceanic chlorophyll-a was lower in 2015/2016, and vice versa.

While patterns of change in regional oceanic chlorophyll-a during extreme El Niño followed a geographic pattern of a northeast-southwest gradient (Figure 5b), patterns of change in IME magnitude did not follow any obvious geographic pattern (Figure 6). For 41% of atolls, the average monthly IME magnitude was consistently higher during the extreme El Niño events relative to neutral ENSO conditions, while 34% had a consistently lower average monthly IME magnitude during extreme events. Across atolls where IME increased during both extreme El Niño events, the increase ranged between +0.03 mg/m^3 and +7.71 mg/m^3. The range of IME reduction during El Niño was -0.01 mg/m^3 and -19.98 mg/m^3. 27% of atolls experienced contrasting changes in average monthly IME magnitude, with an increase during one extreme event, and a decrease during the other.

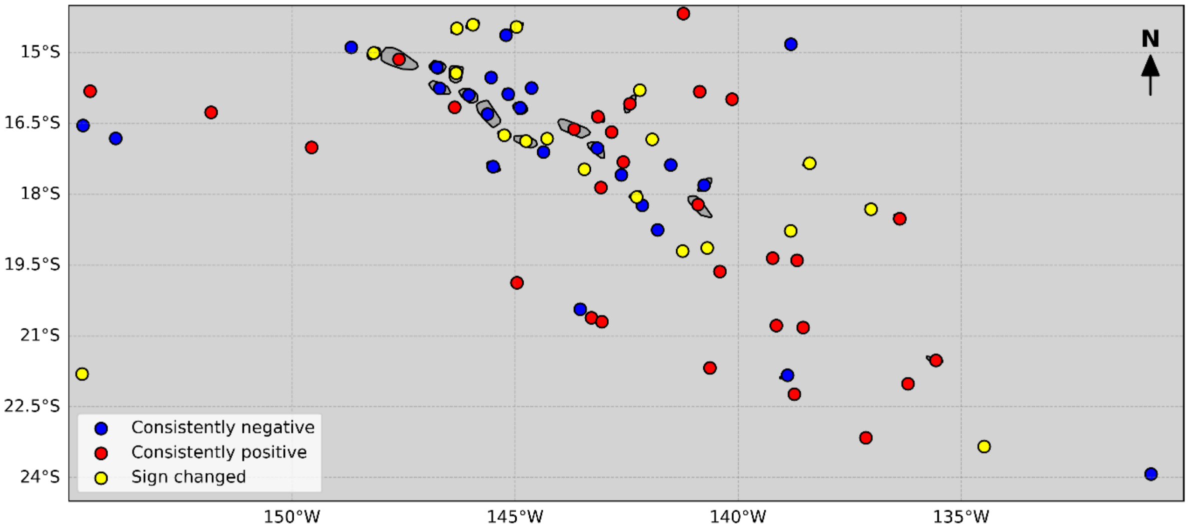

Figure 6. Lack of geographic pattern in island mass effect (IME) magnitude during extreme El Niño events. For some atolls, average monthly IME magnitude was consistently higher (red) or lower (blue) during the extreme events relative to neutral ENSO conditions. Some atolls experienced contrasting changes in average monthly

IME magnitude, with an increase during one extreme event, and a decrease during the other (yellow).

4 Discussion

Pelagic production plays a more significant role in fueling coral reef food webs than is commonly acknowledged (Morais et al., 2025; Morais & Bellwood, 2019), in particular during marine heatwaves, when corals are nutritionally compromised (Fox et al., 2023). In this study, we provided new insights into variability in atoll IME across atolls of different size and lagoon openness, during marine heatwaves, and during the 2015/2016 and 2023/2024 extreme El Niño events.

4.1 Variability in island mass effect across Pacific atolls

We found that the IME was typically present nearly year-round (i.e., at least 10 months) for 50% of atolls. This seasonally persistent IME presence is likely supported by a year-round vertical mixing enhancement described by De Falco et al. (2022). While a nearly year-round IME was common, we also found that for 17% of atolls, IME was present for less than 6 months a year, on average. The observed variability in the average annual IME duration opens interesting questions about the ecological implications of temporal patterns in IME.

The typical annual IME magnitude varied across two orders of magnitude (5×10^2) among the surveyed atolls. Annual IME magnitude scaled with atoll size, with larger atolls associated with greater IME. The size effect indicates strong local-scale control of the IME, and could be explained by both physical and biological processes (Vollbrecht et al., 2021). With regards to physical processes, greater island diameter is associated with enhanced eddy generation downstream of the island (De Falco et al., 2022). Eddy currents may cause upwelling and thereby support greater nutrient provision to the euphotic layer (De Falco et al., 2022; Dufois et al., 2016). In addition to physical processes, biological processes that contribute towards a higher productivity of the lagoonal waters (flowing out of the atoll) may also explain the greater IME observed around larger atolls (Gove et al., 2016; Vollbrecht et al., 2021). These processes include, for example, benthic nitrogen fixation in the reef and lagoon sediments (Cardini et al., 2014; Charpy-Roubaud et al., 2001; Vollbrecht et al., 2021) and the leaching of guano into lagoonal waters from atoll islets on which seabirds roost and breed (Graham et al., 2018). Total atoll ecosystem processes are expected to scale with atoll area, thus offering a potential explanation for the observed positive effect of atoll size on IME magnitude (Gove et al., 2016).

The rate of tide- and wave-driven flushing of the lagoonal waters varies from atoll to atoll due to differences in lagoon openness to the ocean (Dufour et al., 2001; Pagès et al., 2001). However, we found no support for the hypothesis that IME magnitude scales with atoll lagoon openness. Future studies using more detailed metrics for lagoon openness (beyond the closed vs. open binary) could provide further insights into the role of lagoonal water outflow in supporting the IME (see e.g. Andrefouët et al., 2001).

4.2 Marine heatwaves and extreme El Niño

4.2.1 Marine heatwaves

The two extreme El Niño events (2015/2016 and 2023/2024) that occurred during our study period have been linked to environmental disasters worldwide (Jiang et al., 2024; Santoso et al., 2017). For example, the 2015/2016 event was associated with the third global-scale coral bleaching event since the 1980s (Hughes et al., 2017). While we found that both extreme events were associated with severe marine heatwaves in the South Pacific, the geographic pattern of heatwave intensity differed between the two events. For atolls in the northeast, maximum heatwave intensities were lower in 2023/2024 compared to 2015/2016, while the opposite was true for atolls in the southwest. This pattern is in line with the northeast-southwest dipolar pattern of ENSO-related SST anomalies in the South Pacific shown by Pagli et al. (2025). Notably, the location of the northeast-southwest boundary of contrasting ENSO-related SST anomalies differs between ENSO events of different levels of severity, giving rise to spatially and temporally diverse impacts of ENSO across the South Pacific (Pagli et al., 2025). Indeed, although the 2015/2016 El Niño was globally more severe than the 2023/2024 event, we found that the location of the northeast-southwest boundary was slightly more shifted to the west during the 2023/2024 El Niño due to a broadly warmer western Pacific compared to 2015/2016 (see Figure S5, Supplementary materials). This can explain why atolls in the southwest experienced greater maximum heatwave intensities in 2023/2024 compared to 2015/2016. Better understanding how regional spatial patterns of marine heatwaves are associated with El Niño could enable predicting atoll exposure to marine heatwaves 1-12 months in advance (Jacox et al., 2022).

