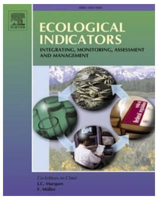
Ecological Indicators 170 (2025) 113042

Contents lists available at ScienceDirect

Ecological Indicators

journal homepage: www.elsevier.com/locate/ecolind



Original Articles

Re-connecting ecosystems: Integrating coral reefs into monitoring of island restoration

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ARTICLE INFO

Keywords:
Island restoration
Rat eradication
Coral reefs
Cross-ecosystem response
Seabird nutrients

ABSTRACT

Ecosystems are intrinsically linked, such that management actions in one ecosystem can influence adjacent ecosystems. However, adequate data, and even protocols, for monitoring cross-ecosystem responses to conservation initiatives are lacking. Here, we evaluate potential indicators, operating on different spatial, temporal, and biological scales, for measuring the effects of island-based restoration on coral reef ecosystems. We show that island restoration status had consistent effects on populations of tropical seabirds across spatial scales from 100 m to entire islands. Seabirds, in turn, provided nutrient subsidies that were incorporated by marine algae and coral-reef fishes, with the most pronounced effects closer to shore, at leeward sites, and at low trophic levels. Microbes and macroalgae exhibited assemblage-level responses to seabird-derived nutrients entering the marine environment, but there were few differences in coral reef benthic and fish assemblages. By identifying and focusing on specific indicators such as macroalgal nutrients, managers can better monitor cross-ecosystem responses to conservation interventions with limited resources.

1. Introduction

Marine and terrestrial ecosystems have been largely siloed in both ecological literature and current management practices, often treated as if they are not connected. However, ecosystem boundaries are porous, with marine and terrestrial ecosystems connected by the movement of material and organisms to form 'meta-ecosystems' (Polis et al. 1997; Loreau et al. 2003). As such, threats, or conversely conservation actions, in one system can have substantial cross-realm impacts (Carlson et al. 2021). Therefore, conservation planning that jumps this gap to explicitly incorporate cross-ecosystem connections should be most effective (Álvarez-Romero et al. 2011; Schiesari et al. 2019; Tulloch et al. 2021).

Although conservation interventions that re-connect ecosystems have the potential to provide wide-ranging benefits, we lack monitoring data and protocols to evaluate the efficacy of such efforts. Restoration in particular is increasingly prioritized as a necessary conservation intervention (Perring et al. 2015; United Nations Environment Agency 2019), and there is growing recognition that restoration activities should consider links among habitats and ecosystems (Hjältén et al. 2016; Bullock et al. 2022; Vozzo et al. 2023). Despite considerable progress in

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https://doi.org/10.1016/j.ecolind.2024.113042
Received 4 October 2024; Received in revised form 9 December 2024; Accepted 24 December 2024

developing standardized indicators for restoration outcomes, and the inclusion of external exchanges with other ecosystems as a key attribute of ecological recovery, monitoring the impacts of these connections on recipient ecosystems is overlooked (Gann et al. 2019). Comprehensive monitoring of restoration outcomes is difficult even within ecosystems (Wortley et al. 2013; Prach et al. 2019), and cross-ecosystem monitoring is more challenging – recovery times are longer, effects are more diffuse, and multi-disciplinary collaboration is required to quantify any impacts. Thus, there is an urgent need to develop efficient ways to monitor cross-ecosystem responses to restoration activities.

Islands are an ideal focus for restoration actions, as their smaller size and relative isolation mean that terrestrial biodiversity is disproportionately unique and threatened, but also that island restoration is often highly successful (Kier et al. 2009; Tershy et al. 2015; Jones et al. 2016; Wood et al. 2017; Russell & Kueffer 2019). For example, eradicating invasive species is one component of island restoration programs that provides extensive benefits for native species and ecosystems (Jones et al. 2016; Graham et al. 2024). As a result, invasive vertebrate eradications have now been attempted on nearly 1000 islands worldwide (Spatz et al. 2022). Moreover, island restoration, including eradicating invasive species, is now also recognized for its potential to provide cross-ecosystem benefits to nearshore marine systems (Sandin et al. 2022; Dunn et al. 2024; Graham et al. 2024). However, a limited understanding of land-sea nutrient pathways in island systems may hamper the identification of critical connections and diminish efforts to restore key ecosystem functions (Delevaux et al. 2018b).

Tropical coral reefs, in particular, are situated to gain much-needed benefits from island restoration initiatives, as they are highly vulnerable and rely on cross-ecosystem linkages to support high biodiversity in nutrient-poor tropical waters. One way that island restoration can benefit coral reefs is by promoting recovery of tropical seabird populations. Tropical seabirds are threatened by the presence of invasive rats and non-native coconut palms on islands via direct predation and replacement of preferred habitat, respectively (Jones et al. 2008; Young et al. 2010; Benkwitt et al. 2022). Where abundant, seabirds connect multiple ecosystems as they deliver essential nutrients from their offshore pelagic feeding grounds to island and coastal systems when they return to breed or roost (Mulder et al. 2011). This nutrient pump is particularly important on tropical atolls, where seabirds deposit an average of 65,000 kg of nitrogen per atoll per year across the Indo-Pacific (Steibl et al. 2024). On nearby coral reefs, seabird-derived nutrients are assimilated by various organisms (Graham et al. 2018), leading to faster growth rates of coral and fish (Graham et al. 2018; Savage 2019; Benkwitt et al. 2021b; Benkwitt et al. 2023), greater fish biomass, productivity, and ecosystem functioning (Graham et al. 2018; Benkwitt et al. 2020), and more resilient reefs (Benkwitt et al. 2023). However, these benefits have primarily been documented by comparing coral reefs near rat-free versus rat-infested islands, with only one study additionally examining these dynamics on rat-eradicated islands (Benkwitt et al. 2021a). Moreover, there is no information on how island restoration affects coral reefs in an integrated way across multiple responses and levels of biological organization.

Here, we integrate multitrophic terrestrial and marine data at a single time point to evaluate potential indicators of effective island restoration on coral reef ecosystems. Using a space-for-time substitution, we first determine whether differences in island restoration status correspond to differences in the density and biomass of breeding and roosting seabirds across multiple spatial scales. We then determine whether seabird-derived nutrients enter coral-reef ecosystems, how far offshore they persist, and which seabird metrics best predict these cross-ecosystem nutrient flows. Finally, we test whether seabird-derived nutrients influence microbial, macroalgal, and fish assemblages, as well as benthic composition. Combined, these findings can be used to focus future coral reef monitoring efforts on metrics that best predict cross-ecosystem responses to land-based restoration.

