ECOGRAPHY

Research article

Seascape configuration determines spatial patterns of seabird-vectored nutrient enrichment to coral reefs

Courtney E. Stuart ✉[1], Simon J. Pittman[1], Kostantinos A. Stamoulis[2], Cassandra E. Benkwitt[3], Hannah E. Epstein[4,5], Nicholas A. J. Graham[3], Andrew C. Smith[6], Jack H. Lacey[6], Kalia S. I. Bistolas[5], Jayna L. DeVore[7,8], Simon Ducatez[9] and Lisa M. Wedding[1]

[1]School of Geography and the Environment, University of Oxford, Oxford, UK
[2]Seascape Solutions, Mililani, HI, USA
[3]Lancaster Environment Centre, Lancaster University, Lancaster, UK
[4]School of Life Sciences, University of Essex, Essex, UK
[5]Department of Microbiology, Oregon State University, Corvallis, OR, USA
[6]British Geological Survey, Nottingham, UK
[7]Tetiaroa Society, Tetiaroa, French Polynesia
[8]University of French Polynesia, ILM, Ifremer, IRD, Faa'a, Tahiti, French Polynesia
[9]IRD, ILM, Ifremer, UPF, Faa'a, Tahiti, French Polynesia

Correspondence: Courtney E. Stuart (courtney.stuart@mansfield.ox.ac.uk)

Ecography
2025: e07863
doi: 10.1002/ecog.07863
Subject Editor: Scott Bennett
Editor-in-Chief: Miguel Araújo
Accepted 26 May 2025

NORDIC SOCIETY OIKOS

www.ecography.org

Pelagic-feeding seabirds deliver nutrient subsidies that enhance the productivity, biodiversity, and resilience of terrestrial and marine ecosystems, particularly in nutrient-poor tropical environments. However, the biogeophysical variables governing the fluxes of these nutrients within and among interconnected ecosystems remain poorly understood. To address this, we examined the spatial distribution of seabird-vectored nutrients in the seascape of Tetiaroa, a semi-enclosed coral atoll in French Polynesia, where seabird populations and associated nutrient cycles are recovering after recent rat eradication. We focus on the nitrogen isotope (δ^{15}N) signatures of a dominant marine alga as evidence of seabird-vectored nutrient uptake. Integrating stable isotope analysis within a seascape ecology framework, we show that breeding seabird biomass, depth, distance to land, geographic location within the atoll, and seafloor curvature drive spatial patterns of nutrient enrichment. Specifically, our models account for up to 88% of the variation in algal δ^{15}N signatures and reveal peak enrichment in shallow, nearshore areas where water flow slows and converges due to localised seafloor curvature. These results extend previous research by highlighting seafloor geomorphology, notably curvature, as a modulator of fine-scale nutrient delivery patterns. Although a complex model incorporating 11 high-resolution biogeophysical variables enhanced spatial predictions by revealing fine-scale variations, a simpler model using only five of these variables was comparably effective in capturing overall spatial trends. This study identifies the key seascape configuration and complexity characteristics likely to affect the spatial patterns of recovery potential following the restoration of seabird-driven nutrient cycles, offering valuable guidance for ongoing restoration efforts in this coupled island-reef system. Future investigations could assess how the effects of

---

biogeophysical variables on nutrient delivery vary in magnitude and direction across different geographic, geological, and anthropogenic contexts.

Keywords: atoll, marine subsidies, restoration, seabirds, seascape ecology, stable isotopes

Introduction

Nutrients play a fundamental role in shaping ecosystem structure, function, and resilience by regulating key biogeochemical processes such as photosynthesis and respiration (Howarth 1988, Atkinson 2011). In marine environments, nitrogen and phosphorus are often limiting nutrients, directly and indirectly influencing net primary and ecosystem productivity (Howarth 1988). Nutrient forms and ratios vary by source, and individual species have specific nutrient requirements and preferences (Raven et al. 1992, Pedersen and Borum 1996). Consequently, nutrient loading can lead to complex, context-dependent effects (Shantz and Burkepile 2014). For instance, anthropogenic nutrient inputs can disrupt the mutualism between coral hosts and their symbiotic dinoflagellates (Symbiodiniaceae), compromising coral growth and altering habitat availability for coral-associated species (Shantz and Burkepile 2014, Burkepile et al. 2020). Excessive nutrient enrichment from sewage effluent, fertiliser runoff, and other anthropogenic sources often fuels the proliferation of fleshy macroalgae at the expense of reef-building scleractinian corals, driving phase shifts that degrade reef structure and function with limited capacity for natural recovery (Hughes 1994, McManus and Polsenberg 2004, Graham et al. 2013). These impacts are compounded by ocean warming, habitat destruction, and other human-driven pressures (Ban et al. 2014, Wedding et al. 2022), accelerating the breakdown of natural (i.e. non-anthropogenic) nutrient pathways within and across ecosystems (Davis et al. 2009). Consequently, opportunities to identify, restore, and protect the natural nutrient cycles that sustain marine ecosystem biodiversity and resilience are diminishing under multiple interacting stressors, highlighting the urgent need for investigation to support effective management and restoration planning.

One natural cross-ecosystem nutrient cycle that has garnered increasing attention in recent decades is the sea-land-sea transport of nutrients by seabirds (McCauley et al. 2012, Lorrain et al. 2017, Graham et al. 2018, Benkwitt et al. 2019, 2021a, 2021b, Savage 2019). Seabirds forage on pelagic fishes and invertebrates, thereby concentrating nutrients across marine trophic levels and producing nutrient-rich excrement (guano) (Polis et al. 1997). While anthropogenic sources provide an imbalanced nutrient supply, often dominated by nitrogen, seabird guano offers a more balanced nitrogen-to-phosphorus ratio, along with essential micronutrients such as iron, manganese, zinc, and copper (Wiedenmann et al. 2013, Honig and Mahoney 2016, Savage 2019, Browning et al. 2023, Wiedenmann et al. 2023, Appoo et al. 2024). Notably, seabird guano is enriched with the heavy nitrogen isotope ^{15}N, leading to elevated ^{15}N:^{14}N ($\delta^{15}N$) values, which can be detected through stable isotope analysis. Additionally, 60–80% of guano nitrogen occurs in soluble organic forms, while 40–55% of phosphorus is present as soluble phosphate (Staunton-Smith and Johnson 1995, Szpak et al. 2012), making it readily available for uptake by primary producers and a potent organic fertiliser (Polis et al. 1997). On islands where seabirds breed and roost, their nutrient-rich guano, eggs, and carcasses enhance soil fertility, boost plant biomass, and influence the composition of both above- and below-ground communities (Fukami et al. 2006, Graham et al. 2018, Grant et al. 2022, Appoo et al. 2024).

Seabird-vectored nutrients, in addition to their terrestrial impacts, enhance productivity in adjacent marine ecosystems through direct deposition, tidal pumping, rainfall runoff, and submarine groundwater discharge (McCauley et al. 2012). These nutrients have been detected in macroalgae, turf algae, Symbiodiniaceae, corals, sponges, and fishes, with subsidies extending hundreds of metres offshore (McCauley et al. 2012, Honig and Mahoney 2016, Lorrain et al. 2017, Graham et al. 2018, Benkwitt et al. 2019, 2021a, 2021b, Savage 2019). For instance, Savage (2019) demonstrated that a dominant branching coral near seabird-rich islands exhibited growth rates up to four times greater than those of conspecifics at the same depth on reefs lacking seabird nutrients. Benkwitt et al. (2019) found that seabird nutrient enrichment enhanced crustose coralline algal cover at the reef scale following disturbances, potentially providing settlement substrate for coral larvae and facilitating their post-settlement survival. Furthermore, seabird-vectored nutrients affect reef fish biomass and demographic rates, altering herbivory, predation, and the availability of culturally and economically important species (Graham et al. 2018, Benkwitt et al. 2019, 2021a, 2021b). Thus, evidence suggests that coral reef recipients respond more positively to the forms and ratios of nitrogen and phosphorus provided by seabirds compared to those from typical anthropogenic sources (Shantz and Burkepile 2014, Savage 2019).

Despite growing evidence of the ecological benefits of seabird-vectored nutrients across land and sea, the biological and geomorphological (hereafter 'biogeophysical') factors that govern their spatial distribution in marine systems remain largely unexplored. Most marine studies have focused on factors like depth, offshore distance, and island categories based on seabird density (Lorrain et al. 2017, Graham et al. 2018, Savage 2019). However, a substantive body of literature from terrestrial and freshwater systems has demonstrated the importance of geomorphological features such as slope, curvature, and terrain roughness in shaping the transport and deposition of matter and energy (Zevenbergen and Thorne 1987, Moore et al. 1991, Varanka et al. 2015, Chadwick and Asner

2016, Florinsky 2017, Rutledge and Chow-Fraser 2019). For example, Evans et al. (2016) showed that in agricultural lands, steep slopes accelerate surface runoff, depositing soil phosphorus in flatter, downslope areas where runoff converges and slows due to local curvature. Applying these insights to coupled island-reef systems, we hypothesise that seabird-vectored nutrient enrichment is likely elevated where upslope terrestrial and downslope marine ecosystems are connected by steep midslopes, and further enhanced where seafloor curvature causes flow to decelerate and converge, increasing residence time and promoting nutrient retention. Incorporating these and other biogeophysical variables into seabird nutrient models may therefore offer novel insights, improving predictions of nutrient fluxes and their ecological impacts.

By bringing together geospatial and stable isotope analytics within a seascape ecology conceptual framework focused on linking spatial patterns and ecological processes, we explore the knowledge gap of where and how seabird-vectored nutrients accumulate in the coastal seascape (Pittman 2018, Palola et al. 2025, Wedding et al. 2025). We apply this novel integrative methodology to examine how seascape configuration, context, and complexity shape the spatial distribution of these nutrients within the semi-enclosed coral atoll of Tetiaroa, French Polynesia. Building on evidence from terrestrial and freshwater analogues, we assess how variations in bathymetric depth, slope, curvature, offshore distance, and other biogeophysical variables, along with seabird populations across islands, influence nutrient enrichment patterns in the atoll lagoon. Specifically, we ask: how can incorporating high-resolution biogeophysical variables within a seascape ecology framework improve the modelling and prediction of seabird-vectored nutrient flows, and what key variables are most critical for this improvement? We then use insights from this approach to support ongoing atoll restoration efforts by identifying seascape characteristics that are likely to influence spatial patterns of recovery resulting from restored seabird-driven nutrient cycles.

Material and methods

Study area

Tetiaroa (149.5666°W, 17.0164°S) is a coral atoll located ~ 55 km north of Tahiti in French Polynesia (Fig. 1). The atoll features a central lagoon surrounded by 12 vegetated coral islands (motu), which have a maximum elevation of 5.7 m, and is encircled by an outer reef with a perimeter of approximately 28 km. Positioned within the Southeast Trade Winds zone, Tetiaroa experiences warm and humid weather, with a dry season from May to October and a wet season from November to April (Jeanson et al. 2014). The Southeast Trade Winds and resulting currents are prevalent throughout the year and are particularly strong in the dry season. However, organised depressions can induce north to northwest winds in the wet season, often coinciding with passing tropical storms. The atoll has a narrow tidal range of less than 0.5 m (Jeanson et al. 2014).

The Tetiaroa Society manages the atoll under a Conservation and Sustainable Use Plan that prohibits urban development, safeguarding both terrestrial and marine ecosystems (Tetiaroa Society 2016). Onetahi is the only inhabited motu, hosting the Tetiaroa Society Ecostation and the Brando Hotel. Importantly, the limited infrastructure on Onetahi is not considered a significant nutrient source, as wastewater is treated on-site and reused for irrigation. Organic by-products and food waste are processed into fertiliser, while non-organic wastes are transported to Tahiti for recycling (Pacific Beachcomber Group 2024).