4.2.1 IME during marine heatwaves and El Niño

We found that atolls typically experiencing a higher annual IME relative to other atolls had more persistent IME during marine heatwaves, and also retained a higher IME magnitude during the heatwave periods. This suggests that the atoll geomorphological characteristics predicting annual IME magnitude may also be leveraged to understand variability in the magnitude and presence of IME during marine heatwaves. Our findings are in line with Vollbrecht et al. (2021) who found that offshore and nearshore waters around Rangiroa atoll were characterized by different dynamics in chlorophyll-a during warming events. In the open ocean, chlorophyll-a tends to be lower during heatwaves as a result of stronger water column stratification (Radenac et al., 2012; Vollbrecht et al., 2021). However, chlorophyll-a in the nearshore waters around an atoll may instead stay stable or even increase (Vollbrecht et al., 2021). Indeed, due to complex atoll-current interactions, patterns of change in local-scale processes that support enhanced primary production near atolls may be different from patterns of change in regional-scale processes (Fox et al., 2023; Vollbrecht et al., 2021). Examples of such local-scale processes include localized upwelling and vertical mixing due to internal waves (De Falco et al., 2022; Fox et al., 2023). Nevertheless, the mechanisms explaining the observed stability of chlorophyll-a in nearshore waters during heatwaves are currently poorly understood (Vollbrecht et al., 2021). One likely reason for this knowledge gap is that the relevant hydrodynamic and biogeochemical processes may take place below the surface layer of the water column, and are therefore not detectable using satellite or airborne data (Fox et al., 2023).

We found that both extreme El Niño years were associated with reduced regional oceanic chlorophyll-a (relative to neutral ENSO conditions) across the South Pacific atolls, in line with Radenac et al. (2012). The magnitude of the reduction followed a northeast-southwest gradient, with the southwestern atolls experiencing the lowest reduction or even an increase in oceanic chlorophyll-a. This is consistent with the dipolar regional pattern of El Niño influence in the South Pacific, discussed by Pagli et al. (2025).

Atolls varied in terms of patterns of change in IME magnitude during the extreme El Niño events: some atolls (41%) had a higher, some (31%) a lower average monthly IME magnitude during the El Niño years, relative to the neutral ENSO year. This variability did not follow the northeast-southwest geographic pattern observed for regional oceanic chlorophyll-a, suggesting that atoll geomorphology plays an important role in mediating the impacts of El Niño-driven changes in ocean currents, wind speed, and mixed layer depth on atoll IME.

Our observations provide an example of the variability of El Niño impacts, underlining the need to better understand heterogeneity in the regional- and local-scale ecological effects of El Niño events of varying levels of severity (Pagli et al., 2025). Future studies leveraging high temporal resolution (daily) satellite data (Bourdin et al., 2024; Kämpf et al., 2023), field measurements (Fox et al., 2023), and computational modeling (De Falco et al., 2024; Kämpf et al., 2023) will be critical in describing how the physical processes that support IME may change during extreme El Niño events across atolls characterized by different geomorphologies.

In addition to an improved description of the regional and local-scale impacts of El Niño events, we identify here two further research needs that must be addressed to quantitatively estimate atoll resilience and predict the ecological impacts of marine heatwaves. First, there is a need to determine thresholds of sea surface temperature anomalies that have significant ecological impacts across different atolls (Hughes et al., 2003; Marzonie et al., 2023): coral reef benthic assemblages on different atolls may be characterized by different heat tolerances (Dietzel et al., 2021; Naugle et al., 2024; Pérez-Rosales et al., 2021). In addition to differences in heat tolerance, coral species differ in the flexibility of their trophic strategies and capacity to exploit allochthonous nutritional resources (Conti-Jerpe et al., 2020). Second, an important next step would be to model the extent to which pelagic production, supported by the island mass effect, gets transported into the atoll food web. Such modeling would allow estimating the level of near-atoll chlorophyll-a enhancement that makes an ecologically meaningful contribution to buffer corals from heatwave impacts. Better understanding what level of IME magnitude is ecologically significant could allow developing predictions of atoll resilience, e.g. identifying a threshold in size from which an atoll starts to be more resilient to extreme heatwaves.

4.3 Comparison with previous literature and limitations

Our estimated average annual IME magnitudes are orders of magnitude smaller than Messié et al. (2022). Our results are not directly comparable due to a difference in scope (we did not include high islands nor submerged reefs). However, we also used a more conservative approach to compute the IME, focusing our study on regionally extreme chlorophyll-a values observed near each atoll. The iterative algorithm developed by Messié et al. (2022) expands the IME region until 1) a minimum threshold value is met, 2) the IME region is too large, touching the domain borders or continent masks, or 3) regions of high chlorophyll-a are found farther than ~150 km away from any island. In 95% of cases studied by Messié et al. (2022), algorithm iteration stopped due to criterion 2. This method results in a much broader spatial definition of the IME, with a single IME region often encompassing entire island groups. While the method proposed by Messié et al. (2022) is well-suited for examining far-reaching IME impacts and understanding large-scale patterns of primary production, our focus here was on near-atoll primary production that we expect to be tightly linked to atoll food webs. We used higher-resolution data (1 km^2 instead of 4 km^2) than the previous large-scale satellite studies (Gove et al., 2016; Messié et al., 2022), which enabled us to take a more zoomed-in perspective on near-atoll primary production. Indeed, we suggest that different methods for IME detection and quantification may be appropriate depending on the specific research questions being asked.

As per Gove et al. (2016) and Messié et al. (2022), we used surface water chlorophyll-a as a proxy for phytoplankton biomass (and thereby, primary production) in the first optical depth, which in our study region corresponds to a depth of around 10-30 m (Messié et al., 2022; Platt & Sathyendranath, 1988). Thus, we did not quantify patterns in subsurface primary production. While available field observations suggest that near-island surface and subsurface chlorophyll-a enrichments are often characterized by similar long-term patterns (Gove et al., 2016), further in situ vertical profiles would be needed to confirm this. In particular, field data collection during extreme El Niño events would be valuable: island-scale impacts of El Niño on upwelling and pelagic primary production are currently poorly understood (Fox et al., 2023), especially in the South Pacific (Pagli et al., 2025).

A further limitation of our study is the application of a shallow water mask over a large area around each atoll, leading to the exclusion of productive offshore waters that likely provide an important contribution to the near-atoll IME (Gove et al., 2016). Our estimates of IME magnitude should therefore be considered highly conservative (Gove et al., 2016; Morais et al., 2025). This limitation may be addressed in future studies, as more accurate satellite algorithms for mapping chlorophyll-a in optically shallow waters are becoming available (Palola et al., 2025).

Finally, we note that beyond atoll-induced chlorophyll-a enhancement, near-atoll pelagic productivity may be significantly influenced by the “dynamic” or “delayed” IME originating from other islands. For example, atolls in the Tuamotu archipelago are likely impacted by delayed IME transported from the high islands of Marquesas (Martinez & Maamaatuaiahutapu, 2004; Signorini et al., 1999). Thus, local atoll-scale phenomena are influenced by large-scale oceanic processes that connect ecosystems located hundreds of kilometers away from each other (Fox et al., 2023). Future work should seek to understand concomitant changes in near-atoll IME and the transportation of dynamic/delayed IME, and how these patterns may differ across atolls.

5 Conclusions

Atolls rely on coral reefs for island-building sediment supply, yet they are threatened by increasingly frequent and intense marine heatwaves. The nearshore enhancement of pelagic production, i.e., the IME, can provide important energy and nutrient subsidies into the atoll system during marine heatwaves, buffering the effects of thermal stress on corals. Our study provides the first description of variability in nearshore surface-water enhancement of pelagic primary production around atolls during marine heatwaves. Our approach allows identifying atolls that may be more buffered from marine heatwave impacts due to the persistence of IME during the heatwaves. Our findings can be leveraged to better understand the enabling conditions of atoll resilience to climate change and identify priority sites for atoll restoration action. Further research is needed to investigate patterns of primary production in subsurface nearshore waters.