2. Methods

2.1. Study sites

This study was designed to capitalize on the unique ecosystems of Tetiaroa, an atoll consisting of 12 *motu* (small islets) in the tropical South Pacific Ocean (Fig. 1). We conducted a comparative study across three motu to emulate different stages of island management: 1) Rimatu'u – Polynesian rats (*Rattus exulans*) are still present and planted coconut palms are abundant (78 % cover along the coastal margin adjacent to marine sampling sites) to represent pre-recovery and pre-restoration dynamics ("unrestored"), 2) Reiono – Polynesian rats and coconut palms were both introduced, but rats were recently eradicated (2018) and there are few remaining palms (6 % cover along the coastal margin adjacent to marine sampling sites) as they have been replaced by native *Pisonia*, to represent a restoration site and show short-term recovery dynamics ("recovering"), and 3) 'Ă'ie – historically rat-free and palm-free as a proxy for a restoration target and long-term recovery dynamics ("reference") (Russell et al. 2011) (Guillaume Molle, personal communication). Minimal contemporary human impacts on Tetiaroa, aside from the historical introductions of rats and coconut palms, allow us to examine the impacts of island restoration initiatives without the confounding effects of other local disturbances.

On each motu, we sampled both leeward and windward sides for a total of six sites. We targeted leeward and windward sites to account for wind-driven differences in mixing and water flow that may affect dissipation of nutrients (e.g., Steven & Atkinson 2003). At each site, we surveyed seabirds and marine nutrients, as well as microbes, macroalgal, broad benthic, and fish assemblages. All fieldwork occurred from October to November 2021, with the exception of fish nutrient sampling, which occurred from July to December 2021. Importantly, these marine metrics represent different time scales of nutrient response and/or integration, from immediate (i.e., microbes) to long-term (i.e., benthic communities). While Tetiaroa is characterized by consistent south-east trade winds over most of the year, we confirmed similarity among wind regimes and island exposure across affected time scales according to each marine metric (Table S1, Fig. S1). A full description of the methods is provided in the Supplemental Material, with a brief overview below.

2.2. Seabirds

The number of breeding seabirds and total seabirds (breeding + roosting) were counted within 100×5 m transects along the coastal margin of the three motu. From these surveys, we calculated four metrics – breeding seabird density, breeding seabird biomass, total seabird density, and total seabird biomass. To further test which measures are most relevant for understanding marine outcomes, we also aggregated data at four different spatial scales – the 100-m transect immediately adjacent to marine sampling sites ('100 m'), the two 100-m transects closest to marine sampling sites ('200 m'), the entire side of the motu adjacent to marine sampling sites ('side'), and both sides of the motu ('motu').

2.3. Nutrients

To capture the cross-system flow of seabird-provided nutrients, we quantified nitrogen stable isotope values in macroalgae and reef fishes. Seabird guano has high δ^{15}N values relative to other nutrient sources, so enhanced δ^{15}N values are a reliable indicator of seabird-derived nutrients within coral-reef organisms (Lorrain et al. 2017; Graham et al. 2018; Benkwitt et al. 2021a). To explore nutrient loading integrated over timescales of 1–3 months (Donovan et al. 2020), we analyzed the δ^{15}N in macroalgae (*Turbinaria ornata* leaflets) collected at 10-, 20-, 30-, and 40-m from shore along triplicate transects at each site (see Supplemental Methods for details). We also analyzed the δ^{15}N in dorsal

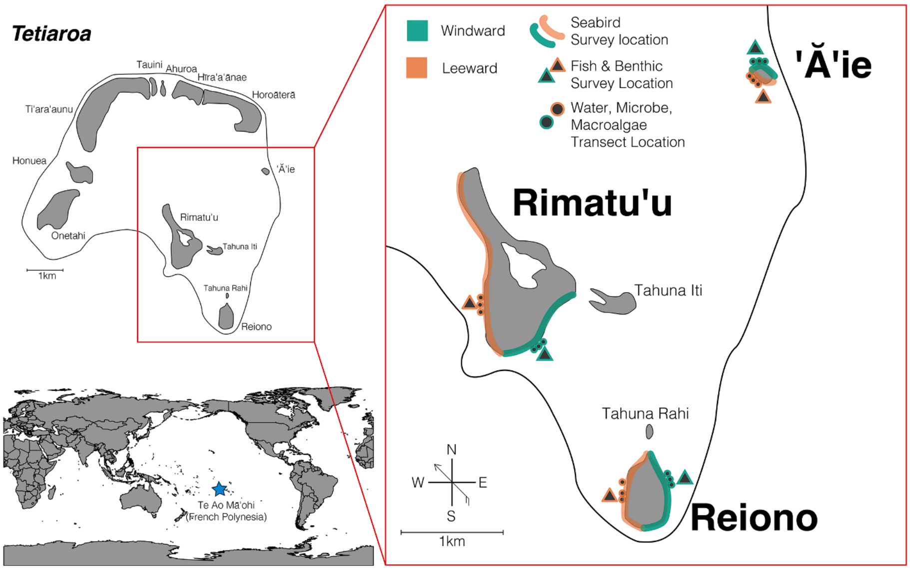

Fig. 1. Locations of field sampling sites on the windward and leeward sides of the three focal motu on Tetiaroa atoll (17°0′S 149°33′W), located 53 km (33 mi) north of Tahiti within the Society Islands of Te Ao Mā'ohi (French Polynesia; blue star). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

muscles of fishes representing several feeding and taxonomic groups collected at one site per motu, and expected to reflect diets over timescales of approximately 3–8 months (Vander Zanden et al. 2015). *T. ornata* leaflets and dorsal white muscle from fish were dried at 60 °C for 48 h, and analyzed for bulk δ^{15}N at Lancaster University using a Vario MICRO cube Elementar Analyzer coupled with an Isoprime 100 Isotope Ratio Mass Spectrometer.

2.4. *Microbes*

Microbial communities of coral and seawater can respond quickly to changes in nutrients (hourly to daily) and can have large implications for organismal and ecosystem health. Seawater and small ($<$2 cm^2) tissue samples of *Porites lobata* (stony coral) were collected using aseptic technique at 10-, 20-, 30- and 40-m from shore on triplicate off-shore transects at each site (Fig. 1), paired with *T. ornata* isotope samples as described above. One liter of collected seawater was run through a 0.22 µm Sterivex^{TM} filter cartridge (Millipore) using a Masterflex peristaltic pump (Cole-Parmer). Coral fragments were rinsed and preserved in RNA/DNA shield (Zymo Research Corporation). Both water filters and coral samples were frozen for storage and transportation. DNA was extracted using the ZymoBiomics MiniPrep DNA extraction kit (Zymo Research Corporation) and the V4 region of the 16S rRNA gene was amplified. Sequencing libraries were prepared using Nextera (Illumina) dual-index barcodes and sequenced by the Center for Quantitative Life Sciences (Oregon State University). All raw sequencing data are available on the NCBI Sequence Read Archive (SRA) under accession PRJNA11146751. Downstream bioinformatic processing and taxonomic identification of amplicon sequence variants (ASVs) were performed using QIIME2 (Boleyn et al. 2019) (https://github.com/hannaheps/TARP_motu_comparison). Further details of collection, sequencing and bioinformatic processing can be found in the Supplementary Methods. Microbial alpha diversity metrics (ASV richness, shannon diversity, evenness and phylogenetic diversity), community composition, and top abundant taxa were tested against nutrient data.