The marine waters are under the jurisdiction of the Government of French Polynesia, which established a no-fishing zone in the southern lagoon in 2014 to protect Tetiaroa's marine biodiversity (Tetiaroa Society 2016). Classified as an Important Bird and Biodiversity Area, Tetiaroa serves as a breeding and roosting ground for thousands of seabirds from eleven species (BirdLife International 2024; Supporting information). Historically, European settlers had reduced the availability of suitable vegetation for seabirds by replacing indigenous plants with monocultures of coconut palms *Cocos nucifera*. The introduction of Polynesian *Rattus exulans* and/or black rats *R. rattus* to nine of the 12 motu further exacerbated seabird population declines by preying on their eggs and chicks (Russell et al. 2011, Tetiaroa Society 2016; Supporting information).

To support the recovery of seabird communities and their associated nutrient contributions, the Tetiaroa Atoll Restoration Project (TARP) began rat eradication efforts on Reiono in 2018. Following this initial success, further eradication efforts were launched on Onetahi and Honuea in 2020, with the remaining invaded motu targeted in 2022. Although some Polynesian rats persist on two motu, efforts to eliminate the remaining individuals and monitor for reinvasion are ongoing. Additionally, TARP may undertake reforestation initiatives to restore the native vegetation preferred by seabirds (Young et al. 2010, McCauley et al. 2012, Carr et al. 2021).

Algal field sampling and isotopic analysis

To provide evidence of seabird-vectored nutrient enrichment in Tetiaroa's seascape, we collected samples of *Turbinaria ornata*, a common brown macroalga that assimilates these nutrients, in 2021 and 2023 (Fig. 1). In November 2021, we gathered individual thalli of *T. ornata* around the perimeters of ten motu. We sampled points parallel to the shoreline, spaced approximately 50 m apart, with a median offshore distance of 15 m and a median depth of 0.5 m. We conducted additional collections in November 2021 and September 2023 along underwater transects perpendicular to the shores of ʻĀ'ie, Reiono, Rimatu'u, and Onetahi (Fig. 1). We spaced the transects at least 15 m apart and collected specimens at 10-m intervals along each transect. The collection points along transects varied in depth (0.19–1.66 m) and offshore distance (6.6–61.85 m).

We cleaned *T. ornata* samples of epibionts, placed them in labelled dishes, and dried them for 24–48 hours at 60°C

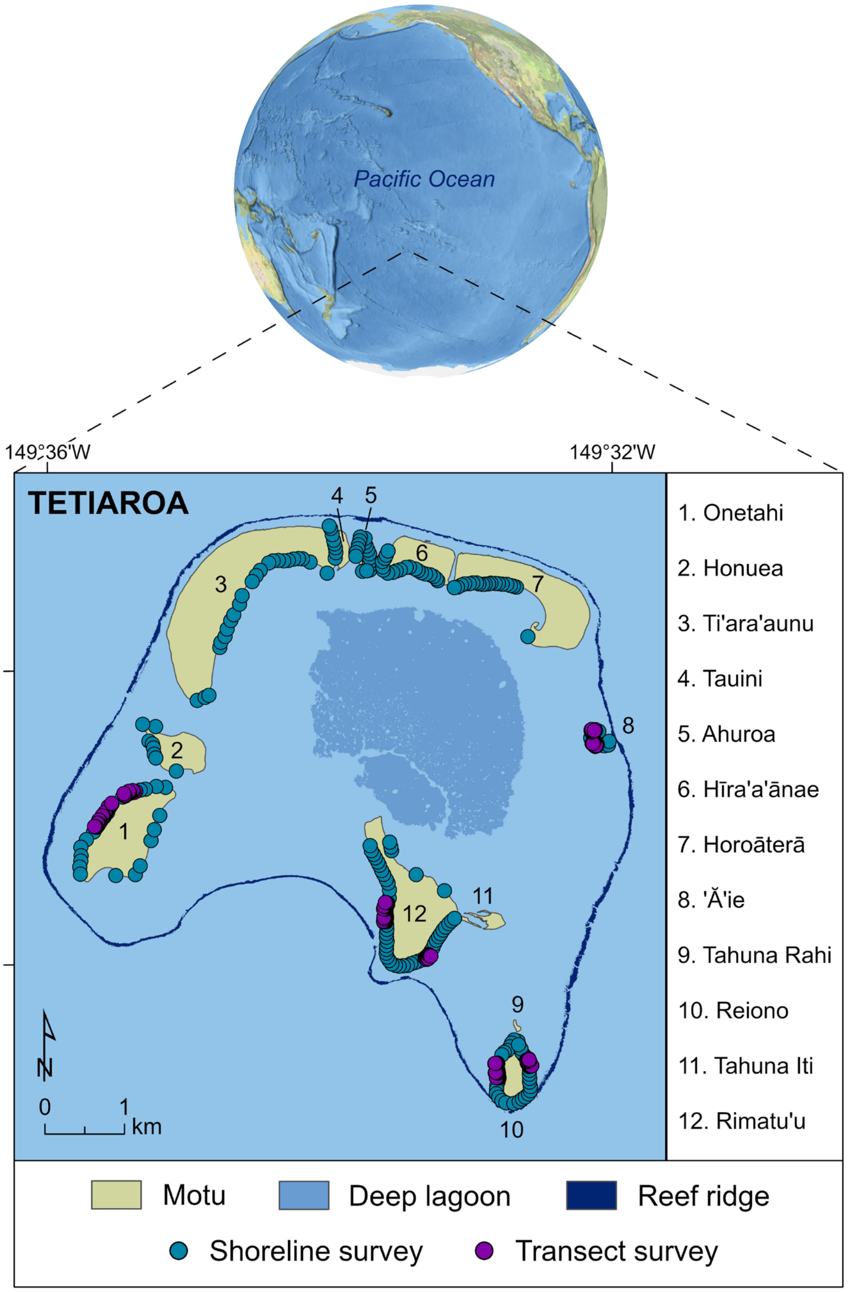

Figure 1. Locations of *Turbinaria ornata* surveys conducted in Tetiaroa, French Polynesia, in 2021 and 2023. Data are referenced to the WGS 1984 UTM Zone 6S coordinate system (European Petroleum Survey Group ID 32706).

in a constant-temperature drying oven at the Tetiaroa Society Ecostation. We ground the dried samples using a ball mill or mortar and pestle and stored them in separate vials for transport. For analysis, we combusted the 2021 samples using an Elementar vario MICRO cube Elemental Analyser and analysed them with an IsoPrime 100 Isotope Ratio Mass Spectrometer at Lancaster University (Lancaster, UK), using international standards IAEA 600 and USGS 41 (Benkwitt et al. 2021a, 2021b). Similarly, we combusted and analysed the 2023 samples using an Elementar vario ISOTOPE cube coupled to an IsoPrime precisION gas chromatography combustion isotope ratio mass spectrometer at the British Geological Survey (Nottingham, UK), referencing certified materials BGS B2162, BGS BROC3, USGS 61, USGS 62, and USGS 63. Reproducibility for all standards was within ± 0.1‰ (1σ) based on repeat analyses. We focus on $\delta^{15}N$ as a reliable proxy for seabird nutrient enrichment, given that guano $\delta^{15}N$ values generally range from 10 to 20‰, although higher values can also occur. In contrast, atmospheric and oceanic $\delta^{15}N$ values are around 0‰ and 2–6‰, respectively (Young et al. 2010, Lorrain et al. 2017, Graham et al. 2018, Appoo et al. 2024). We analysed samples in duplicate or triplicate and tested a subset at both laboratories to ensure consistency ($R^2 = 0.99$, intercept = 0.15, slope = 0.99). This study used a total of 405 records of *T. ornata* nutrients.

Interpolating seabird biomass

We collected seabird survey data across motu with differing histories of rat infestation and coconut monocropping by walking coastal transects (each approximately 100-m long) along the fringing vegetation at the perimeter of each motu (Supporting information). We counted all seabirds within 5 m of the vegetation edge and identified the species, nest status, sex (where possible), and life stage of each individual. These surveys covered the entire coastline of each motu, except for Onetahi, where only the northern third was surveyed due to limited coastal access in the south caused by the presence of the hotel. We conducted surveys from mid-October to early November 2021, coinciding with initial algal collection. We repeated the surveys in late August 2023, one year after the atoll-wide rat removal attempt and around the second wave of algal sampling.

Given the atoll's total land surface (~ 550 ha) and thick vegetation, whole-island surveys were not logistically feasible. Inland nesting activity is limited to only four motu – Reiono, Tahuna Iti, Tahuna Rahi, and 'Ă'ie – and these motu also have the highest coastal seabird abundance. By standardising our approach to coastal transects across all motu, we adopted a conservative strategy that prioritises relative variation in seabird biomass between motu over absolute biomass estimates. While we acknowledge that inland nesting seabirds may influence lagoon nitrogen concentrations via groundwater seepage from freshwater lenses beneath the motu, the hydrology of the atoll is poorly understood, and we lack the data to account for groundwater-derived nitrogen inputs at this time.

Based on the surveys conducted along the coastal vegetated fringe, we identified apparently occupied nests (AONs) by filtering for the presence of a nest, egg, adult on egg, chick, or fledgling. We then calculated seabird biomass (kg ha^{-1}) based on the AONs, applying species-specific body mass scaling (del Hoyo et al. 1992, 1996, Wilman et al. 2014) and survey area data, and assuming two adults per nest. Given the short time since rat removal, seabird populations showed minimal signs of recovery by 2023. Therefore, we averaged total seabird biomass across 2021 and 2023 for each transect. Since nutrient inputs scale with seabird biomass and seabird-vectored nutrients decline approximately linearly with offshore distance, we applied inverse distance weighting with linear decay to interpolate transect-level data across the atoll. This was implemented using the 'gstat' (ver. 2.1-1; Pebesma 2004, Gräler et al. 2016) and 'raster' (ver. 3.6-26; Hijmans 2023b) packages in the RStudio environment (R ver. 4.3.0, www.r-project.org). The resulting predictor, henceforth referred to as 'spatialised seabird biomass', represents the anticipated contribution of island-roosting and -nesting seabirds to nutrient conditions in the surrounding marine environment.

Quantifying seafloor terrain morphology and distance to land

By applying an integrative seascape ecology approach with geospatial pattern metrics (Pittman et al. 2021, Wedding et al. 2011), we derived a suite of biogeophysical variables that may influence marine spatial patterns of seabird-vectored nutrient flows (Table 1, Supporting information). We quantified terrain morphometrics from a 30 cm resolution digital terrain model (DTM) generated from airborne LiDAR (light detection and ranging) in 2017 (Ural et al. 2019). Water depth, slope magnitude and direction (eastness, northness), curvature (mean, planform, and profile), and rugosity (surface area to planar area [SAPA]) were quantified using the 'MultiscaleDTM' package (ver. 0.8.2; Ilich et al. 2023). These calculations assumed a quadratic local fit using the standard three by three cell neighbourhood. Additionally, we calculated a 'distance to land' raster from the DTM using the 'terra' package (ver. 1.7-55; Hijmans 2023a), treating all cells with pixel values greater than the mean tidal range (≥ 0.5 m) as land.

Classifying benthic patch types

To explore the potential influence of habitat context on the assimilation of seabird-vectored nutrients by *T. ornata*, we acquired a high-resolution (2 m) remotely sensed benthic map of the atoll from the Global Reef Expedition of the Khaled bin Sultan Living Oceans Foundation (Purkis et al. 2019). We converted the benthic map with 18 discrete patch types to a raster and resampled it to a 30 cm resolution using the 'fasterize' (ver. 1.0.4; Ross 2022) and 'raster' (ver. 3.6-26) packages. For simplicity, we reclassified this raster into three broad categories: coral and hardbottom, rock, and unconsolidated sediments (Supporting information). We then extracted benthic patch type, approximated seabird biomass influence, and terrain morphometric values at each algal collection point using the 'raster' package (Hijmans 2023b).