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Supplementary materials

Contents

1 Additional notes on the island mass effect detection method

In this study, we quantified the magnitude of monthly IME for each atoll by identifying extreme chlorophyll-a values relative to regional oceanic conditions (Gove et al., 2016; Jena, 2016). Specifically, we identified pixels in a 30-km zone around each atoll (Gove et al., 2016) that exceeded a threshold of regional oceanic mean chlorophyll-a plus two standard deviations, computed monthly. An advantage of this method is that it can capture enhanced primary production regardless of whether the enhancement occurs symmetrically or asymmetrically around the island: IME is neither computed in zones extending symmetrically to all directions around the island (Gove et al., 2016), nor is the enhancement assumed to always occur strictly downstream of the island (Messié et al., 2022). Indeed, depending on the physical processes that underlie IME and that vary depending on island geomorphology, IME could be symmetrically or asymmetrically distributed (De Falco et al., 2022). Our method is also less sensitive to single pixel variability and data quality issues than the algorithm developed by Messié et al. (2022), as we do not use a single pixel value as a threshold. Reducing sensitivity to single pixel variability is particularly important in oligotrophic and ultra-oligotrophic regions, such as the South Pacific Subtropical Gyre, where the signal from the ocean relative to the signal from the atmosphere is low (Bourdin et al., 2024; Hu et al., 2013). Consequently, a small error in atmospheric correction leads to a greater relative error in chlorophyll-a estimation in these regions (Hu et al., 2013).

2 Bayesian regression model diagnostics

Table S1. Bayesian regression model diagnostics. All the diagnostics indicate robust predictive performance.

Diagnostic	**Value**
Leave-one-out cross validation: Pareto k estimates	<0.7
Leave-one-out cross validation: expected log pointwise predictive density	-94.7 (standard error = 6.3)
Gelman diagnostic	All values equal to 1
Geweke diagnostic	All values between -2 and +2
$\hat{R}$	All values equal to 1
Effective Sample Size	All values >13,000
Bayesian Fraction of Missing Information	All values between 0.83 and 0.86

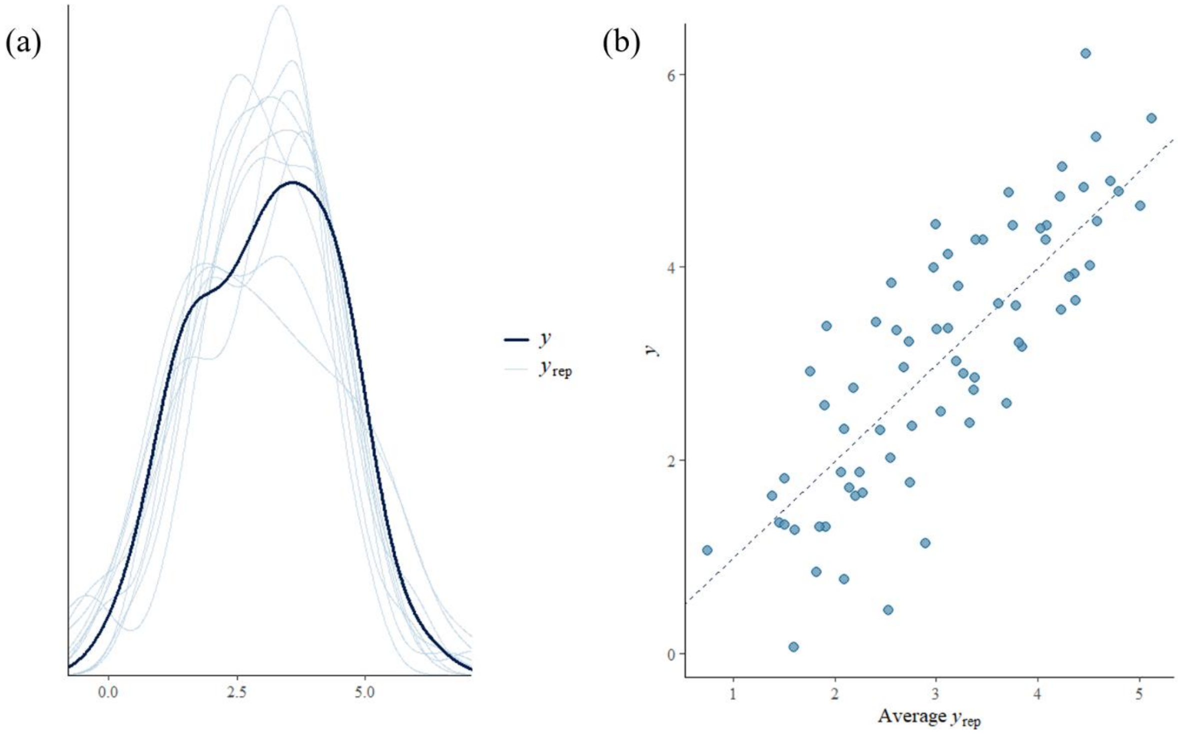

Figure S1. Posterior predictive check. (a) The observed data y (in black) and replicated data y_{rep} generated from the posterior predictive distribution (in light blue). (b) Scatterplot showing observations y (x-axis) against the average predicted values (posterior predictive mean) (y-axis).

3 Additional results

Table S2. Island mass effect: average number of months and magnitude of the island mass effect between 2003 and 2024 for each atoll (n = 71).

Atoll	**Number of months (average)**	**Number of months (std)**	**Magnitude (average)**	**Magnitude (std)**
Ahe	8	1.91	17.41	16.87
Ahunui	7	2.28	5.09	7.08
Amanu	8	2.35	10.91	6.54
Anaa	12	0.66	51.05	34.9
Anuanuraro	4	1.95	1.57	1.43
Anuanurunga	7	2.2	6.53	5.86
Apataki	11	1.41	88.09	52.83
Aratika	9	2.1	23.83	12.61
Arutua	12	0	496.62	109.35
Faaite	12	0.29	125.22	35.22
Fakahina	4	1.7	3.68	4.31
Fakarava	12	0.21	253.95	98.66
Fangatau	6	2.14	3.68	2.81
Fangataufa	11	1.25	28.41	13.39

Hao	10	2.05	24.98	15.14
Haraiki	12	0.39	85	37.01
Hereheretui	12	0.66	72.44	24.88
Hikueru	12	1.34	72.62	32.14
Kauehi	11	1	34.95	15.44
Kaukura	12	0	209.88	97.26
Makemo	10	2.59	55.44	41.9
Manihi	9	2.15	15.26	18.21
Manuhangi	5	2.09	2.15	2.23
Maria	10	1.4	6.53	3.31
Maria_Est	4	1.93	2.31	3.33
Marokau	12	0.77	83.79	54.4
Marutea_Nord	12	0.69	113.14	38.94
Marutea_Sud	8	2.7	5.84	3.64
Mataiva	10	1.62	20.58	12.67
Maupihaa	12	0.39	84.06	44.07
Morane	8	2.26	5.28	3.93
Moruroa	12	0.21	62.39	26.16
Motu_One	7	2.69	3.11	3.14

Motutunga	11	1.14	72.35	35.44
Napuka	9	1.48	29.67	37.71
Nengonengo	11	0.91	44.73	20.22
Niau	11	1.62	37.56	30.5
Nihiru	7	2.51	18.08	16.85
Nukutepipi	7	2.94	13.06	11.81
Oeno	12	0.29	54.49	14.68
Paraoa	8	3.74	15.58	14
Pinaki	4	2.09	2.9	6.84
Pukarua	6	3.28	3.87	4.12
Rangiroa	11	1.5	102.4	50.25
Raraka	10	1.6	38.43	18.58
Raroia	11	1.24	36.43	15.56
Ravahere	10	1.3	28.93	12.21
Reao	4	2.66	3.79	5.37
Reitoru	12	0.8	46.25	27.64
Rekareka	3	1.8	1.06	0.99
Scilly	12	0	154.89	71.92
Taenga	8	3.1	13.32	9.6