2.5. *Macroalgae, benthos, and fish communities*

We conducted focused surveys of macroalgal communities, as macroalgae are the benthic group expected to respond most strongly and rapidly to changes in nutrient regimes. Nearshore macroalgal percent cover and species-specific community composition were recorded *in situ* along four replicate belt transects (20–25 m × 50 cm). At each site, transects were run parallel to shore at 10- and 40-m from shore, encompassing the nutrient and microbial transect stations. Observations included: brown algae (Phaeophyceae), green algae (Chlorophyta), and red algae (Rhodophyta), along with some benthic, filamentous Cyanobacteria genera that were also included as 'macroalgae'.

Separate to nearshore macroalgal surveys, the total benthic composition and fish communities were surveyed offshore of each site (45–175 m from shore; Fig. 1) along four replicate 30-m transects spaced at least 10-m apart. These surveys were conducted as close to other marine sampling stations as possible but were constrained by shallow water depths. The species and body size (to the nearest cm) of all non-cryptic, diurnal fishes were recorded by one observer, with all mobile species counted within a 5-m wide band during a first pass of the transect, and all site-attached Pomacentridae (damselfishes) counted within a 2-m wide band during a second pass of the same transect. Structural complexity along each transect was visually estimated using a standard scale from 0 (no vertical relief) to 5 (exceptionally complex) (Polunin and Roberts 1993), which has been shown to provide a rapid and reliable assessment of complexity (Wilson et al. 2007). The benthic cover was assessed using two methods – *in situ* point-intercept surveys at 50-cm intervals and video surveys, because both are commonly used in coral reef monitoring programs, yet have clear trade-offs between experience necessary in the field, post-processing time, and ability to revisit data. Because we found high congruence among video and *in situ* estimates of percent cover, with positive correlations among all major groups (see Supplemental Methods), we present video estimates in the main text and *in situ* estimates in the Supplement.

2.6. *Statistical analyses*

We first examined correlations among our different seabird metrics and spatial scales to inform appropriate metrics and scales for seabird censuses. Following our correlation analysis findings (see Supplementary Methods and *Results*) and previous literature (e.g., Graham et al. 2018), we then focused on seabird breeding biomass as our response and tested the effects of island restoration status, exposure, spatial scale, and all two-way interactions using multiple linear regression.

To determine which seabird metric(s) was most associated with the amount of seabird-derived nutrients entering the marine environment, we then tested for correlations between each seabird metric and algal δ^{15}N. Based on these findings (see *Results*), we focused on breeding seabird biomass on the side of the motu adjacent to marine study sites. The effect of seabird biomass on algal δ^{15}N was then tested using a linear mixed effects model ('LMM'), with site as a random effect. We included interactions between seabird biomass*distance from shore and seabird biomass*exposure as fixed effects, as there are *a priori* reasons to expect the effect of seabird biomass on marine nutrients to depend on both distance to shore and wind exposure (e.g., seabird nutrients are likely to be more evident closer to shore, and on protected reefs). To examine whether restoration status also influenced seabird-derived nutrient flows to coral reefs, we ran an LMM with algal δ^{15}N as the response, but replaced seabird biomass with restoration status in the fixed effects.

For the remaining analyses, we focused on algal δ^{15}N as a predictor because we paired sampling locations of algal nutrients with our other responses. Thus, algal δ^{15}N better represents the amount of seabird-derived nutrients in the marine environment in the immediate vicinity of each metric. We had data on fish δ^{15}N at only three sites (one per motu), resulting in complete overlap between site and algal δ^{15}N values. Therefore, we analyzed fish δ^{15}N as a function of offshore algal δ^{15}N, fish species, and their interaction using a multiple linear regression rather than a LMM. To visualize community data (microbial, macroalgal, benthic, and fish), we ran separate non-metric multidimensional scaling (NMDS) using Bray-Curtis dissimilarity and algal δ^{15}N fitted as an environmental overlay. We then used permutational distance-based redundancy analyses ('distlm') to test for an effect of algal δ^{15}N*exposure on overall community structure. Models for fish communities included structural complexity as an additional covariate due to its well-documented effects on coral-reef fishes (e.g., Wilson et al. 2007; Darling et al. 2017). Finally, because distance-based redundancy analyses cannot account for random effects, we ran individual linear mixed-effects models with the same fixed effects but with site as a random effect on key metrics – microbiome: richness, evenness, Shannon index, and Faith's phylogenetic diversity; macroalgae: percent cover, species richness, evenness, and Shannon index; benthic: hard coral percent cover; fish: total biomass, species richness, species evenness, and Shannon diversity.

All statistical analyses were conducted in R (R Core Team 2022), with associated packages detailed in the Supplement.

3. Results

3.1. Island restoration status influences seabird populations, with high correlations across metrics and spatial scales

Seabird metrics (breeding biomass, breeding density, adult biomass, and adult density) were highly correlated both within and across spatial scales (100 m closest to marine site, 200 m closest to marine site, side of motu adjacent to marine site, and both sides of motu) (Spearman correlation coefficients within scales ≥0.83, across scales ≥0.84; Fig. S2). Four species of seabirds were present, with red-footed boobies (*Sula sula*) accounting for 88 % of biomass and 57 % of density, brown noddies (*Anous stolidus*) accounting for 12 % of biomass and 40 % of density, and white terns (*Gygis alba*) and black noddies (*Anous minutus*) accounting for <1 % of biomass and <2 % of density (Fig. S3).

Island restoration status was the primary predictor of seabird breeding biomass, which was estimated to be 278.76, 103.36, and 3.92 kg/ha along the coast of the reference, recovering, and unrestored motu, respectively (Fig. 2, Tables S2 and S3, $p < 0.001$). There was also a marginal interaction between island ecosystem status and exposure ($p = 0.07$), such that breeding biomass was 2.3 times higher on the leeward side of the reference motu, but there was no difference between windward and leeward sides on the other motu (Tables S2 and S3).