Spatial autocorrelation and multicollinearity analyses

Given Tetiaroa's small geographic extent and the dense distribution of algal collection points, we assessed spatial autocorrelation in algal $\delta^{15}N$ values before modelling. The Moran's I statistic, calculated using the 'spdep' package (ver. 1.2-8; Pebesma and Bivand 2023) under the assumptions of normality or randomisation, indicated significant positive spatial autocorrelation in the $\delta^{15}N$ data ($p < 0.05$). We plotted empirical variograms and fitted variogram models using the 'gstat' package (ver. 2.1-1), which revealed that $\delta^{15}N$ values were positively autocorrelated up to ~ 1050 m. Spatial filtering of *T. ornata* $\delta^{15}N$ records to remove spatial autocorrelation was not feasible, as it would excessively reduce the dataset, making model construction impractical. As detailed below, we instead incorporated the spatial structure of the response variable into the subsequent models as an additional covariate (Beale et al. 2010), and then examined model residuals for any remaining spatial autocorrelation using the same Moran's I and variogram procedure.

Table 1. Biogeophysical variables used to predict the δ^{15}N signatures of *Turbinaria ornata*, where δ^{15}N serves as a proxy for seabird nutrient enrichment. Ranges reflect values at algal collection points; full atoll ranges are provided in the Supporting information. Methods were conducted in RStudio (R ver. 4.3.0, www.r-project.org).

Predictor	Range and units	Description	Hypothesised effect on seabird-derived nutrients	Method
Spatialised seabird biomass	0–1870.42 kg ha^{-1}	Breeding seabird biomass on the adjacent motu, spatially interpolated over the surrounding marine environment with a linear decay function	Nutrient delivery and uptake are hypothesised to scale with breeding seabird biomass on the adjacent motu	*gstat* and *interpolate* functions of the 'gstat' (ver. 2.1-1) and 'raster' (ver. 3.6-26) packages
Depth	−1.79 to −0.04 m	Bathymetric depth	Nutrient availability is expected to decrease with increasing depth	*mask* function of the 'raster' package (ver. 3.6-26)
Slope	0–59.31°	Rate of maximum change in depth	Steep slopes along the land–sea ecotone are expected to facilitate the initial transport of nutrients from land, while gradual seafloor slopes are hypothesised to enhance nutrient delivery and uptake due to slower flow	*Qfit* function of the 'MultiscaleDTM' package (ver. 0.8.2)
Profile curvature	−2.62 to 1.98 m^{-1}	First derivative of slope calculated parallel to the direction of maximum slope: upwardly convex (−), linear (0), or concave (+)	Profile curvature influences flow deceleration (convex) or acceleration (concave), while planform curvature influences flow convergence (concave) or divergence (convex). Nutrient delivery and uptake are hypothesised to be most elevated where benthic flow decelerates and converges	*Qfit* function of the 'MultiscaleDTM' package (ver. 0.8.2)
Planform curvature	−2.94 to 4.09 m^{-1}	First derivative of slope calculated perpendicular to the direction of maximum slope: laterally convex (+), linear (0), or concave (−)		*Qfit* function of the 'MultiscaleDTM' package (ver. 0.8.2)
Eastness	−1 to 1 unitless	Relative eastness of the slope: due west (−1) to due east (+1)	Slopes facing the prevailing Southeast Trade Winds are hypothesised to be more exposed to wind- and wave-driven circulation, reducing water residence time and diminishing nutrient assimilation opportunities	*Qfit* function of the 'MultiscaleDTM' package (ver. 0.8.2)
Northness	−1 to 1 unitless	Relative northness of the slope: due south (−1) to due north (+1)		*Qfit* function of the 'MultiscaleDTM' package (ver. 0.8.2)
Distance to land	2.82–61.85 m	Distance to the nearest point on land	Nutrient delivery and uptake are hypothesised to decrease with increasing offshore distance	*gridDist* function of the 'terra' package (ver. 1.7-55)
Benthic patch type	3 classes	Benthic habitat classified as coral/hardbottom, unconsolidated sediment, or rock	Competition for nutrients will be higher in coral/hardbottom areas compared to rock or unconsolidated sediments, resulting in lower δ^{15}N values	*fasterize* and *resample* functions of the 'fasterize' (ver. 1.0.4) and 'raster' (ver. 3.6-26) packages

We assessed correlation and multicollinearity among predictors prior to modelling to prevent model instability and to enhance interpretability (Supporting information). Predictor selection was guided by statistical criteria as well as ecological reasoning to ensure that the models reflected meaningful relationships. We evaluated Pearson pairwise correlation coefficients (r) and variance inflation factors (VIF) using the 'usdm' package (ver. 1.1-18; Naimi et al. 2014), applying thresholds of $|0.7|$ and 5, respectively (Welch et al. 1994, Dormann et al. 2013). Two variables had collinearity issues – rugosity and mean curvature. Rugosity, which was positively correlated with slope ($r=0.84$), was excluded in favour of slope, as the latter had a broader range of values and was expected to more strongly influence water flow and nutrient transport. Mean curvature was positively correlated with both profile ($r=0.68$) and planform ($r=0.77$) curvatures. We retained the latter two predictors due to their anticipated effects on water flow acceleration (deceleration) and convergence (divergence), respectively. All predictors retained for modelling had pairwise correlation values less than $|0.6|$ and VIF values below 3.

Modelling

We constructed two generalised additive models (GAMs) to evaluate whether biogeophysical predictors derived from high-resolution remote sensing data enhance our understanding and prediction of seabird-vectored nutrient distributions. GAMs extend multiple linear models by using smooth functions, like splines, to capture non-linear relationships between variables (Hastie and Tibshirani 1990, Wood 2017). Splines flexibly approximate relationships without requiring modellers to assume a predefined predictor-response form, making GAMs both adaptable and interpretable. Unlike ensemble methods, GAMs allow exploration of individual predictor effects while controlling for others and provide a framework for hypothesis testing and confidence interval estimation (Hastie and Tibshirani 1990, Wood 2017).

We fitted and evaluated GAMs iteratively over the 405 algal $\delta^{15}N$ records using leave-one-out cross-validation (LOOCV) with the *gam* function of package 'mgcv' (ver. 1.8-42; Wood 2004, 2017), employing restricted maximum likelihood (REML) estimation as recommended by Wood (2017). LOOCV involves removing one row at a time from the dataset, fitting the model on the remaining rows, and evaluating the fitted model by using it to predict the response value of the withheld observation.

The first model (GAM1) fitted *T. ornata* $\delta^{15}N$ values as a function of the full suite of biogeophysical predictors. In this model, benthic patch type was included as a factor, while depth, slope, planform and profile curvatures, eastness, northness, distance to land, and spatialised seabird biomass were modelled as smooth terms using thin plate regression splines. To account for possible temporal variation (sampling in 2021 and 2023) and the positive spatial autocorrelation of the algal $\delta^{15}N$ response variable, we incorporated two additional components into the model: year (as a factor) and a two-dimensional (2D) Duchon spline of latitude and longitude. This approach allowed the model to address both unintended temporal effects and spatial dependencies. The second model (GAM2) included only thin plate regression splines for depth, distance to land, and spatialised seabird biomass as predictors, along with the factor term for year and the 2D spline of latitude and longitude. This simpler model aimed to test whether variables commonly measured in situ were sufficient to model spatial patterns of seabird-vectored nutrients across the atoll.

We created partial dependence plots using the 'gratia' package (ver. 0.8.2; Simpson 2024) to visualise the relationship between algal $\delta^{15}N$ signatures and each biogeophysical predictor, while accounting for the average effects of the other predictors in the model. We also produced diagnostic plots using the *gam.check* function of 'mgcv' to assess model fit and adherence to assumptions. To compare model performance quantitatively, we calculated the Akaike information criterion (AIC), adjusted R^2, and root mean squared error (RMSE) values. AIC balances model fit and complexity, with lower values indicating a more parsimonious model. Adjusted R^2 reflects the proportion of variance explained by the independent variables, accounting for the number of predictors, with higher values indicating better fit. RMSE measures predictive accuracy, where lower values denote better performance.

To examine the results spatially, we mapped $\delta^{15}N$ predictions alongside residuals at each algal collection point to highlight areas where the models performed well versus those where they over- or under-predicted $\delta^{15}N$. We also used the fitted models to extrapolate the $\delta^{15}N$ predictions within a 400-m buffer around each motu to visualise spatial trends and identify potential hot and cold spots. The 400-m buffer distance was chosen based on previous studies documenting seabird-vectored nutrient enrichment in marine organisms up to this distance offshore (Lorrain et al. 2017, Graham et al. 2018, Savage 2019, Benkwitt et al. 2021a). Predictions were clamped to a $\delta^{15}N$ range of 0–30‰ at this stage, as GAMs with spatial smooths may extrapolate poorly when making predictions for locations with conditions that differ substantially from those in the training data (Guisan et al. 2002). This approach mitigates the risk of generating implausible $\delta^{15}N$ values due to the model's reliance on localised regression techniques.

Results

Algal $\delta^{15}N$ spatial patterns and relationships with biogeophysical predictors

The $\delta^{15}N$ signatures of *T. ornata* varied considerably across the atoll (median = 6.73‰, range = 2.73–16.96‰; Supporting information). Algae were generally enriched in ^{15}N in the north-central, northeast, and southeast, with the highest $\delta^{15}N$ values found along the northeastern side of Reiono (16.96‰) and the southeastern side of Ahuora (16.64‰). In contrast, *T. ornata* collected near Onetahi, Honuea, and Ti'ara'aunu in the western half of the atoll were relatively depleted in ^{15}N, with a median $\delta^{15}N$ value of 4.14‰ (Supporting information). Over 95% of these western specimens had $\delta^{15}N$ signatures below 6‰, and roughly 34% fell below 4‰.

The splines for spatialised seabird biomass, depth, and distance to land were similar in form and statistically significant at the 95% confidence level in both GAMs (Fig. 2). Spatialised seabird biomass exhibited a significant positive relationship with *T. ornata* $\delta^{15}N$ signatures in both models (Fig. 2). Partial dependence plots indicated that algal $\delta^{15}N$ signatures increase with seabird biomass up to approximately 1000 kg ha^{-1}, after which the effect stabilises around zero. However, substantial uncertainty exists at higher biomass values, as indicated by the wide confidence intervals. In general, algal $\delta^{15}N$ signatures exhibited a negative relationship with both depth and distance to land in the raw data, with the top 10% of $\delta^{15}N$ values (indicating the greatest enrichment) recorded at collection points shallower than 1.0 m and within approximately 25 m from shore (Supporting information). Holding all numeric predictors at their median and factors at their reference levels, GAM1 suggests that $\delta^{15}N$ would return to the upper oceanic reference level of 6‰ at approximately 203 m offshore, and to the lower oceanic reference level of 2‰ at around 290 m offshore. Similarly, GAM2 suggests that $\delta^{15}N$ would return to the upper and lower oceanic reference levels at approximately 231 m and 323 m offshore, respectively. The smooth term for depth in both models suggests a negative relationship between $\delta^{15}N$ and depths of approximately 0.5–1.5 m below the surface, with an uptick in predicted $\delta^{15}N$ values beyond this range indicating a shift toward a positive relationship. However, the narrow depth sampling window and widening confidence intervals at greater depths suggest that predictions in deeper waters are less reliable and should be interpreted with caution (Fig. 2).