Tahanea	12	0.39	119.52	48.03
Taiaro	6	2.26	7.56	12.13
Takapoto	10	1.81	28.53	21.95
Takaroa	9	2.55	12.26	10.41
Takume	9	2.28	25.22	17.43
Tatakoto	4	2.62	3.58	7.13
Tauere	7	3.19	5.56	4.2
Tekokota	8	2.07	10.14	7.63
Temitangi	10	1.75	10.56	6.86
Temoe	11	1.78	19.34	11.87
Tepoto	6	2.78	30.85	26.69
Tetiaroa	12	0.29	81.15	32.02
Tikehau	11	1.12	49.24	23.96
Toau	12	0.39	132.57	40.14
Tupai	11	0.92	118.52	79.14
Tureia	10	1.59	10.03	3.85
Vahitahi	8	3.21	6.1	5.07
Vairaatea	5	2.54	18.41	23.82
Vanavana	6	2.24	5.11	7.28

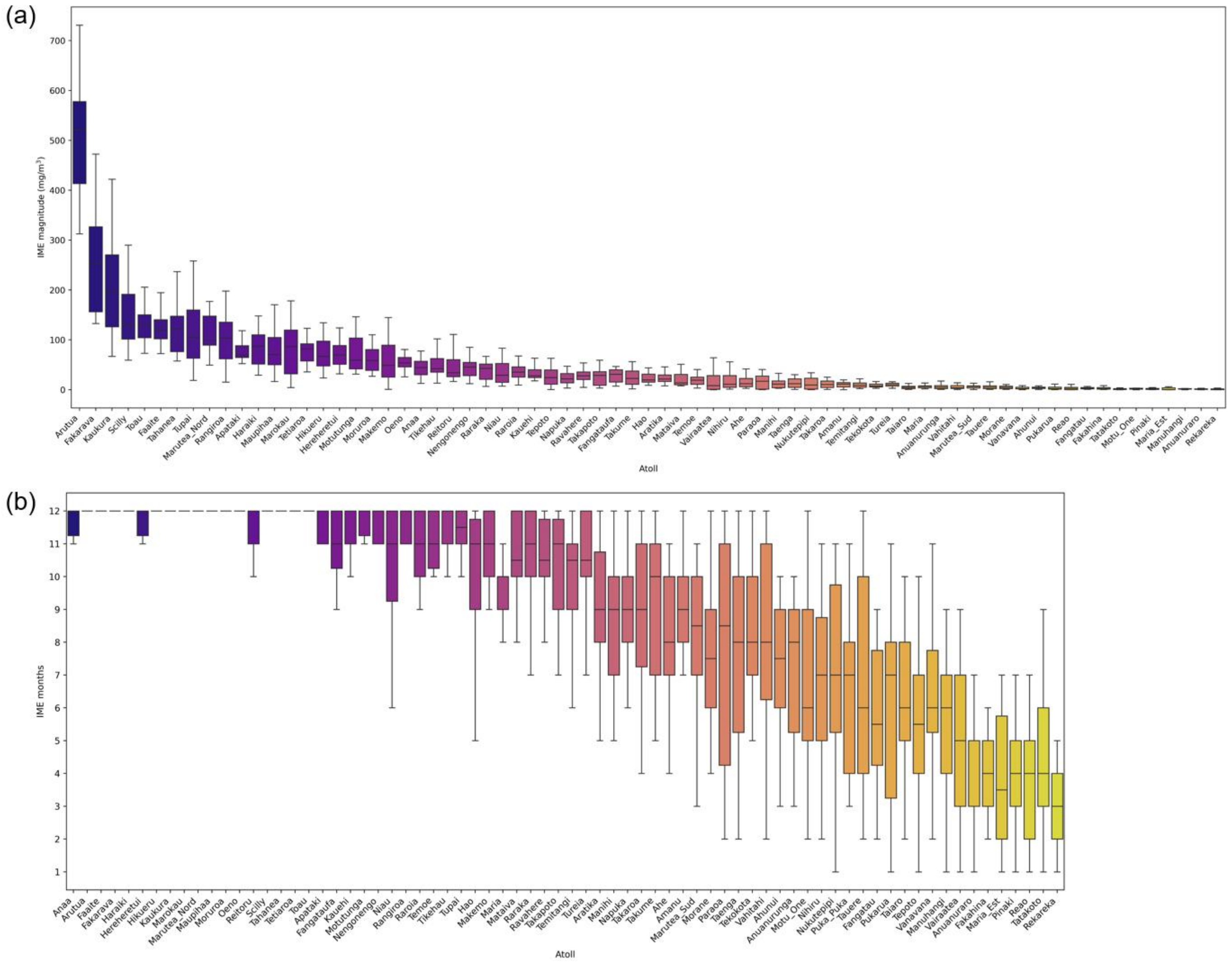

Figure S2. (a) Island mass effect magnitude: annual chlorophyll-a enhancement (mg/m^3) relative to oceanic conditions (average over 2003-2024) per atoll. (b) Island mass effect consistency: number of months during which island mass effect is “on” every year (average over 2003-2024) per atoll.

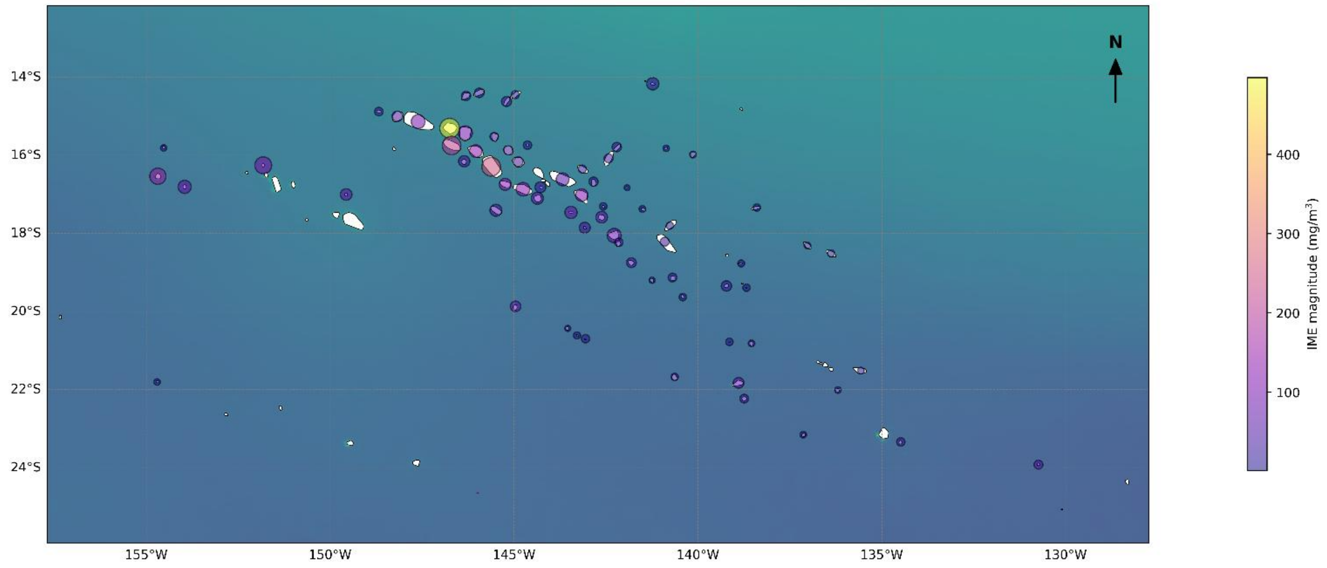

Figure S3. Island mass effect magnitude: annual chlorophyll-a enhancement (mg/m^3) relative to oceanic conditions (average over 2003-2024) per atoll. The marker size is scaled based on interannual variability (standard deviation).