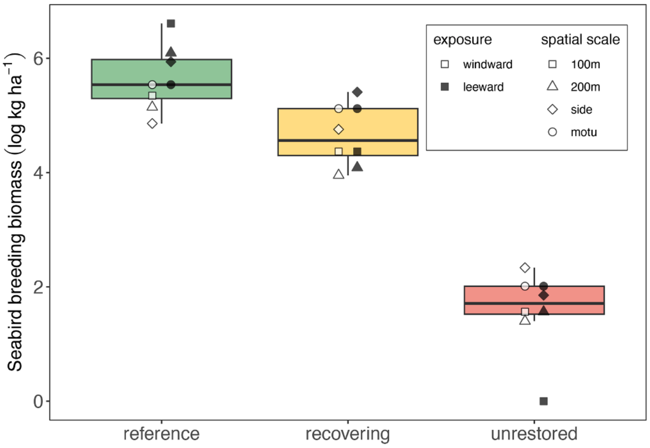

Fig. 2. Effect of island ecosystem restoration status, exposure, and spatial scale on seabird breeding biomass. 'Reference' refers to a historically rat and palm-free motu representing long-term recovery dynamics, 'recovering' refers to a motu with recent restoration interventions representing short-term recovery dynamics, and 'unrestored' refers to a motu with abundant rats and palms representing pre-recovery and pre-restoration dynamics. Points represent raw data, boxplots display median (thick horizontal line), first and third quantiles (box edges), and range of values no further than 1.5*inter-quantile range (whiskers). Note the log scale of the y-axis.

3.2. Seabird nutrients enter nearshore marine habitats and coral-reef food webs

Correlations between algal δ^{15}N values and seabird metrics were overall positive, with breeding seabird biomass by side of motu showing the highest correlation with nearshore algal δ^{15}N (Spearman coefficient = 0.94; Fig. S4). The effect of seabird breeding biomass on algal δ^{15}N depended on both distance to shore and exposure (Fig. 3ab, Table S4, $p < 0.001$). At leeward sites, there was a positive log-linear effect of seabird breeding biomass on algal δ^{15}N at all distances, with the strongest effects occurring closer to shore (Table S5, all $p < 0.001$). With each doubling of seabird biomass, algal δ^{15}N at 10-m from shore increased by 0.95, whereas at 40-m from shore it increased by 0.49. By contrast, at windward sites there was no significant effect of seabird biomass at any distance from shore (Table S5, all $p > 0.55$). Similarly, when using restoration status rather than seabird biomass as a predictor, algal δ^{15} N values decreased with distance to shore around both the reference and recovering motu, but there was no effect of distance to shore around the unrestored motu (Fig. 3c and d, Tables S4 and S6). Moreover, the reference and recovering motu had consistently higher algal δ^{15}N than the unrestored motu at leeward, but not windward, sites (Fig. 3c and d, Tables S4 and S7). These patterns were driven by high algal δ^{15}N values at the exposed side of the unrestored motu (Rimatu'u) across all distances from shore, potentially due to the existence of large seabird populations on nearby rat-free Tahuna Iti (Fig. 1). To investigate this possibility, we incorporated seabird counts from the southwest coast of Tahuna Iti, which begin <50 m from the exposed side of Rimatu'u, into the estimates for this side of the motu. When doing so, both seabird breeding biomass and distance to shore were significant predictors of algal δ^{15}N, but there were no longer any significant interactions (Fig. 3e, Table S4). Algal δ^{15}N increased by 0.42 with each doubling of seabird biomass, but decreased with increasing distance to shore.

Seabird-derived nutrients that entered the marine realm were transferred up the food chain, as indicated by increasing fish δ^{15}N values with increasing offshore algal δ^{15}N (Fig. 4, $F = 21.43$, $p < 0.001$). However, the strength of this pattern varied by fish species (species $F = 3.40$, $p = 0.03$, δ^{15}N*species $F = 4.25$, $p < 0.01$), with the strongest effects on omnivorous damselfish and herbivorous surgeonfish, and the weakest effect on predatory snapper (Fig. 4, Fig. S5, Table S8).

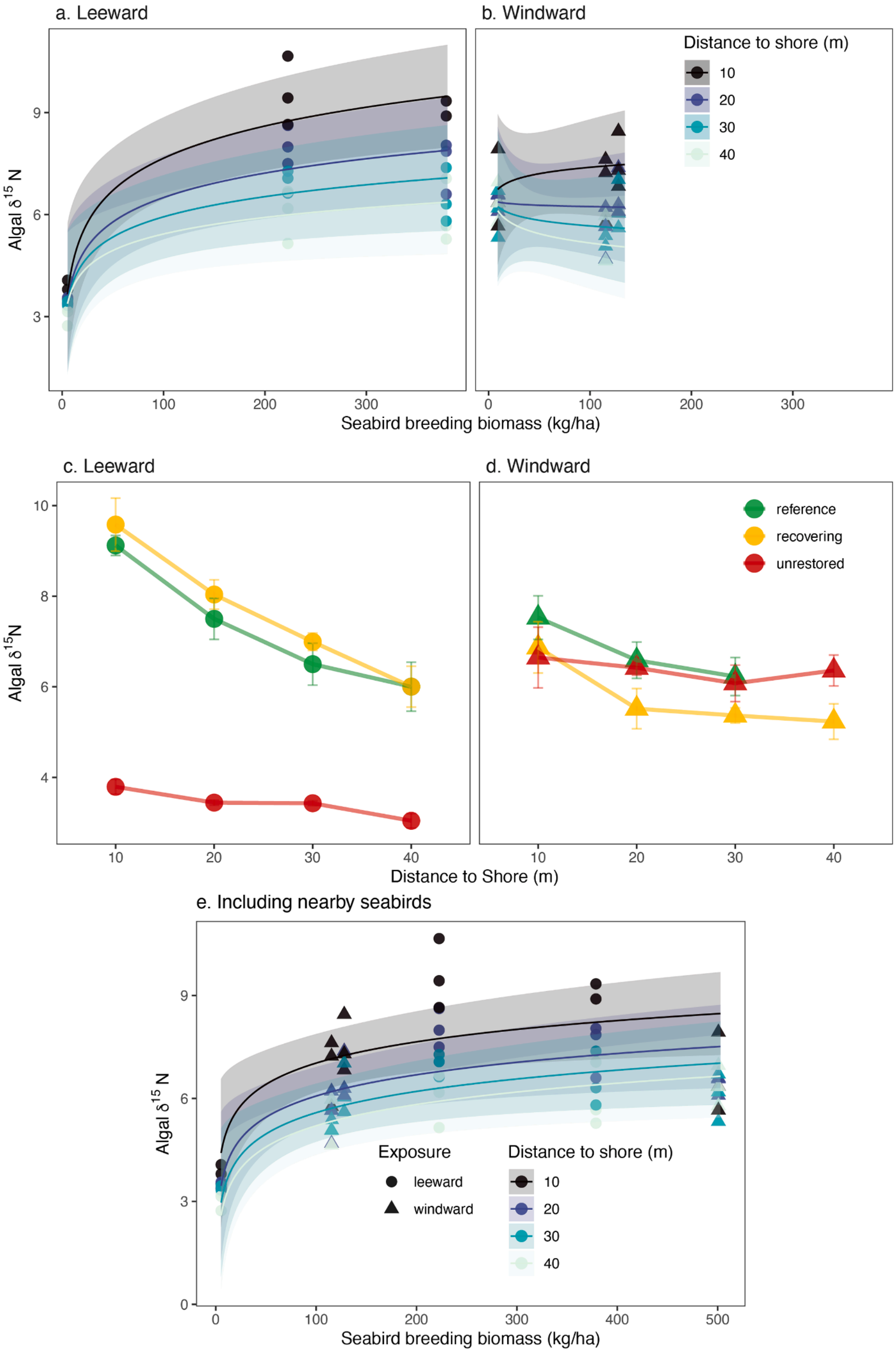

Fig. 3. Effects of exposure, distance to shore, seabird breeding biomass, and restoration status on δ^{15}N of macroalgae. (a-b) Seabird breeding biomass by side of motu (kg/ha), (c-d) restoration status, (e) seabird breeding biomass by side of motu (kg/ha), but including nearby seabird populations for the exposed side of the unrestored motu. (a,b,e) Points represent raw data, lines represent model fits, shaded areas represent 95 % confidence intervals. (c,d) Points represent means, with error bars for standard error.