Beyond spatialised seabird biomass, depth, and offshore distance, GAM1 identified profile and planform curvatures

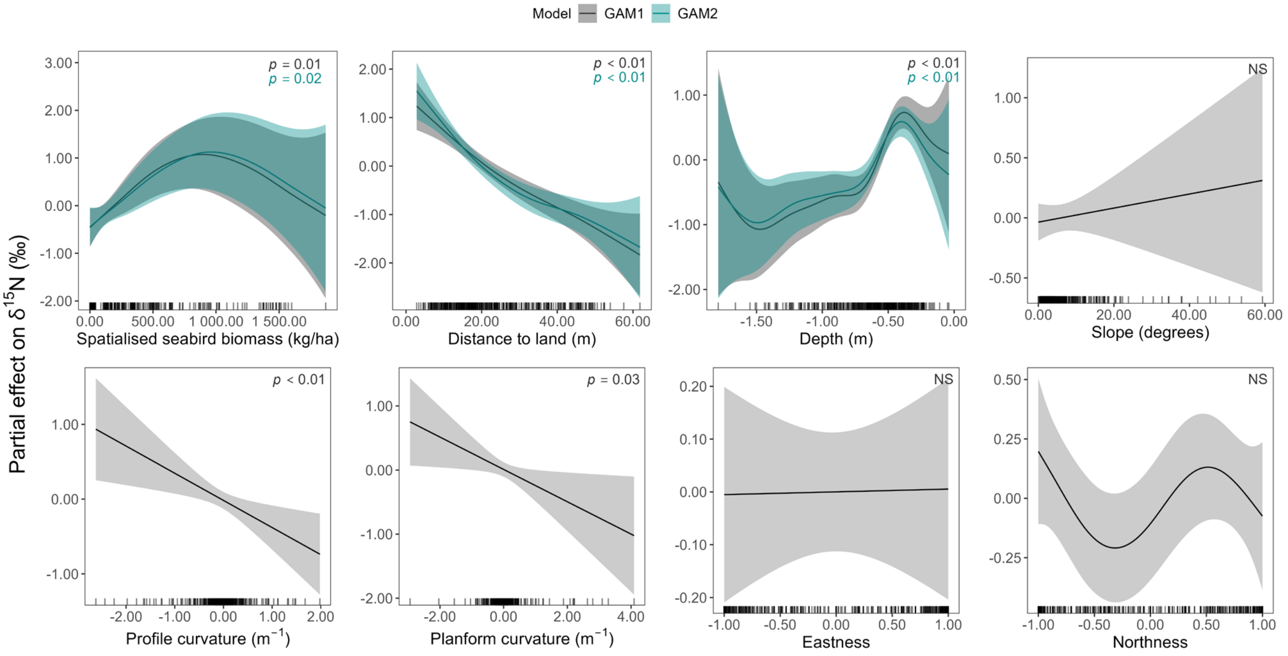

Figure 2. Results of the generalised additive models (GAMs) showing the effects of biogeophysical variables on *Turbinaria ornata* δ^{15}N signatures. GAM1 (grey) includes all predictors, while GAM2 (cyan) is limited to three key predictors. The y-axes represent the marginal effects of each variable on predicted δ^{15}N, holding other variables constant. Solid lines show the smoothed response relationships, with shading indicating 95% confidence intervals. Approximate significance of the smooth terms is shown by p-values, with "NS" denoting non-significance. Tick marks along the x-axes ('rug') show the distribution of observed data points. Results for the two-dimensional (2D) smooths of latitude and longitude are provided in Fig. 3.

as statistically significant predictors of algal δ^{15}N (Fig. 2). Negative values of profile curvature (i.e. convexities in the direction of the maximum slope) were associated with higher δ^{15}N values. Similarly, nutrient enrichment corresponded to negative values of planform curvature (i.e. concavities perpendicular to the direction of the maximum slope). In contrast, the splines for slope, northness, and eastness were non-significant and highly uncertain. In GAM1, benthic patch type as a factor yielded statistically significant results. For the reference year 2021, there was no significant difference in δ^{15}N signatures of algae growing on rock compared to unconsolidated sediments. However, δ^{15}N was estimated to be 0.45‰ lower for algae on coral reef/hardbottom compared to unconsolidated sediments ($p = 0.01$). According to GAM1, δ^{15}N was, on average, 0.21‰ higher in 2023 compared to 2021, regardless of benthic patch type; however, this effect of year was not statistically significant.

The 2D spline of latitude and longitude, included to address spatial dependence in the algal δ^{15}N response variable, was highly statistically significant in both models (Fig. 3).

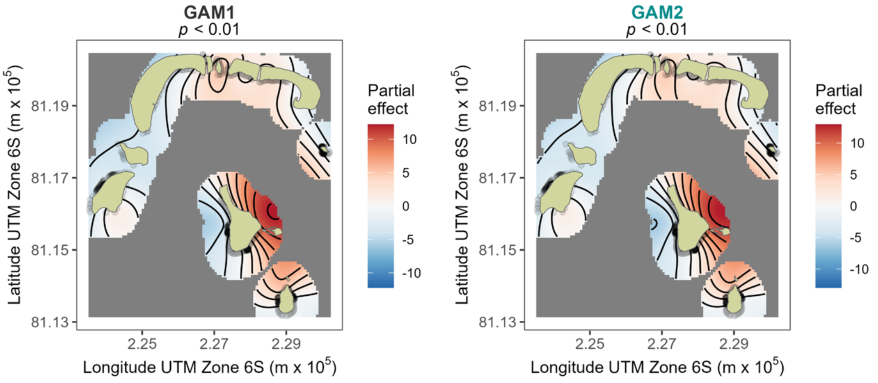

Figure 3. Heatmaps of the two-dimensional Duchon splines of latitude and longitude from the generalised additive models (GAMs) used to account for spatial dependence in the *Turbinaria ornata* δ^{15}N response variable. Transparent black circles represent the locations of the original observations, while contour lines connect points with the same predicted δ^{15}N values. Partial effect values represented by cool tones indicate relative nutrient depletion, while warm tones indicate relative nutrient enrichment.

After accounting for the average effects of other predictors, GAM1 and GAM2 suggested that δ^{15}N values increase notably in the eastern and particularly southeastern regions of the atoll. Conversely, δ^{15}N signatures decrease toward the western part of the atoll. Contour lines, which represent areas of constant predicted algal δ^{15}N values, showed strong alignment across both models. According to Moran's I and variogram analyses, the inclusion of the 2D geographic spline effectively removed spatial autocorrelation from the residuals of both models (Moran's I statistic ≈ 0, $p > 0.05$).

Comparison of model performance and predictions

Based on AIC, GAM1 demonstrated a better goodness of fit compared to GAM2 (Table 2). Although GAM1 included additional predictors, with planform and profile curvatures being statistically significant (Fig. 2), both models produced the same adjusted R^2 value. RMSE values were also consistent across GAM1 and GAM2. These findings align with diagnostic plots, which suggested that the two models exhibited similar fit and adherence to model assumptions (Supporting information). The numerical distribution of errors around predicted algal δ^{15}N signatures was similar across the two models: approximately 36% of GAM1 predictions and 32% of GAM2 predictions fell within ± 0.5‰ of observed values, while ~ 60% of predictions in both models were within ± 1‰ (Supporting information). Likewise, the spatial distributions of predicted algal δ^{15}N values and associated residuals were comparable across models when mapped (Supporting information).

Table 2. Summary of the two generalised additive models (GAMs) used to model *Turbinaria ornata* δ^{15}N signatures. Benthic patch type and year were included as factors, longitude and latitude as a two-dimensional Duchon spline (Lat:Lon), and all other variables as thin plate regression splines. Abbreviations: AIC (Akaike information criterion); R^2 (adjusted R^2); RMSE (root mean square error); edf (effective degrees of freedom); Ref df (reference degrees of freedom).

Model	Formula	AIC	R^2	RMSE
GAM1	δ^{15}N ~ Benthic_Patch_Type + Year + s(Spatialised_Seabird_Biomass) + s(Depth) + s(Slope) + s(Planform_Curvature) + s(Profile_Curvature) + s(Eastness) + s(Northness) + s(Distance_to_Land) + s(Longitude_UTM6S, Latitude_UTM6S)	1320.4	0.88	1.29
Parametric coefficients				
Term	Estimate	SE	t-value	Pr(> |t|)
Intercept	7.65	0.13	57.45	< 0.01
Benthic_Patch_Type2[Rock]	−0.14	0.24	−0.59	0.56
Benthic_Patch_Type3[Coral reef]	−0.45	0.17	−2.57	0.01
Year2023	0.21	0.17	1.27	0.21
Approximate significance of smooth terms				
Term	edf	Ref df	F	p-value
s(Spatialised_Seabird_Biomass)	2.69	3.38	3.34	0.01
s(Depth)	5.73	6.92	7.17	< 0.01
s(Slope)	1.00	1.00	0.44	0.51
s(Eastness)	1.00	1.00	0.00	0.95
s(Northness)	3.08	3.80	1.79	0.17
s(Planform_Curvature)	1.00	1.00	4.81	0.03
s(Profile_Curvature)	1.00	1.00	7.42	0.01
s(Distance_to_Land)	2.01	2.56	20.51	< 0.01
s(Longitude_UTM6S, Latitude_UTM6S)	29.63	31.57	38.49	< 0.01
Model	Formula	AIC	R^2	RMSE
GAM2	δ^{15}N ~ Year + s(Spatialised_Seabird_Biomass) + s(Depth) + s(Distance_to_Land) + s(Longitude_UTM6S, Latitude_UTM6S)	1327.9	0.88	1.30
Parametric coefficients				
Term	Estimate	SE	t-value	Pr(> |t|)
Intercept	7.38	0.08	96.74	< 0.01
Year2023	0.26	0.17	1.51	0.13
Approximate significance of smooth terms				
Term	edf	Ref df	F	p-value
s(Spatialised_Seabird_Biomass)	2.64	3.30	3.31	0.02
s(Depth)	5.38	6.56	5.58	< 0.01
s(Distance_to_Land)	2.74	3.47	17.39	< 0.01
s(Longitude_UTM6S, Latitude_UTM6S)	29.74	31.61	39.67	< 0.01

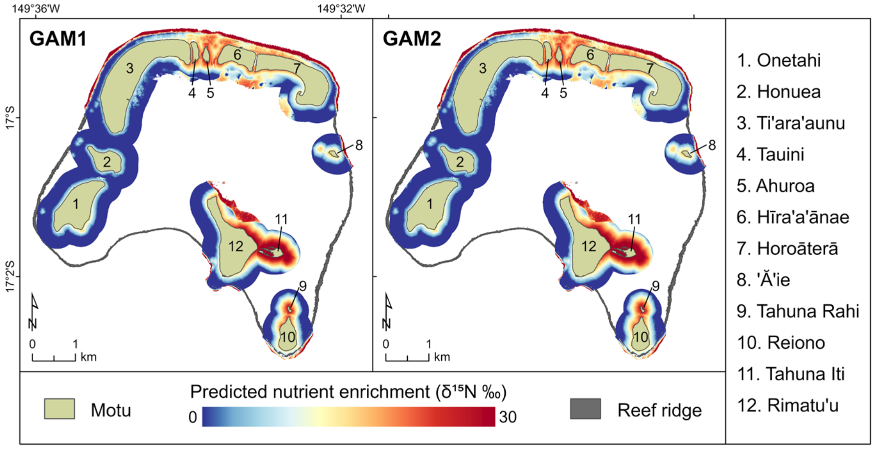

Figure 4. Predicted seabird nutrient enrichment within 400 m of Tetiaroa's motu, based on generalised additive models (GAMs) fitted to *Turbinaria ornata* δ^{15}N signatures. Predictions are shown for the most recent sampling year, 2023.