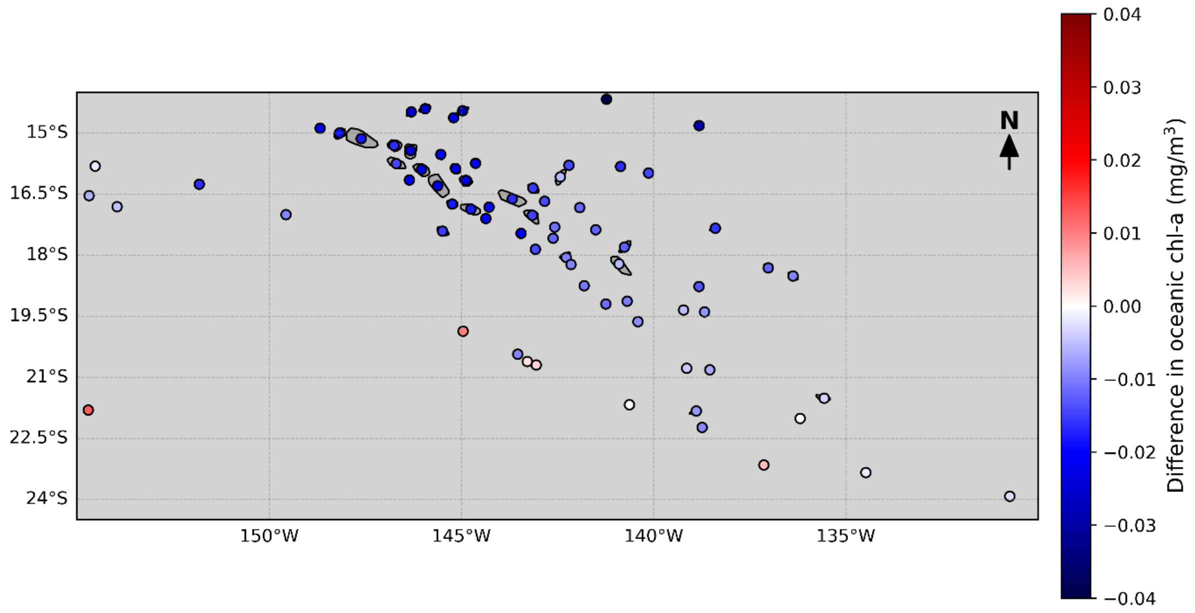

Figure S4. Comparing regional oceanic mean chlorophyll-a across atolls during the neutral ENSO year (2013/2014) and the extreme El Niño year (2023/2024). Positive values indicate that oceanic chlorophyll-a was higher in 2023/2024, and vice versa.

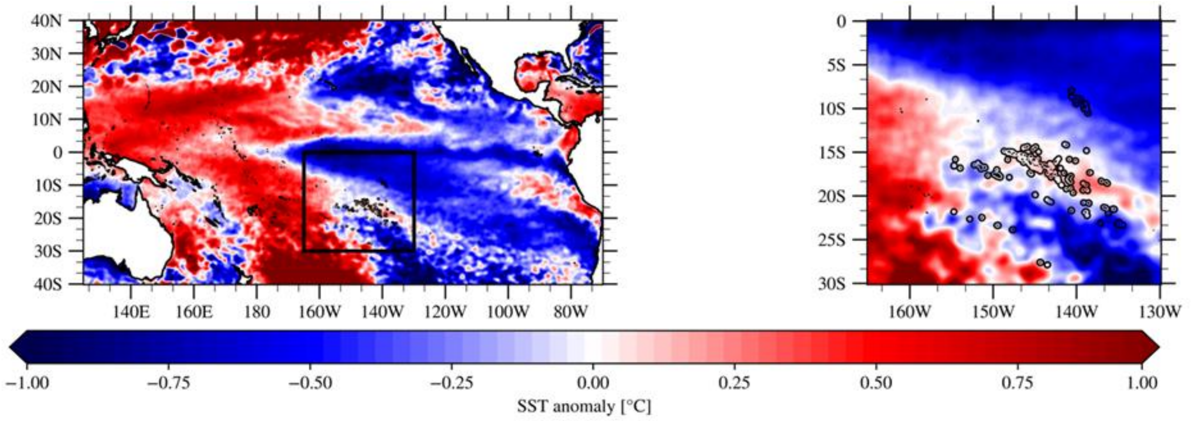

Figure S5. Comparison between November 2015 – April 2016 and November 2023 – April 2024 SST anomalies with respect to climatology computed using the NOAA 0.25° Daily Optimum Interpolation Sea Surface Temperature (OISST) (Huang et al., 2021). The baseline used to compute the climatology was 1993-2024. Positive values indicate SST anomalies during 2023/24 El Niño were stronger than during the 2015/16 El Niño.

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8 Conclusion

Climate change and local human activities are rapidly altering coastal environments worldwide. Monitoring where, how, and why coastal environments are changing is essential for the success of local management and restoration efforts. In this DPhil thesis, I developed conceptual and analytical tools to better understand change in coastal environments. I focused my research on tropical islands with coral reefs, where climate change impacts are particularly acute: increasingly frequent marine heatwaves are causing mass coral bleaching and mortality.

Developing environmental management strategies that support the resilience of island-reef systems to climate change requires understanding the enabling conditions of ecosystem resistance and recovery – in other words, what determines the shape of the "stability landscape" (see section 2.1 of this thesis). To gain such understanding, we need a whole-system approach that takes into account feedback loops between different system components and drivers of change (Chapter 2). In Chapter 2, I proposed a novel scientific framework, nutrientscape ecology, to support the operationalization of a whole-system approach in coastal nutrient connectivity research. The need for a whole-system approach and understanding multiple drivers of change was also underlined in Chapter 1, where I found that continued reforestation and estimated reduction in land use-based pressure have not been sufficient to halt coral cover decline in northeastern Puerto Rico. Thus, to better understand the past and future of coral reef communities in Puerto Rico, it will be necessary to consider the effects of land use-based pressure not in isolation, but in the context of other stressors, such as marine heatwaves and coral diseases.

A key recommendation presented in Chapters 1 and 2 was to leverage recent advancements in remote sensing and machine learning in order to develop our understanding of coastal ecosystem components, connectivity, and drivers of change. Traditional field-based surveys can generally only cover a limited geographic area and a narrow temporal window, and remote sensing could provide the critical data needed to support a whole-system understanding (Chapters 1 and 2). It is important to note, however, that remote sensing cannot and should not fully replace traditional field surveys. Instead, new technologies and traditional field surveys can be combined strategically. For example, novel remote sensing algorithms that leverage probabilistic machine learning allow quantifying pixel-wise uncertainty in satellite-derived maps (Chapter 3). Field campaigns can then target locations where the satellite-derived maps have most uncertainty. Furthermore, field surveys provide very detailed information on ecological community compositions at fine taxonomic scales (genus, species) and can be designed to detect visually and/or behaviourally cryptic species. Such a detailed characterization of an ecological community cannot be achieved using satellite- or drone-based mapping. Additionally, marine field surveys will remain necessary in highly turbid coastal waters, where the optical signal of the benthos is not detectable from the water surface. In summary, thoughtfully combining remote sensing with targeted field surveys can advance our understanding of coastal ecosystem dynamics across multiple spatial and temporal scales.

Chapters 1 and 2 identified the need for new marine remote sensing products specifically designed for optically shallow reef environments. In particular, developing more accurate methods for water quality mapping would represent a significant advancement for coral reef research and management, both because water quality is one of the most important determinants of coral health and resilience at a local scale, and because water quality constituents can be used as a proxy for cross-ecosystem flows of nutrients and energy (Chapters 1, 2, and 4). To address this research need, Chapter 3 developed a novel algorithm that leverages a state-of-the-art approximate Bayesian inference method to estimate water quality constituents in shallow coastal waters, assuming brown coral cover. The new algorithm provides exciting opportunities for further development and novel insights in marine remote sensing and ocean optics, for example enabling the visualization and analysis of the combinatory parameter space that results in a given optical signal. Finally, in Chapter 4, I provided a concrete example of using satellite remote sensing to examine variability in the enabling conditions of reef resilience to climate change across South Pacific atolls.