3.3. *Water column microbes are influenced by both seabird-derived nutrients and location*

Algal δ^{15}N significantly impacted water microbial community dissimilarity, with marginal evidence that this effect varied by exposure (distlm: δ^{15}N $p = 0.03$, exposure $p = 0.23$, δ^{15}N*exposure $p = 0.07$; Fig. 4b; Table S9). Water microbial richness also increased with increasing algal δ^{15}N, with a stronger effect on windward compared to leeward sites (LMM: δ^{15}N $p < 0.001$, exposure $p = 0.72$, δ^{15}N*exposure $p < 0.001$; Fig. 4a; Table S10). By contrast, the relative abundance of three of the dominant water column taxa – SAR116 (Alphaproteobacteria), SAR86 (Gammaproteobacteria), and an autotrophic marine bacterium of the genus *Synechococcus* – significantly decreased with increasing algal δ^{15}N, regardless of exposure (Table S11a; Fig. S7b-d). However, the patterns for richness, SAR86 and *Synechococcus* appeared to be driven by localized conditions around ’Ă’ie (the reference motu). There was anomalously low richness and high *Synechococcus* near the protected side of ’Ă’ie, while SAR86 was anomalously low on both sides of ’Ă’ie. On removing these samples from the dataset, the pattern for both richness and SAR86 held, but relative abundance of *Synechococcus* was no longer significantly driven by algal δ^{15}N (Table S11a; Fig. S6, S7a-c). Seabird-derived nutrients had minimal

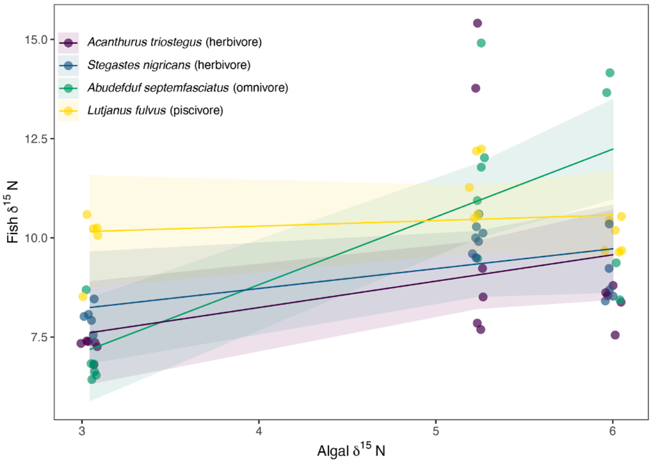

Fig. 4. Effect of algal δ^{15}N on δ^{15}N of four coral-reef fish species across 3 sites. Points represent raw data, lines represent model estimated marginal effects, shaded areas represent 95 % confidence intervals.

effects on other metrics of seawater microbial diversity (Shannon index, evenness, Faith's phylogenetic diversity), with patterns instead seemingly driven by location (i.e., restoration status or motu; Fig. S7a; Table S12a).

3.4. Coral microbiomes are impacted by seabird-derived nutrients

Coral microbial ASV richness increased with increasing seabird-derived nutrients, with an estimated 10.8 % increase on windward sides and 17.8 % increase on leeward sides with every doubling of algal δ^{15}N (LMM: δ^{15}N $p < 0.001$, exposure $p = 0.23$, δ^{15}N*exposure $p = 0.06$; Fig. 5a; Table S10). Evenness also increased with increasing algal δ^{15}N, but only at windward sites (LMM: δ^{15}N $p = 0.01$, exposure $p = 0.01$, δ^{15}N*exposure $p = 0.01$; Fig. S8b; Table S10). However, neither algal δ^{15}N nor exposure significantly impacted overall community dissimilarity (distlm: δ^{15}N $p = 0.58$, exposure $p = 0.26$, δ^{15}N*exposure $p = 0.69$; Fig. 5d), Shannon diversity (LMM: δ^{15}N $p = 0.19$, exposure $p = 0.59$, δ^{15}N*exposure $p = 0.34$), or Faith's phylogenetic diversity (LMM: δ^{15}N $p = 0.29$, exposure $p = 0.70$, δ^{15}N*exposure $p = 0.88$) (Fig. 5c and d, Fig. S8, Tables S9 and S10). In addition, in most cases, algal δ^{15}N did not explain variances in the relative abundances of the most dominant taxa in the coral microbiome, and instead the relative abundance of several top taxa seemed to be driven by location (Tables S11 and S12b). For