Overall, the spatial predictions from the two models were largely consistent (Fig. 4). Both models indicated elevated nutrient enrichment in the channels between the northern motu Ti'ara'aunu, Tauini, Ahuroa, and Hīra'a'ānae. The southern stretches of these channels, despite their greater depth (~ 3–4.5 m), were predicted to have high δ^{15}N values, particularly in flat-bottomed sections flanked by steeper slopes. Both models predicted especially high seabird-vectored nutrient levels near Tahuna Iti, along the east coast of Rimatu'u, and to a lesser extent around Tahuna Rahi and the northern tip of Reiono. Nutrient levels were predicted to fall within oceanic reference ranges (2–6‰) around Onetahi, Honuea, and Ti'ara'aunu, except for the northeastern-most stretches of the latter. Additionally, predicted δ^{15}N signatures were expected to return to these levels rapidly around the other motu (Fig. 4, Supporting information).

Discussion

Pelagic-feeding seabirds provide allochthonous nutrient subsidies that enhance the growth, resilience, and diversity of terrestrial and marine ecosystems, particularly in oligotrophic tropical systems (McCauley et al. 2012, Graham et al. 2018, Benkwitt et al. 2021a, 2021b, Grant et al. 2022, Appoo et al. 2024). Using a seascape ecology approach and high-resolution remote sensing products, we examined biogeophysical predictors of seabird-vectored nutrient distribution in Tetiaroa, French Polynesia, where invasive rats were eradicated to support seabird recovery. Spatialised seabird biomass, depth, distance to land, and location within the atoll were found to be the primary drivers of nutrient enrichment, with profile and planform curvatures refining these patterns at finer scales. However, a model excluding curvature metrics performed similarly, capturing the same general trends. These results inform conservation and restoration strategies by identifying areas where seabird nutrient enrichment is most likely to contribute to ecosystem recovery.

Algal δ^{15}N spatial patterns and relationships with biogeophysical predictors

δ^{15}N signatures of the marine alga *T. ornata* indicated that seabird-vectored nutrient enrichment was highest in Tetiaroa's north-central, northeast, and southeast seascape regions. The highest signals of nutrient enrichment were recorded in algae collected adjacent to Reiono and Ahuroa. δ^{15}N values were also elevated (> 10.5‰) around Tauini, Hīra'a'ānae, and Horoāterā, where large species like the brown booby *Sula leucogaster*, red-footed booby *S. sula*, and great frigatebird *Fregata minor* nest year-round, providing substantial nutrient subsidies (Appoo et al. 2024, Tetiaroa Society 2024). Elevated δ^{15}N values (> 14‰) were similarly recorded along the east coast of Rimatu'u near Tahuna Iti, which is locally known as "Bird Island". Tahuna Iti has never been invaded by rats and supports an abundant seabird population, including several species that breed exclusively there (Tetiaroa Society 2024). Conversely, algae from Honuea and Onetahi showed notably low δ^{15}N means (< 5‰). These western motu have the lowest seabird biomasses in the atoll due to their long histories of rat infestation, proximity to anthropogenic influence, and highly modified vegetation (Russell and Faulquier 2009, Russell et al. 2011).

Predicted spatial patterns of nutrient enrichment closely aligned with spatialised seabird biomass in the atoll, which was a significant positive predictor of algal δ^{15}N signatures. However, the positive effect of seabird biomass diminished beyond ~ 1000 kg ha^{-1}, where additional biomass had negligible or even negative effects, accompanied by greater uncertainty. Notably, the spatial distribution of seabirds aligns with that of native island vegetation, reflecting many species' preference for nesting in native flora rather than in monospecific coconut stands (Carr et al. 2021). Crucially, not all nutrients provided by seabirds become available to marine algae; a significant portion is likely assimilated by terrestrial vegetation, bound to island soils, or buried in marine sediments (Davis et al. 2009, Kolb et al. 2010). Further work integrating terrestrial nutrient retention with marine fluxes would help clarify the potential for nutrient saturation effects across the land–sea interface.

Previous studies suggest that a critical threshold of seabird density is required to elicit measurable nitrogen responses in seagrasses and macroalgae (Kolb et al. 2010, Appoo et al. 2024). Surprisingly, our findings point to the potential existence of another threshold, beyond which the influence of seabird biomass or density plateaus or transitions to a negative effect. Many studies rely on categorical comparisons between seabird-rich and seabird-poor (or seabird-absent) islands, rather than directly quantifying seabird biomass, density, or nutrient inputs. This highlights the need for future research to move beyond island categories and directly measure seabird demographic metrics or nutrient inputs to better understand organism responses to seabird fertilisation and to verify the existence of such thresholds.

Turbinaria ornata stable isotope signatures exhibited a negative relationship with depth and distance to land, with the highest $\delta^{15}N$ values found in shallow, nearshore areas. Our models suggest that in Tetiaroa, holding all other variables at their medians or reference values, the $\delta^{15}N$ signatures of *T. ornata* are expected to return to oceanic reference levels (2–6‰) within 200–300 m from shore. The rapid decrease in seabird nutrient enrichment with increasing offshore distance in Tetiaroa aligns with previous studies from Hawai‘i (Honig and Mahoney 2016), New Caledonia (Lorrain et al. 2017), Fiji (Savage 2019), and the Chagos Archipelago and Scattered Islands (Graham et al. 2018, Benkwitt et al. 2021a). These patterns were consistent in form and statistical significance across our GAMs, further validating their robustness and showing that the observed relationships are not dependent on model complexity.

Slope magnitude and direction (eastness, northness) were not statistically significant predictors of *T. ornata* $\delta^{15}N$ signatures. This contrasts with our hypotheses and previous terrestrial studies that have demonstrated a strong influence of slope metrics on surface runoff and nutrient mobility (Chadwick and Asner 2016, Evans et al. 2016, Rutledge and Chow-Fraser 2019). Similarly, Guinan et al. (2009a, 2009b) found that these variables influence cold-water coral distribution, attributing this to their effects on water circulation and the supply of suspended food particles. However, our finding that slope magnitude had a weak positive influence on predicted algal $\delta^{15}N$ values aligns with Varanka et al. (2015), who reported a minor positive effect of mean basin slope on nutrient concentrations in Finland's boreal rivers. They note that slope likely acts as a secondary factor, influencing water quality metrics through other environmental factors, such as water flow and residence time, rather than playing a dominant role (Varanka et al. 2015).

Rather than slope itself, profile and planform curvatures – which represent the rate of change in slope parallel and perpendicular to its steepest direction – emerged as statistically significant drivers. Negative profile curvatures, indicative of convex slopes, were associated with elevated algal $\delta^{15}N$, while positive values, corresponding to concave slopes, were related to lower algal $\delta^{15}N$ signatures. Similarly, negative (positive) planform curvatures, associated with concavities (convexities) perpendicular to the direction of maximum slope, were linked to higher (lower) seabird nutrient enrichment levels. These findings support our hypothesis that seabird-vectored nutrients accumulate in areas where seafloor curvature slows and converges benthic flow, consistent with terrestrial and freshwater studies on curvature's role in transporting sediments, nutrients, and water. For example, high relief positions on convex hillslopes in the southwestern Amazon were associated with higher soil nutrient concentrations (Chadwick and Asner 2016). Similarly, modelling by Sharma (2013) showed that curvature affects the saturated volume and average saturation of hillslopes, even under constant rainfall, with concave hillslopes exhibiting higher saturation, subsurface flow concentration, and pore-water pressure. While curvature and other seafloor terrain metrics have been widely studied in relation to fish distributions and marine protected area (MPA) placement (reviewed by Borland et al. 2021), few marine studies have explicitly examined how these factors influence nutrient fluxes beyond surface-level analyses (but see Hearn et al. 2001, Signa et al. 2013).

Our algal $\delta^{15}N$ response variable exhibited a property characteristic of ecological data: spatial autocorrelation (Legendre 1993). Spatial autocorrelation poses a challenge because it violates a common assumption of many conventional statistical methods – that residuals are independent and identically distributed. Consequently, analysing spatially autocorrelated data can result in flawed ecological interpretations and an increased Type I error rate (i.e. the probability of incorrectly rejecting the null hypothesis) (Beale et al. 2010). To prevent these issues, we incorporated spatial effects as an additional 2D spline of geographic coordinates in our models. This approach has been explored in other contexts, including simulation studies (Beale et al. 2010) and research on fish distributions (Stoner et al. 2001, Salazar et al. 2021), forest regeneration dynamics (Moreno-Fernández et al. 2018), and air pollution levels (Pearce et al. 2011). The spatial spline was statistically significant in both our GAMs, reflecting the elevated $\delta^{15}N$ signatures of *T. ornata* collected around the seabird-rich Tahuna Iti, Tahuna Rahi, Tauini, and Ahuroa.

Comparison of model performance

We compared two GAMs of varying complexity to evaluate whether high-resolution biogeophysical predictors enhanced our understanding of seabird-vectored nutrient enrichment patterns. GAM1 had a lower AIC score than GAM2; however, the adjusted R^2 values indicated that both models explained similar variance in $\delta^{15}N$. Their predictive performance was also nearly identical, with RMSE values differing by only 0.01. These results suggest that, while GAM1 included additional statistically significant covariates, they did not substantially improve model performance. In the relatively shallow coral atoll studied, a simpler model based on depth, offshore distance, and spatialised seabird biomass – variables that can be easily measured in the field or derived from available data – may suffice to characterise general patterns of seabird-vectored nutrient enrichment. This finding aligns with Graham et al. (2015), who showed that a simple model using structural complexity and depth predicted post-disturbance reef conditions in the Seychelles with 98% accuracy, performing similarly to a model with 11 reef-level variables. They suggested that factors such as depth and structural complexity, which are relatively stable over time, may provide adequate information for resource-limited agencies tasked with monitoring and restoring coral reef ecosystems (Graham et al. 2015).

Model limitations and future considerations

Although planform and profile curvatures significantly influenced nutrient enrichment in GAM1, these variables exhibited limited ranges at our algae collection points. The same applies to slope, as the seafloor within Tetiaroa's lagoon is relatively homogeneous and shallow, particularly within the depths and offshore distances where we sampled. While our models fit the data well, performed effectively on withheld testing data, and allowed for extrapolation, we do not yet fully understand the extent to which these factors influence nutrient distribution in the atoll. Caution is warranted when interpreting model predictions at locations with predictor values that differ substantially from those used to fit and evaluate our models (Guisan et al. 2002). Our results are specific to the context of this small, shallow atoll lagoon and may not be generalisable to deeper, more topographically complex coral systems. Nonetheless, our modelling approach is transferable. Investigating the influence of various seafloor terrain metrics across broader spatial scales and diverse geological settings presents a promising avenue for further research. Such studies would be especially valuable in regions with greater topographic–bathymetric heterogeneity, such as those near high volcanic islands.

Hydrodynamics, while not explored directly in this study, influences nutrient transport by dictating water motion and residence time (Hench et al. 2008, Wang et al. 2023). However, available hydrodynamic data for Tetiaroa are currently limited to a time series from a meteorological station in 2017 and a brief field experiment conducted in June–July 2019 (Tetiaroa Society 2019). Furthermore, due to its small size relative to the resolution of regional and global models, Tetiaroa's conditions are poorly represented, if at all, in these datasets. Ongoing efforts to model and validate the atoll's wave conditions and water circulation patterns will support the integration of these findings into future models, enhancing the prediction and understanding of spatiotemporal patterns in seabird-vectored nutrient fluxes. Additionally, more hydrodynamic data will allow future models to better assess the role of the fresh groundwater lens in transporting seabird-derived nutrients from motu interiors to the lagoon.

Our models capture spatial variation in seabird nutrient enrichment patterns but do not account for temporal variation, such as seasonal fluctuations. Increased precipitation during the wet season may elevate land–sea nutrient transfer, potentially resulting in higher algal $\delta^{15}N$ signatures than those reported here for the dry season. Seasonal effects on the land–sea transport of anthropogenic nutrients have been observed around the nearby high volcanic island of Moorea, where wave forcing varies throughout the year (Adam et al. 2021). Additional wet-season sampling, along with hydrodynamic data collection as discussed above, could help confirm whether the biogeophysical predictors identified here exert consistent effects over time. Targeted surveys in the waters adjacent to Tahuna Iti and the northern shores of Hīra'a'ānae and Horoāterā – where seabird biomass is especially high – would further clarify temporal nutrient pulses and help ground truth the elevated nutrient predictions produced by our models in these areas.