A key research priority for the future would be additional bio-optical data collection in shallow coral reef waters, ideally covering a range of environmental conditions. A coordinated effort to produce a curated dataset, consisting of in situ hyperspectral reflectance and water quality measurements, will be critical for further remote sensing algorithm development and evaluation. In addition to the continued development and application of data-driven approaches (remote sensing and machine learning), it will be important to continue to strive for an improved theoretical understanding of system dynamics and resilience.

Coral reefs are highly vulnerable to climate change impacts, such as extreme marine heatwaves. Even in an optimistic scenario of significant reductions in global greenhouse gas emissions, the majority of the world’s coral reefs are predicted to be exposed to annual severe bleaching by 2045 (UNEP, 2020). In this thesis, I made alarming observations about the drastic declines in coral cover in northeastern Puerto Rico and the exposure of South Pacific atolls to severe marine heatwaves. However, the impacts of climate change on coral reefs are not uniform but depend on the unique geomorphological and ecological characteristics of each system, as well as their exposure to oceanic and atmospheric processes. Better understanding the differences across coral reef systems – in particular, the heterogeneity in the enabling conditions of reef resilience – would support the development of effective management and restoration interventions. While coral reef ecosystems continue to change due to the combined impacts of multiple stressors, targeted management and restoration efforts can steer the transformation of coral reef ecosystems in a direction that maintains ecological and social values. This thesis contributed analytical and conceptual tools that can be leveraged to better understand the patterns of change in coral reef ecosystems, and ultimately to inform the preservation and restoration of coral reef ecosystems in a rapidly changing climate.

9 Co-authorship statement

Chapter 1: From ridge to reef: combining remote sensing and field surveys to inform coral reef conservation

The authors' contributions to the paper were as follows:

- Pirta Palola: Led the project, developed the research questions, conducted the analyses, and drafted the manuscript.
- Sasha Hills: Supported the statistical analyses and editing the manuscript.
- Simon J. Pittman: Supported data management, designing the methodology, developing the research questions, and editing the manuscript.
- Edwin A. Hernández-Delgado: Conducted the field data collection and contributed to editing the manuscript.
- Antoine Collin: Provided supervision and contributed to editing the manuscript.
- Lisa M. Wedding: Provided supervision and contributed to editing the manuscript.

All authors reviewed the results and approved the final version of the manuscript.

Chapter 2: Nutrientscape ecology: a whole-system framework to support the understanding and management of coastal nutrient connectivity

- Pirta Palola: Led the project, developed the research questions, conducted the literature search, screening, and review, and drafted the manuscript.

- Simon J. Pittman: Contributed to the development of the research questions and editing the manuscript.
- Antoine Collin: Provided supervision and contributed to editing the manuscript.
- Casey E. Benkwitt: Contributed to the development of the research questions and editing the manuscript.
- Eleanor Thomson: Contributed to editing the manuscript.
- Yadvinder Malhi: Contributed to editing the manuscript.
- Nick A. J. Graham: Contributed to the development of the research questions and editing the manuscript.
- Lisa M. Wedding: Provided supervision and contributed to the development of the research questions, and editing the manuscript.

All authors reviewed the results and approved the final version of the manuscript.

Chapter 3: Simulation-based inference advances water quality mapping in shallow coral reef environments

- Pirta Palola: Led the project, conceptualized the research questions, developed the methodology, planned and conducted the field campaign, led data management, acquired funding, and drafted the manuscript.
- Varunan Theenathayalan: Provided advice on field methods (radiometric measurements) and contributed to editing the manuscript.
- Cornelius Schröder: Provided advice on simulation-based inference and contributed to editing the manuscript.

- Victor Martinez-Vicente: Supported laboratory methods (spectrophotometric measurements), provided access to software (EcoLight), and contributed to editing the manuscript.
- Antoine Collin: Provided supervision and advice on field methods (drone surveys) and contributed to editing the manuscript.
- Rosalie Wright: Contributed to field data collection and editing the manuscript.
- Melissa Ward: Contributed to field data collection and editing the manuscript.
- Eleanor Thomson: Piloted the drone, provided advice on drone data processing, and contributed to editing the manuscript.
- Patricia Lopez-Garcia: Supported laboratory methods (fluorometric measurements) and contributed to editing the manuscript.
- Eric Hochberg: Provided access to data (the global benthic reflectance dataset) and contributed to editing the manuscript.
- Yadvinder Malhi: Supported the field campaign and funding acquisition and contributed to editing the manuscript.
- Lisa M. Wedding: Supported the field campaign and funding acquisition and contributed to editing the manuscript.

All authors reviewed the results and approved the final version of the manuscript.

Chapter 4: Variability in the island mass effect and vulnerability to marine heatwaves across South Pacific atolls

- Pirta Palola: Led the project, conceptualized the research questions, developed the methodology, and drafted the manuscript.
- Sebastian Steibl: Contributed to the development of the research questions and methodology, and editing the manuscript.
- Gareth Williams: Contributed to the development of the research questions and methodology, and editing the manuscript.
- Bastien Pagli: Contributed to the development of the research questions and methodology, and editing the manuscript.
- Takeshi Izumo: Contributed to the development of the research questions and methodology, and editing the manuscript.
- Victor Martinez-Vicente: Provided supervision, contributed to the development of the research questions and methodology, and edited the manuscript.
- Antoine Collin: Provided supervision and contributed to editing the manuscript.
- Lisa M. Wedding: Provided supervision and contributed to editing the manuscript.

All authors reviewed the results and approved the final version of the manuscript.

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11 Supplementary materials

11.1 Inherent optical properties – methods

Field data for Chapter 3 were collected on the Tetiaroa atoll in the South Pacific in July and August, 2022. In addition to the field methods and laboratory analyses described in the Methods section of Chapter 3, I collected seawater samples and analyzed them for particulate absorption. This data could not be used for the validation of the algorithm in Chapter 3, as simultaneous measurements of subsurface remote-sensing reflectance and chlorophyll-a concentration would have been necessary. In total, I analyzed ten seawater samples for particulate absorption (two duplicate measurements at five sampling sites). The methods and results are briefly described below.

Particulate absorption measurements were conducted following the IOCCG 2018 protocol (Roesler et al., 2018). For each sample, 4 liters of seawater were filtered under low vacuum onto a 47-mm glass fiber filter (Whatman, GF/F) (Figure S1). Absorption was measured at a 1-nm resolution in the wavelength range of 350-850 nm with a dual beam spectrophotometer equipped with an integrating sphere (Babin & Stramski, 2004; Stramski et al., 2015). To distinguish between the absorption of phytoplankton and non-algal particles (NAP), the filters were analyzed before and after bleaching with 90% methanol (MeOH) solution (Roesler et al., 2018). The spectrophotometric measurements were made at the Plymouth Marine Laboratory, United Kingdom.

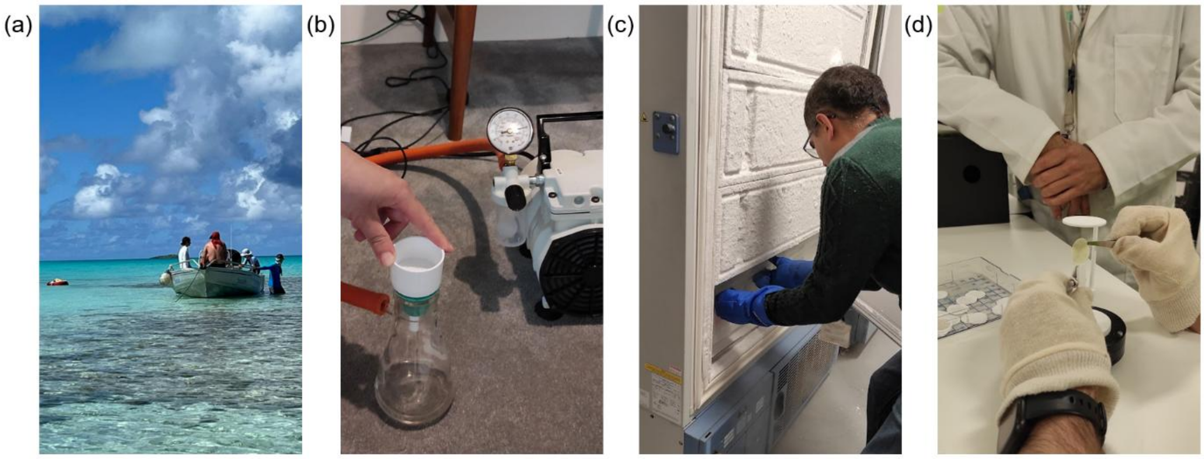

Figure S1. Illustration of the methods. (a) Collecting water samples. (b) Filtering the water samples under low vacuum. (c) Freezing the samples. (d) Conducting spectrophotometric measurements.