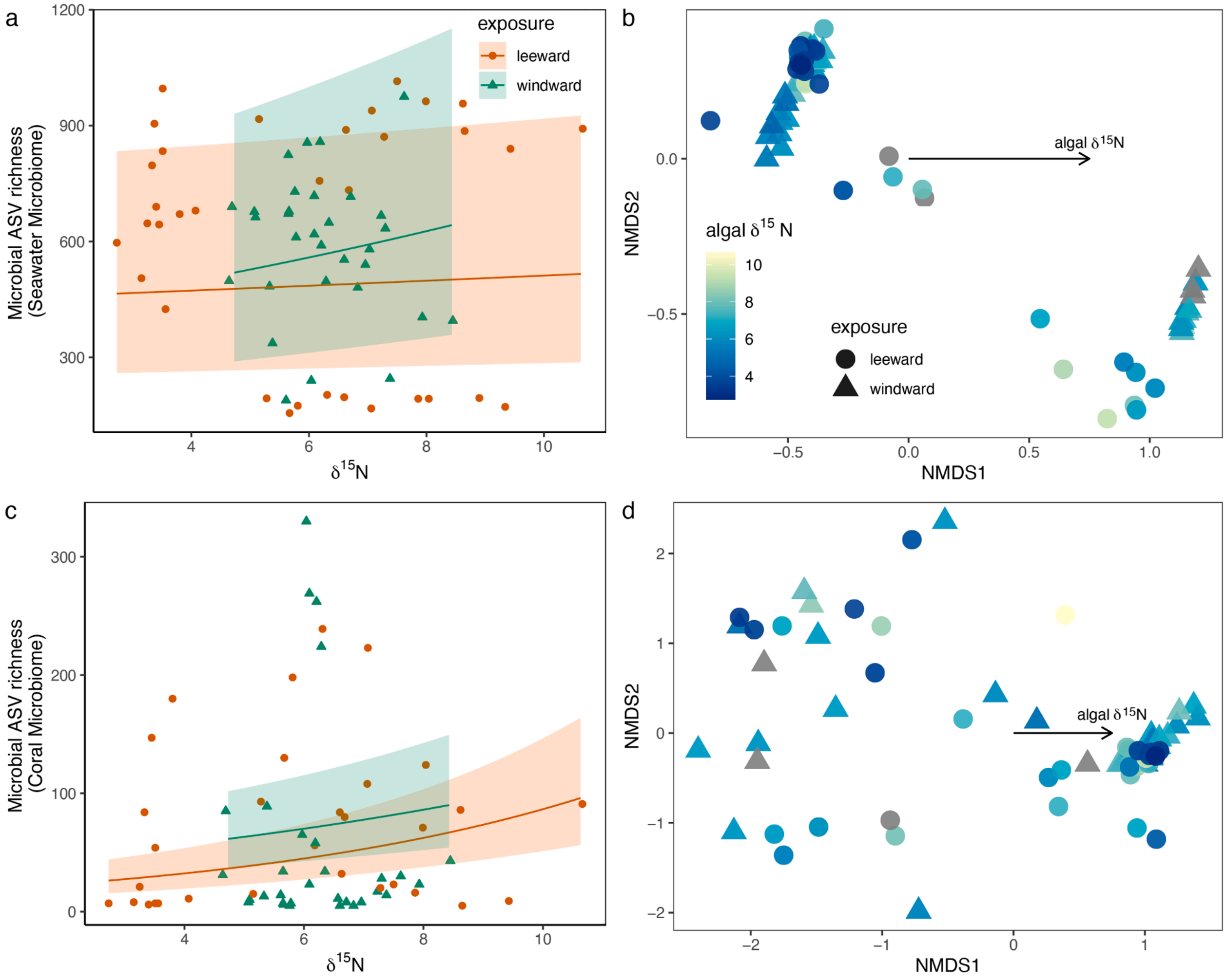

Fig. 5. Effect of algal δ^{15}N on a) seawater-associated and c) coral-associated microbial amplicon sequence variant (ASV) richness, where shading represents 95 % confidence intervals of predicted fit (using a Poisson distribution). NMDS plots of b) seawater microbiomes (stress = 0.035) and d) coral microbiomes (stress = 0.124), colored and rotated by algal δ^{15}N. The length and direction of the arrow for algal δ^{15}N indicates the strength and direction of the effect.

example, relative abundance of *Endozoicomonas* was lowest at the reference motu, showing distinct, localized differences (Fig. S9a). In contrast, an uncultured genus in the family Alteromonadaceae, *Litoricola* and *Neptunibacter* were higher in abundance at the reference motu compared to recovering and unrestored motu, particularly at exposed sites (Fig. S9b-d).

3.5. Macroalgal community diversity and composition vary according to seabird nutrients and distance from shore

Seabird-derived nutrients had strong effects on macroalgal communities 10–40 m from shore, with decreased algal cover, species richness, and Shannon diversity with increasing algal δ^{15}N, regardless of exposure (LMM: all δ^{15}N $p < 0.001$, all exposure $p > 0.29$, all δ^{15}N*exposure $p > 0.28$; Fig. 6a and b, Fig. S10, Table S13). For each one unit increase in algal δ^{15}N, there was a 22.1 % decrease in richness, 17.4 % decrease in relative cover, and 0.22 index unit decrease in Shannon diversity. Macroalgal species evenness also decreased with increasing algal δ^{15}N, although this trend was marginally stronger at windward sites compared to leeward sites (LMM: δ^{15}N $p < 0.001$, exposure $p = 0.69$, δ^{15}N*exposure $p = 0.06$; Fig. 6c, Table S13). For each one unit increase in algal δ^{15}N, macroalgal evenness decreased by 0.11 on windward sites and 0.03 on leeward sites.

Both algal δ^{15}N and exposure also influenced the community composition of macroalgal species (distlm: δ^{15}N $p = 0.001$, exposure $p = 0.04$, δ^{15}N*exposure $p = 0.001$; Fig. 6d). The percent cover of 25 out of 31 species were negatively correlated with NMDS axis 1, corresponding to algal δ^{15}N, with two species of calcifying green macroalgae (*Halimeda distorta* and *H. heteromorpha*), two species of cyanobacteria (*Schizothrix minuta* and *Hydrocoleum coccineum*) and one brown alga (*Lobophora* spp.) displaying the strongest negative correlations (corr = −0.56, −0.38, −0.47, −0.39, and −0.37, respectively). All six species positively related to NMDS1 had relatively weak correlations, with *Halimeda opuntia* having the highest correlation coefficient at 0.25, and all other species having correlation coefficients <0.11. *Turbinaria ornata,* the most abundant algal taxon, was more strongly negatively correlated with NMDS axis 2 than axis 1 (corr = −0.85 and −0.15, respectively), which appeared to be driven by extremely low *Turbinaria* cover (<0.1 %) at one location, 40-m from shore on the windward side of ’Ă’ie (the reference motu), which clustered at the highest values along NMDS2. Overall, leeward sites were also associated with more negative NMDS2 values, matching the observation that *Turbinaria* made up a greater relative percentage of the macroalgal communities at leeward sites (Fig. S11).