Land and sea are inherently interconnected in atoll systems, where terrestrial and marine features dynamically change in form, size, and position (Steibl et al. 2024). Achieving resilience to global change in atoll ecosystems necessitates considering the influences of both terrestrial and marine ecosystems, as well as their interconnectivity. As reviewed by Palola et al. (2025), future research applying an integrated land–sea approach may offer a path forward for understanding the broader 'nutrientscape'. For instance, Delevaux et al. (2018) developed a linked land–sea modelling framework specifically designed for the high relief oceanic islands of Hawai'i. Their novel framework effectively connected land use to coral reefs through the flow of nutrient-rich groundwater at fine spatial resolutions, providing valuable insights for implementing place-based ridge-to-reef management strategies (Delevaux et al. 2018). A similar hydrological systems approach in Tetiaroa would facilitate a more comprehensive investigation of the individual and combined effects of terrestrial and marine socio-ecological context and geomorphology on nutrient fluxes.

Implications for restoration in Tetiaroa and beyond

Beyond rat eradication efforts, TARP is considering the replanting of native vegetation to restore seabird breeding and roosting habitats (Young et al. 2010, Carr et al. 2021, Tetiaroa Society 2023). Our models indicate that western Rimatu'u and parts of Ti'ara'aunu currently exhibit low algal nutrient enrichment, likely due to low-to-intermediate seabird biomass (< 300 kg ha^{-1}) and limited native forest cover. With adjacent shallow coral reefs and varied seafloor curvature, these areas present promising opportunities for reforestation to enhance both terrestrial and marine ecosystems. Aligning terrestrial restoration with key connectivity corridors for herbivorous reef fishes, which support coral dominance and act as nutrient biovectors within the lagoon (Peterson et al. 2024), could enhance restoration efficacy and efficiency, supporting the recovery of socio-ecological co-benefits.

Coral reefs in Tetiaroa, like others in the South Pacific, are at risk of shifting into an algal-dominated state. Notably, *T. ornata* has expanded rapidly in density, spatial distribution, and its competitive interactions with corals in recent decades (Stiger and Payri 1999a, b). This alga thrives even in low-light, low-nutrient conditions and is widespread across lagoonal, barrier, and localised fringing reefs in French Polynesia (Stiger and Payri 1999a, Fong et al. 2017). *Turbinaria ornata* disperses via both short-range spores and long-distance fertile parent thalli (Stiger and Payri 1999a), which, combined with increasing anthropogenic nutrient enrichment, pollution, and climate change impacts, may further enhance its competitive advantages over reef-building corals (Pratchett et al. 2011, Schmitt et al. 2019, Williams et al. 2019, Souter et al. 2021).

Turbinaria ornata is defended by toughened thalli and anti-herbivore compounds, which increase with elevated nutrients and in the presence of grazers (Stiger et al. 2004, Bittick et al. 2016). It provides shelter for understory seaweeds, shielding them from herbivory (Bittick et al. 2010). These algal communities can shade, smother, and kill corals, reduce coral settlement, damage coral recruits, and ultimately lower reef biodiversity and resilience (McManus and Polsenberg 2004, Fong et al. 2017). Herbivorous fish that graze on *T. ornata* are scarce in the lagoons of both Moorea (Bergman et al. 2016) and Tetiaroa (Stuart et al. unpubl.). Monitoring should assess the extent of herbivore grazing on *T. ornata*, as the balance of nutrient input and herbivory will dictate algal dynamics on the reefs. If restored seabird nutrient cycles further enhance the competitive advantage of macroalgae over corals, human-led algal removal may be trialled to kickstart coral recovery, similar to the proposed removal of coconuts on land to reestablish native flora. However, evidence for the success of such resource-intensive *T. ornata* eradication efforts is limited (Bulleri et al. 2018).

Even for Tetiaroa's most pristine motu and coral reefs, it may take years before signs of seabird population recovery and nutrient rebounds are noticeable (Graham et al. 2024). Recovery timelines for seabirds and plants vary by species, with full restoration of the interconnected land–sea system likely taking decades. Thus, long-term monitoring post-restoration, particularly in shallow, structurally complex nearshore waters adjacent to seabird-rich motu in the north and southeast, will be essential.

Conclusion

Our research contributes to the growing field of seascape ecology, which examines the relationships between spatiotemporal patterns and biophysical and ecological processes (Pittman 2018, Wedding et al. 2025). Seascape ecology has been applied to study species habitat use and movement (Moustaka et al. 2024, Stuart et al. 2024), evaluate MPA design (Olds et al. 2016, Carr et al. 2017), and assess ecosystem services post-restoration (Lester et al. 2020, Rummell et al. 2023). However, its application to nutrient fluxes in complex seascapes is rare, despite their importance for conservation and restoration. This study applies seascape ecology to reveal nutrient dynamics in Tetiaroa and introduces a novel method for modelling nutrient enrichment across marine settings, including atolls. While the effects of the biogeophysical predictors explored may be context-dependent, combining stable isotope and geospatial analytics through a seascape lens is transferable, highlighting the multi-scale drivers of nutrient enrichment that affect ecosystem resilience and inform restoration strategies.

Acknowledgements – We thank the Tetiaroa Society for permitting us to conduct this research in their atoll, with special thanks to Vairupe Huioutu Pater, Temakehu Murphy, Lusiano Kolokilagi, and Tuterai Apuarii for their generous support with logistics and transportation. We also thank Yadvinder Malhi, Eleanor Thomson, Ines Lange, Chris Perry, Ruth Dunn, Pirta Palola, and Melissa Ward for their constructive feedback.

Funding – Funding for C.E.S., C.E.B., N.A.J.G., and L.M.W. was provided by the Bertarelli Foundation as part of the Bertarelli Program in Marine Science (2021-819047). C.E.S. was further supported by the Natural Environment Research Council (NERC) through the NERC-Oxford Doctoral Training Partnership in Environmental Research (NE/S007474/1) and the National Environmental Isotope Facility Studentship Support Grant (2718.0823). H.E.E. was supported by the National Science Foundation (NSF) through a Postdoctoral Research Fellowship in Biology (PRFB 2006244). J.L.D. and S.D. were supported by the Agence Nationale de la Recherche (ANR InvEcoF) and the Fondation Fyssen.

Permits – Algae were collected and exported under permit no. ENV23508883AM-1, issued by the Gouvernement de la Polynésie française Direction de l'Environnement.

Author contributions

Courtney E. Stuart: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Funding acquisition (supporting); Investigation (lead); Methodology (lead); Resources (supporting); Validation (lead); Visualization (lead); Writing – original draft (lead). **Simon J. Pittman**: Conceptualization (supporting); Methodology (supporting); Project administration (supporting); Supervision (supporting); Writing – review and editing (equal). **Kostantinos A. Stamoulis**: Data curation (supporting); Investigation (equal); Methodology (supporting); Writing – review and editing (equal). **Cassandra E. Benkwitt**: Data curation (supporting); Investigation (equal); Methodology (supporting); Resources (supporting); Writing – review and editing (equal). **Hannah E. Epstein**: Data curation (supporting); Investigation (equal); Methodology (supporting); Resources (supporting); Writing – review and editing (equal). **Nicholas A. J. Graham**: Funding acquisition (lead); Project administration (supporting); Writing – review and editing (equal). **Andrew C. Smith**: Formal analysis (supporting); Funding acquisition (supporting); Investigation (supporting); Resources (supporting); Writing – review and editing (equal). **Jack H. Lacey**: Formal analysis (supporting); Investigation (supporting); Resources (supporting); Writing – review and editing (equal). **Kalia S. I. Bistolas**: Data curation (supporting); Investigation (supporting); Methodology (supporting); Resources (supporting); Writing – review and editing (equal). **Jayna L. DeVore**: Data curation (supporting); Investigation (equal); Methodology (supporting); Resources (supporting); Writing – review and editing (equal). **Simon Ducatez**: Data curation (supporting); Investigation (equal); Methodology (supporting); Resources (supporting);

Writing – review and editing (equal). **Lisa M. Wedding**: Conceptualization (supporting); Funding acquisition (supporting); Methodology (supporting); Project administration (lead); Supervision (lead); Writing – review and editing (equal).

Transparent peer review

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ecog.07863.

Data availability statement

All data and code supporting the findings in this article are publicly available from the Harvard Dataverse Repository: https://doi.org/10.7910/DVN/5NHHEY (Stuart et al. 2025).

Supporting information

The Supporting information associated with this article is available with the online version.

References

Adam, T. C., Burkepile, D. E., Holbrook, S. J., Carpenter, R. C., Claudet, J., Loiseau, C., Thiault, L., Brooks, A. J., Washburn, L. and Schmitt, R. J. 2021. Landscape-scale patterns of nutrient enrichment in a coral reef ecosystem: implications for coral to algae phase shifts. – Ecol. Appl. 31: e2227.

Appoo, J., Bunbury, N., Letori, J., Hector, A., Gendron, A., Graham, N. A. J., Rocamora, G., Le Corre, M. and Jaquemet, S. 2024. Seabird presence and seasonality influence nutrient dynamics of atoll habitats. – Biotropica 56: e13354.

Atkinson, M. J. 2011. Biogeochemistry of nutrients. – In: Dubinsky, Z. and Stambler, N. (eds), Coral reefs: an ecosystem in transition. Springer, pp. 199–206.

Ban, S. S., Graham, N. A. J. and Connolly, S. R. 2014. Evidence for multiple stressor interactions and effects on coral reefs. – Global Change Biol. 20: 681–697.

Beale, C. M., Lennon, J. J., Yearsley, J. M., Brewer, M. J. and Elston, D. A. 2010. Regression analysis of spatial data. – Ecol. Lett. 13: 246–264.

Benkwitt, C. E., Wilson, S. K. and Graham, N. A. J. 2019. Seabird nutrient subsidies alter patterns of algal abundance and fish biomass on coral reefs following a bleaching event. – Global Change Biol. 25: 2619–2632.

Benkwitt, C. E., Gunn, R. L., Le Corre, M., Carr, P. and Graham, N. A. J. 2021a. Rat eradication restores nutrient subsidies from seabirds across terrestrial and marine ecosystems. – Curr. Biol. 31: 2704–2711.e4.

Benkwitt, C. E., Taylor, B. M., Meekan, M. G. and Graham, N. A. J. 2021b. Natural nutrient subsidies alter demographic rates in a functionally important coral-reef fish. – Sci. Rep. 11: 12575.

Bergman, J. L., Dang, B. N., Tabatabaee, M. M., McGowan, M. M., Fong, C. R., Bittick, S. J. and Fong, P. 2016. Nutrients induce and herbivores maintain thallus toughness, a structural anti-herbivory defense in *Turbinaria ornata*. – Mar. Ecol. Prog. Ser. 559: 35–43.

BirdLife International. 2024. Important bird area factsheet: Tetiaroa, Moorea et Tahiti Marine. – https://datazone.birdlife.org/site/factsheet/tetiaroa-moorea-et-tahiti-marine.

Bittick, S. J., Bilotti, N. D., Peterson, H. A. and Stewart, H. L. 2010. *Turbinaria ornata* as an herbivory refuge for associate algae. – Mar. Biol. 157: 317–323.

Bittick, S. J., Clausing, R. J., Fong, C. R. and Fong, P. 2016. Bolstered physical defences under nutrient-enriched conditions may facilitate a secondary foundational algal species in the South Pacific. – J. Ecol. 104: 646–653.