Following the spectrophotometric measurements, the optical density (OD_f) was calculated for both the unbleached (=particulate) and bleached (=NAP) samples by subtracting the blank filter values. The beta-corrected optical density (OD_s) was then calculated following Equation 1 (Roesler et al., 2018; Stramski et al., 2015). Using the beta-corrected OD_s values, total particulate and NAP absorption coefficients could then be determined (Equation 2). Finally, the absorption coefficient of phytoplankton was calculated by subtracting the contribution of NAP from the total particulate absorption coefficient.

Equation 1. $OD_s = 0.323(OD_f)^{1.0867}$

Equation 2. $a_x(\lambda) = \ln(10)\, OD_s/(V/A)$

where the subscript x defines the water constituent (NAP or total particles), V is the filtered volume (m^3), and A is the effective area of the filter (m^2) (Roesler et al., 2018).

11.2 Inherent optical properties – results

The results of the spectrophotometric measurements are shown in Figures S2 and S3. The absorption spectra are in line with available data from previous studies (see Russell et al., 2019).

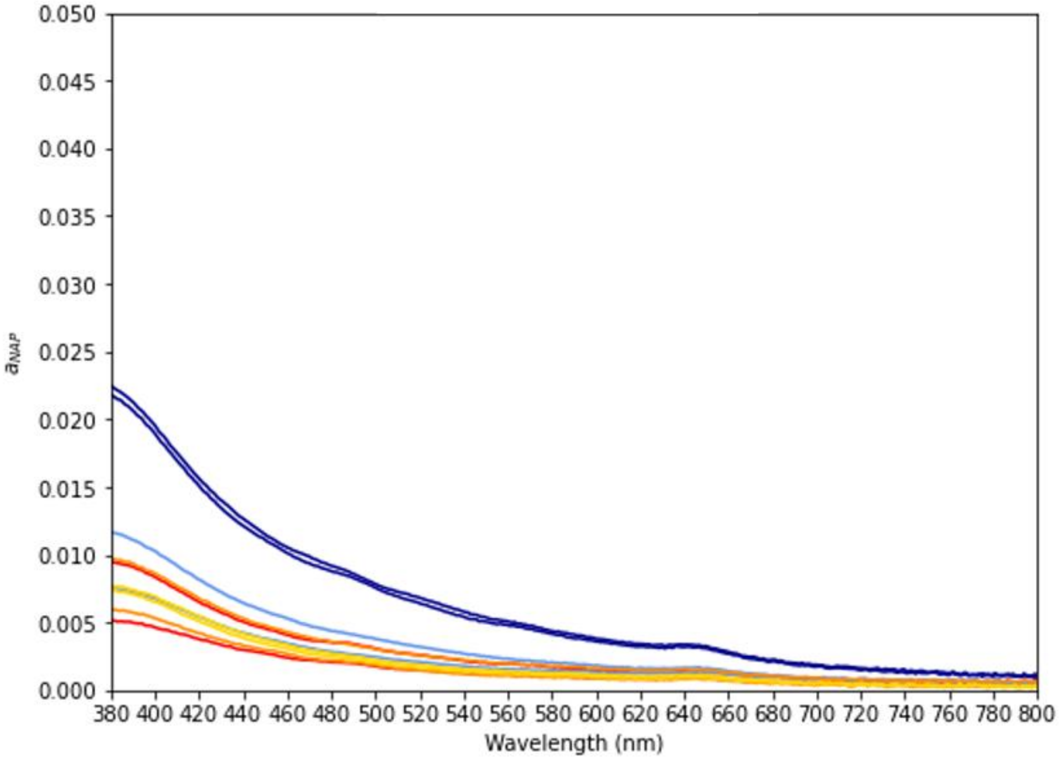

Figure S2. Non-algal particulate absorption spectra. Each color corresponds to a different sampling site (n = 5). Two duplicate samples were taken at each site.

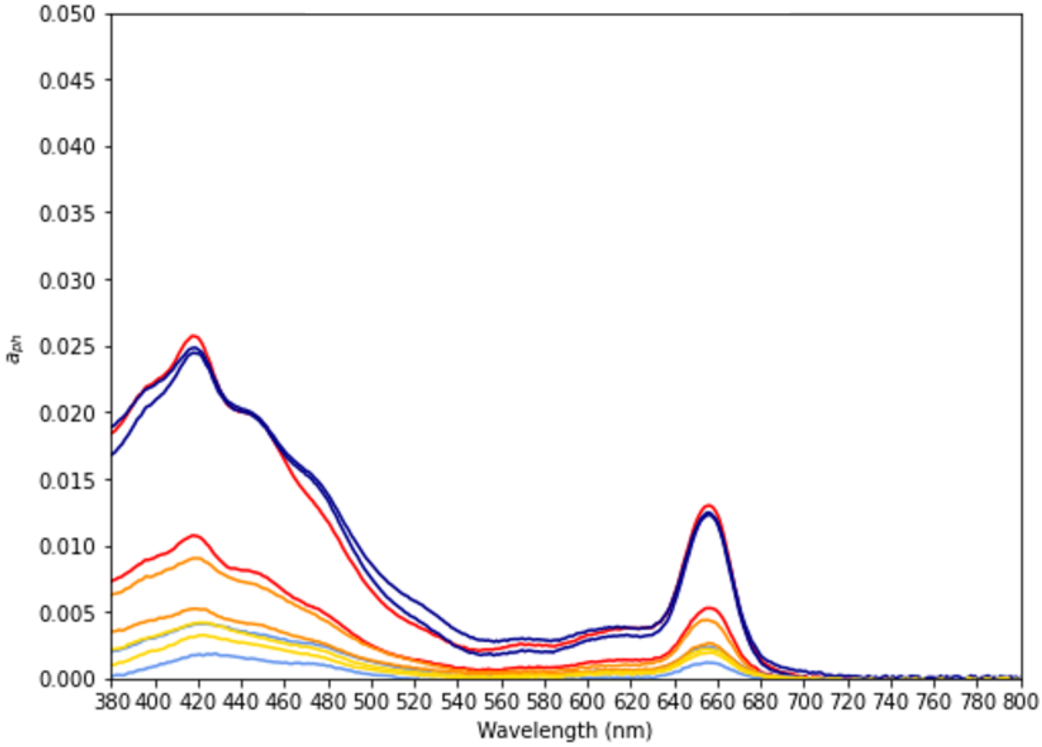

Figure S3. Phytoplankton absorption spectra. Each color corresponds to a different sampling site (n = 5). Two duplicate samples were taken at each site.

11.3 Apparent optical properties – methods

In addition to the just-below-surface hyperspectral measurements described in the Methods section of Chapter 3, I conducted measurements of downwelling irradiance and upwelling radiance at 5-10 cm above the benthos to compute benthic reflectance, as described by Theenathayalan & Shanmugam (2021). The hyperspectral measurements were conducted using a pair of TriOS RAMSES irradiance and radiance radiometers mounted on a frame (Kutser et al., 2013). The underwater radiometer set-up is shown in Figure S4.