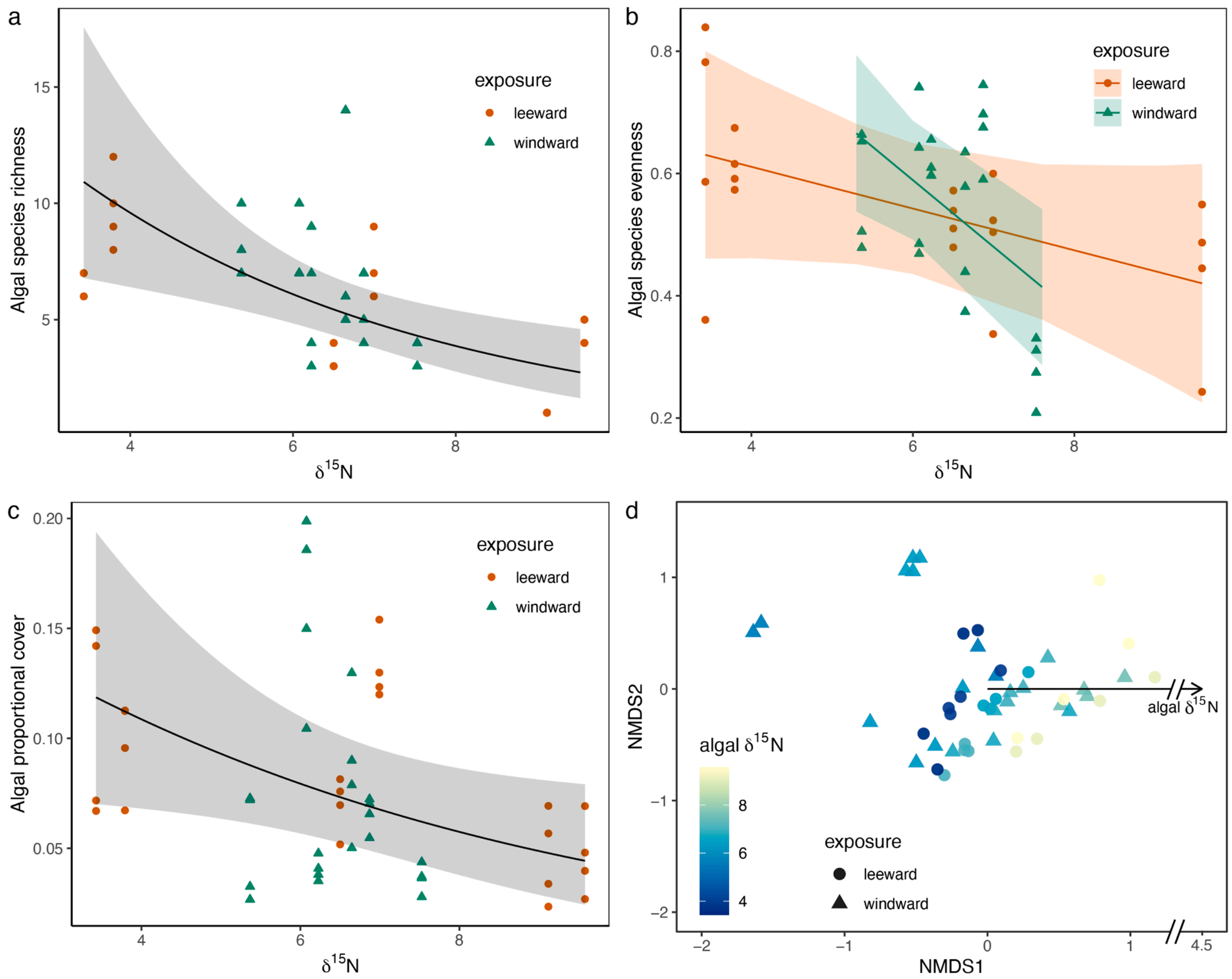

Fig. 6. Effect of algal δ^{15}N and exposure on macroalgal a) species richness, b) species evenness, c) proportional cover, and d) community structure. (a-c) Points represent raw data, lines represent model estimated marginal effects, shaded areas represent 95 % confidence intervals. (d) NMDS plots rotated by algal δ^{15}N (stress = 0.135). The length and direction of the arrow for algal δ^{15}N indicates the strength and direction of the effect. The NMDS axis 1 and arrow are discontinuous between 1.5 and 4.5 to better visualize the distribution of points.

3.6. Seabird nutrients weakly influence total benthic composition and coral-reef fish communities

The benthic habitat farther offshore (45–175 m) primarily consisted of large *Porites* bommies interspersed among sand channels, such that sand and rubble dominated percent cover across all sites (Fig. S12). Hard coral cover increased with increasing seabird-derived nutrients at windward, but not leeward, sites (LMM, δ^{15}N $p = 0.81$, exposure $p = 0.96$, δ^{15}N*exposure $p = 0.002$; Fig. S13ab, Table S14). However, there was weak evidence that seabird-derived nutrients and wind exposure influenced overall benthic community structure (distlm: δ^{15}N $p = 0.80$, exposure $p = 0.76$, δ^{15}N*exposure $p = 0.09$; Fig. 7a, Fig. S13c).

Fish community structure varied according to offshore algal δ^{15}N and structural complexity, but not exposure (distlm: δ^{15}N $p < 0.01$, exposure $p = 0.69$, structure $p = 0.45$, δ^{15}N*exposure $p = 0.22$, δ^{15}N*exposure $p = 0.02$; Fig. 7b). Piscivores and herbivores were the most positively correlated with NMDS axis 1, corresponding to higher algal δ^{15}N, while planktivores and sessile invertebrate feeders were most negatively correlated with NMDS1, corresponding to higher structural complexity (corr = 0.42, 0.39, −0.65, −0.51, respectively). By contrast, there was no effect of offshore algal δ^{15}N on fish total biomass, species richness, evenness, or Shannon's diversity (Table S15, Fig. S14). Overall, structural complexity was highest at low seabird sites and strongly negatively correlated with algal δ^{15}N, making it difficult to disentangle the effects of structure versus seabirds on fish communities (Fig. S15, Spearman's correlation = −0.68, $p < 0.001$).

4. Discussion

Effective monitoring is a key component of any management plan. Here, we integrate metrics operating on different spatial, temporal, and biological scales to evaluate the impacts of island-based restoration on tropical coral reefs. We observed clear relationships between island restoration status and seabird populations, which in turn influenced the amount of seabird-derived nutrients entering marine ecosystems. As a result, seabird nutrients had the strongest effects on microbial and macroalgal communities, with limited effects on broader benthic and fish communities (Fig. 8). However, the strength of several patterns varied by wind exposure. Based on our findings, we highlight considerations for future monitoring programs to most efficiently and effectively capture the cross-ecosystem successes, and failures, of island restoration efforts.

4.1. Seabird nutrients flow from land to nearshore marine habitats and are taken up by coral-reef organisms

Many of the benefits to islands and reefs following island restoration stem from an increase in seabird populations (Mulder et al. 2011; Dunn et al. 2024). Here, we observed the highest seabird populations on the historically rat and palm-free reference motu (ʼĂʼie), intermediate seabirds on the recovering motu (Reiono), and the lowest seabirds on the unrestored motu with rats and palms still present (Rimatuʼu). This gradient is consistent with previous studies on the negative effects of rats and coconut palms on seabirds (Jones et al. 2016; Brooke et al., 2017; Young et al. 2017; Benkwitt et al. 2021a; Benkwitt et al. 2022; Dunn et al. 2024), and population sizes on the reference and recovering motu are within the range observed for other rat-free and rat-eradicated tropical islands (Benkwitt et al. 2021a). That seabird populations on Reiono were already higher than those on Rimatuʼu may indicate a relatively rapid recovery, as rats were only eradicated three years prior to this study. By comparison, in other regions seabirds take decades to recover following rat eradication and sometimes require additional active interventions (e.g., translocations) (Jones 2010; Kappes & Jones 2014; Benkwitt et al. 2021a; Graham et al. 2024). The relatively high seabird densities on the recovering motu may be driven by the existence of nearby source populations on rat-free motu within 200 m − 3 km. It is also possible that seabird biomass was relatively high on Reiono even before the rat eradication due to the high cover of native forest, which may have contributed to the high prevalence of red-footed boobies despite the presence of invasive rats. Red-footed boobies strongly prefer native forest (Young et al. 2010; Young et al. 2017) and are less susceptible to predation by invasive rats than smaller seabird species, yet still exhibit population increases following rat eradication (Le Corre et al. 2015). Although a lack of pre-eradication data precludes distinguishing between these explanations, it is the current gradient in seabird populations that is essential to establish before examining seabird-driven outcomes across ecosystems.