Borland, H. P., Gilby, B. L., Henderson, C. J., Leon, J. X., Schlacher, T. A., Connolly, R. M., Pittman, S. J., Sheaves, M. and Olds, A. D. 2021. The influence of seafloor terrain on fish and fisheries: a global synthesis. – Fish Fish. 22: 707–734.

Browning, T. J., Al-Hashem, A. A., Achterberg, E. P., Carvalho, P. C., Catry, P., Matthiopoulos, J., Miller, J. A. and Wakefield, E. D. 2023. The role of seabird guano in maintaining North Atlantic summertime productivity. – Sci. Total Environ. 897: 165309.

Bulleri, F., Thiault, L., Mills, S. C., Nugues, M. M., Eckert, E. M., Corno, G. and Claudet, J. 2018. Erect macroalgae influence epilithic bacterial assemblages and reduce coral recruitment. – Mar. Ecol. Prog. Ser. 597: 65–77.

Burkepile, D. E., Shantz, A. A., Adam, T. C., Munsterman, K. S., Speare, K. E., Ladd, M. C., Rice, M. M., Ezzat, L., McIlroy, S., Wong, J. C. Y., Baker, D. M., Brooks, A. J., Schmitt, R. J. and Holbrook, S. J. 2020. Nitrogen identity drives differential impacts of nutrients on coral bleaching and mortality. – Ecosystems 23: 798–811.

Carr, M. H., Robinson, S. P., Wahle, C., Davis, G., Kroll, S., Murray, S., Schumacker, E. J. and Williams, M. 2017. The central importance of ecological spatial connectivity to effective coastal marine protected areas and to meeting the challenges of climate change in the marine environment. – Aquat. Conserv. Mar. Freshw. Ecosyst. 27: 6–29.

Carr, P., Trevail, A., Bárrios, S., Clubbe, C., Freeman, R., Koldewey, H. J., Votier, S. C., Wilkinson, T. and Nicoll, M. A. C. 2021. Potential benefits to breeding seabirds of converting abandoned coconut plantations to native habitats after invasive predator eradication. – Restor. Ecol. 29: e13386.

Chadwick, K. D. and Asner, G. P. 2016. Tropical soil nutrient distributions determined by biotic and hillslope processes. – Biogeochemistry 127: 273–289.

Davis, S. E., Lirman, D. and Wozniak, J. R. 2009. Nitrogen and phosphorus exchange among tropical coastal ecosystems. – In: Nagelkerken, I. (ed.), Ecological connectivity among tropical coastal ecosystems. – Springer, pp. 9–43.

del Hoyo, J., Elliott, A. and Sargatal, J. 1992. Handbook of the birds of the world, vol. 1. – Lynx Edicions.

del Hoyo, J., Elliott, A. and Sargatal, J. 1996. Handbook of the birds of the world, vol. 3. – Lynx Edicions.

Delevaux, J. M. S. et al. 2018. A linked land–sea modeling framework to inform ridge-to-reef management in high oceanic islands. – PLoS One 13: e0193230.

Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., García Márquez, J. R., Gruber, B., Lafourcade, B., Leitão, P. J., Münkemüller, T., McClean, C., Osborne, P. E., Reineking, B., Schröder, B., Skidmore, A. K., Zurell, D. and Lautenbach, S. 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. – Ecography 36: 27–46.

Evans, D. A., Williard, K. W. and Schoonover, J. E. 2016. Comparison of terrain indices and landform classification procedures in low-relief agricultural fields. – J. Geospat. Appl. Nat. Resour. 1: 1.

Florinsky, I. V. 2017. An illustrated introduction to general geomorphometry. – Prog. Phys. Geogr. 41: 723–752.

Fong, P., Smith, T. B. and Muthukrishnan, R. 2017. Algal dynamics: alternate stable states of reefs in the Eastern Tropical Pacific. – In: Glynn, P. W. (eds), Coral reefs of the Eastern Tropical Pacific: persistence and loss in a dynamic environment. Coral reefs of the world. – Springer, pp. 339–367.

Fukami, T., Wardle, D. A., Bellingham, P. J., Mulder, C. P. H., Towns, D. R., Yeates, G. W., Bonner, K. I., Durrett, M. S., Grant-Hoffman, M. N. and Williamson, W. M. 2006. Above- and below-ground impacts of introduced predators in seabird-dominated island ecosystems. – Ecol. Lett. 9: 1299–1307.

Graham, N. A., Bellwood, D. R., Cinner, J. E., Hughes, T. P., Norström, A. V. and Nyström, M. 2013. Managing resilience to reverse phase shifts in coral reefs. – Front. Ecol. Environ. 11: 541–548.

Graham, N. A. J., Jennings, S., MacNeil, M. A., Mouillot, D. and Wilson, S. K. 2015. Predicting climate-driven regime shifts versus rebound potential in coral reefs. – Nature 518: 94–97.

Graham, N. A. J., Wilson, S. K., Carr, P., Hoey, A. S., Jennings, S. and MacNeil, M. A. 2018. Seabirds enhance coral reef productivity and functioning in the absence of invasive rats. – Nature 559: 250–253.

Graham, N. A. J., Benkwitt, C. E. and Jones, H. P. 2024. Species eradication for ecosystem restoration. – Curr. Biol. 34: R407–R412.

Gräler, B., Pebesma, E. and Heuvelink, G. 2016. Spatio-temporal interpolation using gstat. – R J. 8: 204–218.

Grant, M. L., Bond, A. L. and Lavers, J. L. 2022. The influence of seabirds on their breeding, roosting and nesting grounds: a systematic review and meta-analysis. – J. Anim. Ecol. 91: 1266–1289.

Guinan, J., Grehan, A. J., Dolan, M. F. J. and Brown, C. 2009a. Quantifying relationships between video observations of cold-water coral cover and seafloor features in Rockall Trough, west of Ireland. – Mar. Ecol. Prog. Ser. 375: 125–138.

Guinan, J., Brown, C., Dolan, M. F. J. and Grehan, A. J. 2009b. Ecological niche modelling of the distribution of cold-water coral habitat using underwater remote sensing data. – Ecol. Inform. 4: 83–92.

Guisan, A., Edwards, T. C. and Hastie, T. J. 2002. Generalized linear and generalized additive models in studies of species distributions: setting the scene. – Ecol. Modell. 157: 89–100.

Hastie, T. J. and Tibshirani, R. J. 1990. Generalized additive models. – Chapman and Hall.

Hearn, C., Atkinson, M. and Falter, J. 2001. A physical derivation of nutrient-uptake rates in coral reefs: effects of roughness and waves. – Coral Reefs 20: 347–356.

Hench, J. L., Leichter, J. J. and Monismith, S. G. 2008. Episodic circulation and exchange in a wave-driven coral reef and lagoon system. – Limnol. Oceanogr. 53: 2681–2694.

Hijmans, R. J. 2023a. terra: spatial data analysis. – https://CRAN.R-project.org/package=terra.

Hijmans, R. J. 2023b. raster: geographic data analysis and modeling. – https://CRAN.R-project.org/package=raster.

Honig, S. E. and Mahoney, B. 2016. Evidence of seabird guano enrichment on a coral reef in Oahu, Hawaii. – Mar. Biol. 163: 22.

Howarth, R. W. 1988. Nutrient limitation of net primary production in marine ecosystems. – Annu. Rev. Ecol. Syst. 19: 89–110.

Hughes, T. P. 1994. Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. – Science 265: 1547–1551.

Ilich, A. R., Misiuk, B., Lecours, V. and Murawski, S. A. 2023. MultiscaleDTM: an open-source R package for multiscale geomorphometric analysis. – Trans. GIS 27: 1164–1204.

Jeanson, M., Anthony, E. J., Etienne, S. and Dolique, F. 2014. Morphodynamic characterization of beaches on a Pacific atoll island: Tetiaroa, French Polynesia. – J. Coast. Res. 70: 176–181.

Kolb, G. S., Ekholm, J. and Hambäck, P. A. 2010. Effects of seabird nesting colonies on algae and aquatic invertebrates in coastal waters. – Mar. Ecol. Prog. Ser. 417: 287–300.

Legendre, P. 1993. Spatial autocorrelation: trouble or new paradigm? – Ecology 74: 1659–1673.

Lester, S. E., Dubel, A. K., Hernán, G., McHenry, J. and Rassweiler, A. 2020. Spatial planning principles for marine ecosystem restoration. – Front. Mar. Sci. 7: 328.

Lorrain, A., Houlbrèque, F., Benzoni, F., Barjon, L., Tremblay-Boyer, L., Menkes, C., Gillikin, D. P., Payri, C., Jourdan, H., Boussarie, G., Verheyden, A. and Vidal, E. 2017. Seabirds supply nitrogen to reef-building corals on remote Pacific islets. – Sci. Rep. 7: 3721.

McCauley, D. J., DeSalles, P. A., Young, H. S., Dunbar, R. B., Dirzo, R., Mills, M. M. and Micheli, F. 2012. From wing to wing: the persistence of long ecological interaction chains in less-disturbed ecosystems. – Sci. Rep. 2: 409.

McManus, J. W. and Polsenberg, J. F. 2004. Coral–algal phase shifts on coral reefs: ecological and environmental aspects. – Prog. Oceanogr. 60: 263–279.

Moore, I. D., Grayson, R. B. and Ladson, A. R. 1991. Digital terrain modelling: a review of hydrological, geomorphological, and biological applications. – Hydrol. Processes 5: 3–30.

Moreno-Fernández, D., Augustin, N. H., Montes, F., Cañellas, I. and Sánchez-González, M. 2018. Modeling sapling distribution over time using a functional predictor in a generalized additive model. – Ann. Forest Sci. 75: 9.

Moustaka, M., Evans, R. D., Kendrick, G. A., Hyndes, G. A., Cuttler, M. V. W., Bassett, T. J., O'Leary, M. J. and Wilson, S. K. 2024. Local habitat composition and complexity outweigh seascape effects on fish distributions across a tropical seascape. – Landscape Ecol. 39: 28.

Naimi, B., Hamm, N. A. S., Groen, T. A., Skidmore, A. K. and Toxopeus, A. G. 2014. Where is positional uncertainty a problem for species distribution modelling. – Ecography 37: 191–203.

Olds, A. D., Connolly, R. M., Pitt, K. A., Pittman, S. J., Maxwell, P. S., Huijbers, C. M., Moore, B. R., Albert, S., Rissik, D., Babcock, R. C. and Schlacher, T. A. 2016. Quantifying the conservation value of seascape connectivity: a global synthesis. – Global Ecol. Biogeogr. 25: 3–15.

Pacific Beachcomber Group. 2024. Corporate social responsibility report. – www.calameo.com/read/00450054530b2c12fdcc5, pp. 1–40.

Palola, P., Pittman, S. J., Collin, A., Benkwitt, C. E., Thomson, E., Malhi, Y., Graham, N. A. J. and Wedding, L. M. 2025. Nutrientscape ecology: a whole-system framework to support the understanding and management of coastal nutrient connectivity. – Landscape Ecol. 40: 1–30.

Pearce, J. L., Beringer, J., Nicholls, N., Hyndman, R. J. and Tapper, N. J. 2011. Quantifying the influence of local meteorology on air quality using generalized additive models. – Atmos. Environ. 45: 1328–1336.

Pebesma, E. J. 2004. Multivariable geostatistics in S: the gstat package. – Comput. Geosci. 30: 683–691.

Pebesma, E. J. and Bivand, R. S. 2023. Spatial data science with applications in R. – Chapman and Hall.

Pedersen, M. and Borum, J. 1996. Nutrient control of algal growth in estuarine waters. Nutrient limitation and the importance of nitrogen requirements and nitrogen storage among phytoplankton and species of macroalgae. – Mar. Ecol. Prog. Ser. 142: 261–272.