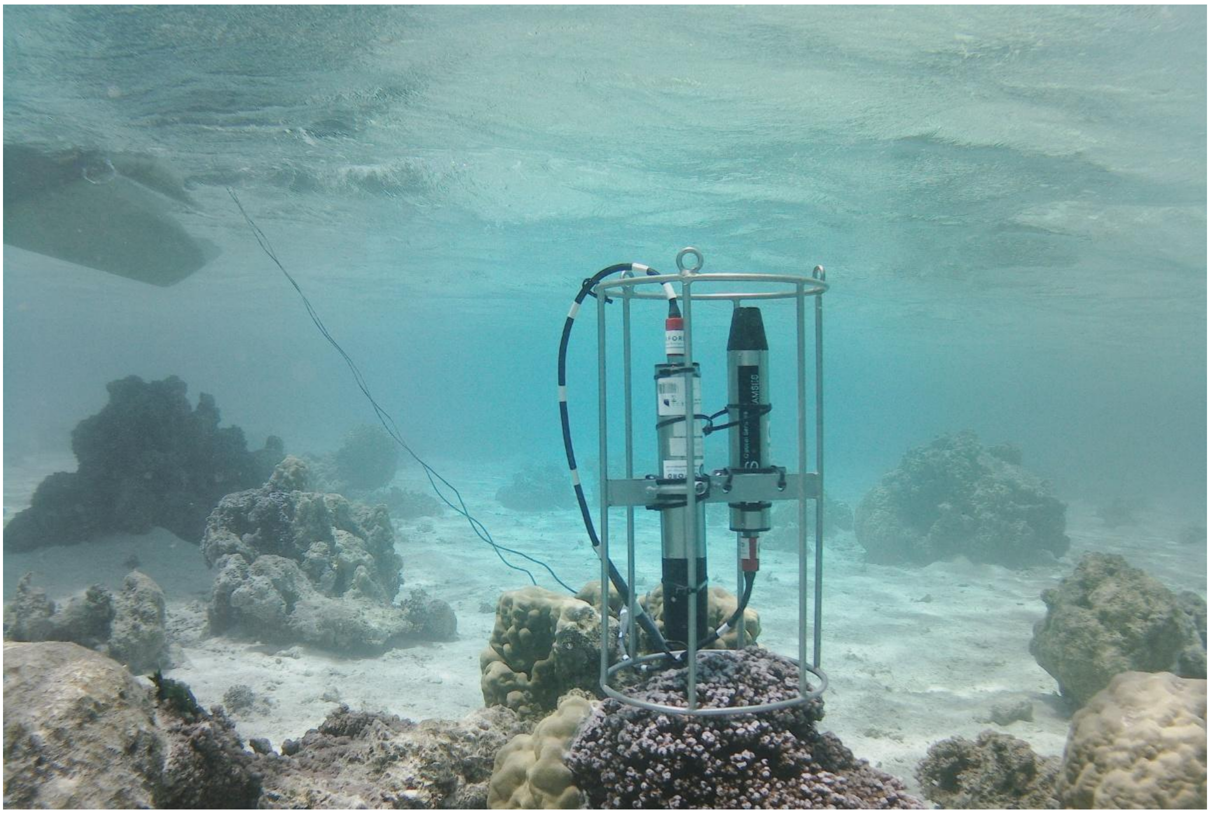

Figure S4. The TriOS RAMSES radiometer set-up for benthic reflectance measurements. Photo credit: Courtney Stuart.

11.4 Apparent optical properties – results

Results of the benthic reflectance measurements are shown in Figure S5. The reflectance spectra are in line with available data from previous studies (see e.g., Hochberg et al., 2003).

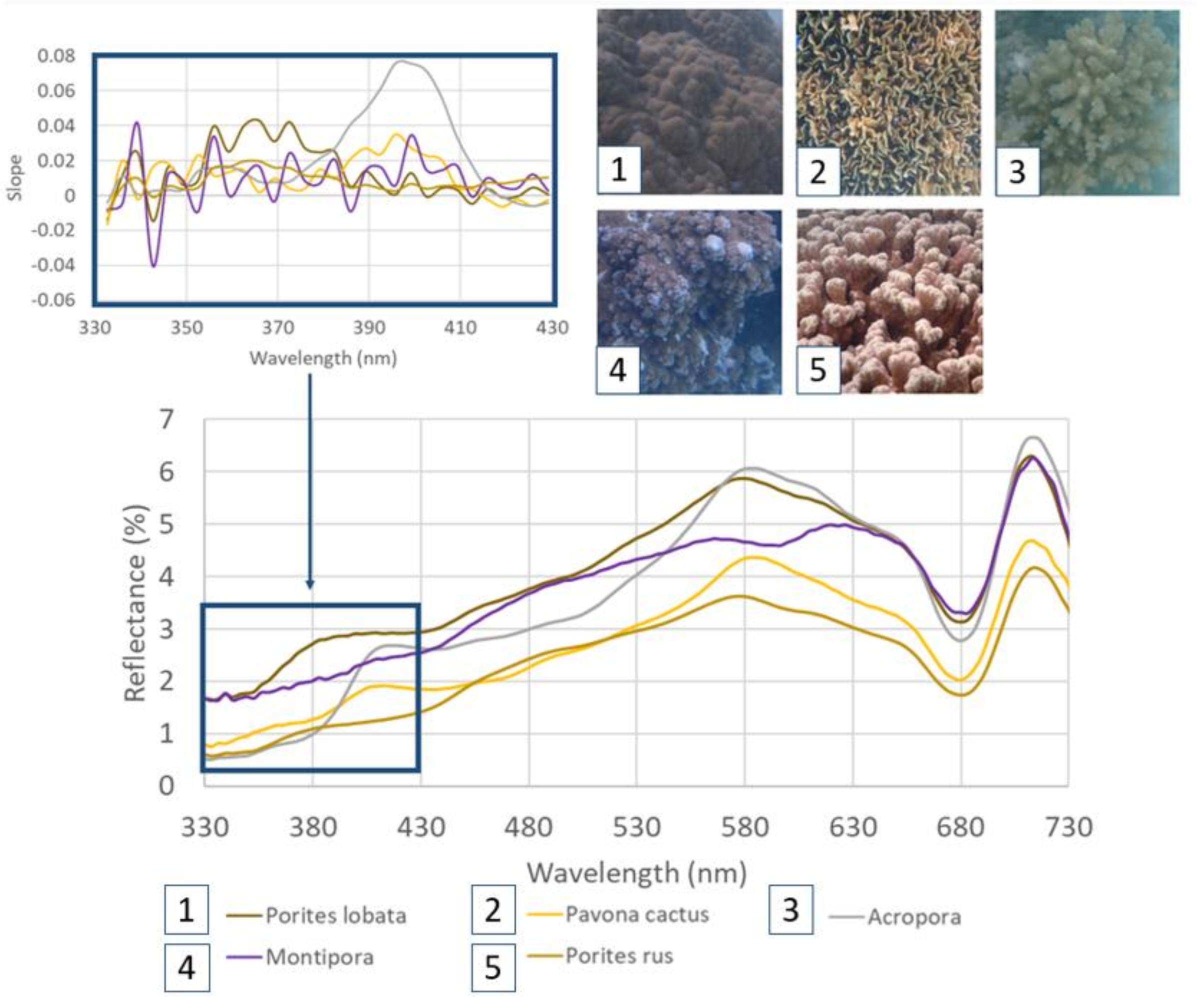

Figure S5. Examples of coral reflectance spectra for *Porites lobata*, *Pavona cactus*, *Acropora* sp., *Montipora* sp., and *Porites rus*. The blue box illustrates how taking the first derivative of the spectra can be used to highlight differences between spectral signatures.

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