Peterson, E. A., Stuart, C. E., Pittman, S. J., Benkwitt, C. E., Graham, N. A. J., Malhi, Y., Salmon, T., Stoll, B., Purkis, S. J. and Wedding, L. M. 2024. Graph-theoretic modeling reveals connectivity hotspots for herbivorous reef fishes in a restored tropical island system. – Landscape Ecol. 39: 145.

Pittman, S. 2018. Seascape ecology. – Wiley Blackwell.

Pittman, S. J. et al. 2021. Seascape ecology: identifying research priorities for an emerging ocean sustainability science. – Mar. Ecol. Prog. Ser. 663: 1–29.

Polis, G. A., Anderson, W. B. and Holt, R. D. 1997. Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. – Annu. Rev. Ecol. Syst. 28: 289–316.

Pratchett, M. S., Munday, P. L., Graham, N. A. J., Kronen, M., Pinca, S., Friedman, K., Brewer, T. D., Bell, J. D., Sibiti, S. M. and Webb, A. 2011. Vulnerability of coastal fisheries in the tropical Pacific to climate change. – Fish. Sci. 6: 167–185.

Purkis, S. J., Gleason, A. C. R., Purkis, C. R., Dempsey, A. C., Renaud, P. G., Faisal, M., Saul, S. and Kerr, J. M. 2019. High-resolution habitat and bathymetry maps for 65,000 sq. km of Earth's remotest coral reefs. – Coral Reefs 38: 467–488.

Raven, J. A., Wollenweber, B. and Handley, L. L. 1992. A comparison of ammonium and nitrate as nitrogen sources for photolithotrophs. – New Phytol. 121: 19–32.

Ross, N. 2022. fasterize: fast polygon to raster conversion. – https://CRAN.R-project.org/package=fasterize.

Rummell, A. J., Borland, H. P., Hazell, J. J., Mosman, J. D., Leon, J. X., Henderson, C. J., Gilby, B. L. and Olds, A. D. 2023. Connectivity shapes delivery of multiple ecological benefits from restoration. – Biol. Conserv. 288: 110358.

Russell, J. C. and Faulquier, L. 2009. Tetiaroa rat and seabird survey (7th–13th July 2009). – Univ. of California, Berkeley, and Société d'Ornithologie de Polynésie MANU.

Russell, J. C., Faulquier, L. and Tonione, M. A. 2011. Rat invasion of Tetiaroa atoll, French Polynesia. – In: Vietch, C. R., Clout, M. N. and Towns, D. R. (eds), Island invasives: eradication and management. – International Union for Conservation Nature (IUCN), pp. 118–123.

Rutledge, J. M. and Chow-Fraser, P. 2019. Landscape characteristics driving spatial variation in total phosphorus and sediment loading from sub-watersheds of the Nottawasaga River, Ontario. – J. Environ. Manage. 234: 357–366.

Salazar, J. E., Benavides, I. F., Portilla Cabrera, C. V., Guzmán, A. I. and Selvaraj, J. J. 2021. Generalized additive models with delayed effects and spatial autocorrelation patterns to improve the spatiotemporal prediction of the skipjack (*Katsuwonus pelamis*) distribution in the Colombian Pacific Ocean. – Reg. Stud. Mar. Sci. 45: 101829.

Savage, C. 2019. Seabird nutrients are assimilated by corals and enhance coral growth rates. – Sci. Rep. 9: 4284.

Schmitt, R. J., Holbrook, S. J., Davis, S. L., Brooks, A. J. and Adam, T. C. 2019. Experimental support for alternative attractors on coral reefs. – Proc. Natl Acad. Sci. USA 116: 4372–4381.

Shantz, A. A. and Burkepile, D. E. 2014. Context-dependent effects of nutrient loading on the coral–algal mutualism. – Ecology 95: 1995–2005.

Sharma, R. H. 2013. Evaluating the effect of slope curvature on slope stability by a numerical analysis. – Aust. J. Earth Sci. 60: 283–290.

Signa, G., Mazzola, A., Tramati, C. D. and Vizzini, S. 2013. Gull-derived trace elements trigger small-scale contamination in a remote Mediterranean nature reserve. – Mar. Pollut. Bull. 74: 237–243.

Simpson, G. L. 2024. gratia: graceful ggplot-based graphics and other functions for GAMs fitted using mgcv. – https://CRAN.R-project.org/package=gratia.

Souter, D., Planes, S., Wicquart, J., Logan, M., Obura, D. and Staub, F. (eds) 2021. Status of coral reefs of the world: 2020 report. – Global Coral Reef Monitoring Network and International Coral Reef Initiative.

Staunton-Smith, J. and Johnson, C. R. 1995. Nutrient inputs from seabirds and humans on a populated coral cay. – Mar. Ecol. Prog. Ser. 124: 189–200.

Steibl, S., Kench, P. S., Young, H. S., Wegmann, A. S., Holmes, N. D., Bunbury, N., Teavai-Murphy, T. H., Davies, N., Murphy, F. and Russell, J. C. 2024. Rethinking atoll futures: local resilience to global challenges. – Trends Ecol. Evol. 39: 258–266.

Stiger, V. and Payri, C. E. 1999a. Spatial and temporal patterns of settlement of the brown macroalgae *Turbinaria ornata* and *Sargassum mangarevense* in a coral reef on Tahiti. – Mar. Ecol. Prog. Ser. 191: 91–100.

Stiger, V. and Payri, C. E. 1999b. Spatial and seasonal variations in the biological characteristics of two invasive brown algae, *Turbinaria ornata* (Turner) J. Agardh and *Sargassum mangarevense* (Grunow) Setchell (Sargassaceae, Fucales) spreading on the reefs of Tahiti (French Polynesia). – Bot. Marina 42: 295–306.

Stiger, V., Deslandes, E. and Payri, C. E. 2004. Phenolic contents of two brown algae, *Turbinaria ornata* and *Sargassum mangarevense* on Tahiti (French Polynesia): interspecific, ontogenic and spatio-temporal variations – Bot. Marina 47: 402–409.

Stoner, A. W., Manderson, J. P. and Pessutti, J. P. 2001. Spatially explicit analysis of estuarine habitat for juvenile winter flounder: combining generalized additive models and geographic information systems. – Mar. Ecol. Prog. Ser. 213: 253–271.

Stuart, C. E., Wedding, L. M., Pittman, S. J., Serafy, J. E., Moura, A., Bruckner, A. W. and Green, S. J. 2024. Seascape connectivity modeling predicts hotspots of fish-derived nutrient provisioning to restored coral reefs. – Mar. Ecol. Prog. Ser. 731: 179–196.

Stuart, C. E., Pittman, S. J., Stamoulis, K. A., Benkwitt, C. E., Epstein, H. E., Graham, N. A. J., Smith, A. C., Lacey, J. H., Bistolas, K. S. I., DeVore, J. L., Ducatez, S. and Wedding, L. M. 2025. Data from: Seascape configuration determines spatial patterns of seabird-vectored nutrient enrichment to coral reefs. – Harvard Dataverse Repository, https://doi.org/10.7910/DVN/5NHHEY.

Szpak, P., Longstaffe, F. J., Millaire, J.-F. and White, C. D. 2012. Stable isotope biogeochemistry of seabird guano fertilization: results from growth chamber studies with maize (*Zea mays*). – PLoS One 7: e33741.

Tetiaroa Society. 2016. Tetiaroa conservation and sustainable use plan. – https://www.tetiaroasociety.org/sites/default/files/research-docs/Tetiaroa-CASUP.pdf.

Tetiaroa Society. 2019. Tetiaroa society field program annual report 2019. – https://www.tetiaroasociety.org/sites/default/files/research-docs/TSFP-Annual-Report-2019.pdf.

Tetiaroa Society. 2023. Tetiaroa Atoll Restoration Project (TARP). – https://www.tetiaroasociety.org/sites/default/files/research-docs/Tetiaroa%20Atoll%20Restoration%20Program.pdf.

Tetiaroa Society. 2024. Birds of Tetiaroa. – https://www.tetiaroasociety.org/island/birds.

Ural, S., Gruen, A. and Kocaman, S. 2019. Point clouds over Tetiaroa – 3D modeling of a tropical island by topo-bathymetric Lidar. – Proc. Asian conference of remote sensing, Daejeon, Korea, pp. 13–19.

Varanka, S., Hjort, J. and Luoto, M. 2015. Geomorphological factors predict water quality in boreal rivers. – Earth Surf. Process. Landf. 40: 1989–1999.

Wang, L., Shang, S., Liu, W., She, D., Hu, W. and Liu, Y. 2023. Hydrodynamic controls on nitrogen distribution and removal in aquatic ecosystems. – Water Res. 242: 120257.

Wedding, L. M., Lepczyk, C. A., Pittman, S. J., Friedlander, A. M. and Jorgensen, S. 2011. Quantifying seascape structure: extending terrestrial spatial pattern metrics to the marine realm. – Mar. Ecol. Prog. Ser. 427: 219–232.

Wedding, L. M., Green, S. J., Reiter, S., Arrigo, K. R., Hazen, L., Ruckelshaus, M., van der Grient, J. M. A., Bailey, R. M., Cameron, M. A., Leape, J., Levi, M., Merkl, A., Mills, M. M., Monismith, S., Ouellette, N. T., van Dijken, G. and Micheli, F. 2022. Linking multiple stressor science to policy opportunities through network modeling. – Mar. Policy 146: 105307.

Wedding, L. M., Stuart, C. E., Govers, L. L., Lilley, R. J., Olds, A., Preston, J., Tavasi, L. E. and Pittman, S. J. 2025. Five ways seascape ecology can help to achieve marine restoration goals. – Landsc. Ecol. 40: 115.

Welch, B. L., Cole, D. N., McArthur, E. D., Booth, G. D., Geier-Hayes, K. and Sloan, J. P. 1994. Identifying proxy sets in multiple linear regression: an aid to better coefficient interpretation. – USDA Forest Service, Intermountain Research Station, Gen. Tech. Rep. INT-GTR-470.

Wiedenmann, J., D'Angelo, C., Smith, E. G., Hunt, A. N., Legiret, F. E., Postle, A. D. and Achterberg, E. P. 2013. Nutrient enrichment can increase the susceptibility of reef corals to bleaching. – Nat. Clim. Change 3: 160–164.

Wiedenmann, J., D'Angelo, C., Mardones, M. L., Moore, S., Benkwitt, C. E., Graham, N. A. J., Hambach, B., Wilson, P. A., Vanstone, J., Eyal, G. and Ben-Zvi, O. 2023. Reef-building corals farm and feed on their photosynthetic symbionts. – Nature 620: 1018–1024.

Williams, I. D., Kindinger, T. L., Couch, C. S., Walsh, W. J., Minton, D. and Oliver, T. A. 2019. Can herbivore management increase the persistence of Indo-Pacific coral reefs? – Front. Mar. Sci. 6: 557.

Wilman, H., Belmaker, J., Simpson, J., de la Rosa, C., Rivadeneira, M. M. and Jetz, W. 2014. EltonTraits 1.0: species-level foraging attributes of the world's birds and mammals. – Ecology 95: 2027–2027.

Wood, S. N. 2004. Stable and efficient multiple smoothing parameter estimation for generalized additive models. – J. Am. Stat. Assoc. 99: 673–686.

Wood, S. N. 2017. Generalized additive models: an introduction with R, 2nd edn. – Chapman and Hall/CRC.

Young, H. S., McCauley, D. J., Dunbar, R. B. and Dirzo, R. 2010. Plants cause ecosystem nutrient depletion via the interruption of bird-derived spatial subsidies. – Proc. Natl. Acad. Sci. USA 107: 2072–2077.

Zevenbergen, L. W. and Thorne, C. R. 1987. Quantitative analysis of land surface topography. – Earth Surf. Process. Landf. 12: 47–56.