To evaluate the efficacy of island restoration for marine ecosystems, it is then necessary to establish whether this leads to differences in cross-ecosystem nutrient flow. Algal δ^{15}N decreased with increasing distance from shore around the reference and recovering motu, but there was no offshore gradient near the unrestored motu. This pattern provides additional evidence that, where abundant, seabirds drive a land-sea link that is reflected in algal δ^{15}N values (Lorrain et al. 2017; Savage 2019; Benkwitt et al. 2021a). Furthermore, given the similarity in algal δ^{15}N values between reference and recovering motu, this metric may provide a rapid early indicator of restored cross-ecosystem flows.

However, enhanced algal δ^{15}N on the reference and recovering motu compared to the unrestored motu was only apparent at leeward sites. Similarly, algal δ^{15}N only increased with larger seabird populations at leeward sites. Thus, seabird-derived nutrients dissipate more quickly on exposed sites, likely due to enhanced mixing and water flow. Similarly, the amount of seabird-derived nitrogen in temperate macroalgae also decreases with increasing wave exposure (Rankin & Jones 2021). Importantly, the difference between leeward and exposed sites was also driven by surprisingly high δ^{15}N values at the exposed side of the

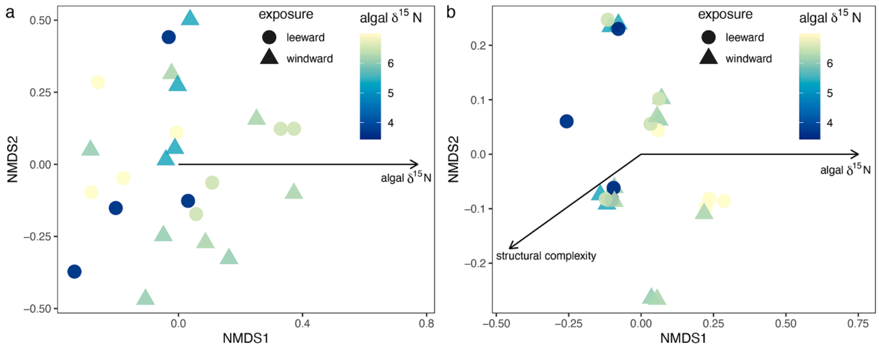

Fig. 7. Effect of algal δ^{15}N and exposure on a) broad benthic community groups (from video surveys) and b) fish feeding groups (log-transformed density). NMDS plots rotated by algal δ^{15}N (stress = 0.06 and 0.09, respectively). The length and direction of the arrows for algal δ^{15}N and structural complexity indicate the strength and direction of the effect.

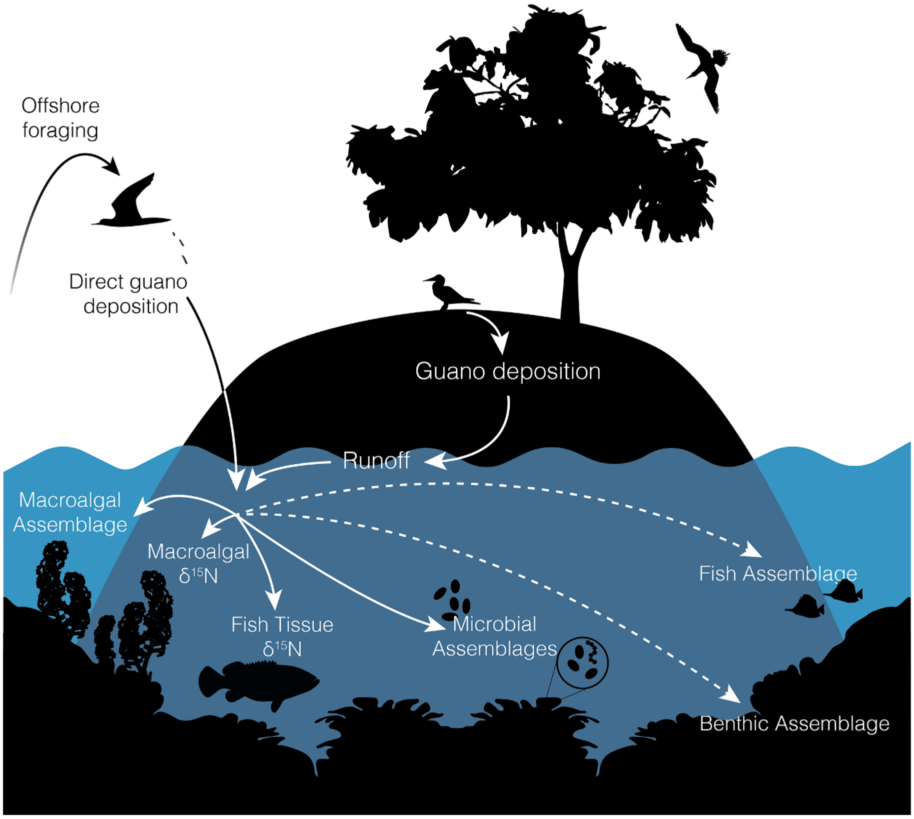

Fig. 8. Schematic representation of the connections between seabird nutrient deposition, the input of seabird nutrients into island-adjacent marine ecosystems and uptake of these nutrients among trophic levels. Line types represent strength of evidence for the connections from the current study, with solid lines indicating strong evidence, while dotted lines indicate modest evidence.

unrestored motu. This pattern suggests that nutrients from another source and/or location are influencing δ^{15}N at this site. Here, there is a large seabird population on another motu immediately adjacent to, and downwind of, this site. When incorporating information on this seabird population into models of algal δ^{15}N, there was a strong effect of seabird biomass, but not exposure, on algal δ^{15}N. While seabirds on another motu offer a parsimonious explanation for the observed δ^{15}N patterns, it is also possible that additional nitrogen sources are playing a role. For example, deep oceanic nitrogen, which can be transported to shallower depths via internal waves, is also enriched in δ^{15}N and may be more prevalent at windward sites (Leichter et al. 2003; Williams et al. 2018). Overall, these results highlight the importance of considering the broader seascape context when trying to understand cross-ecosystem nutrient flows.

There was also evidence that seabird-derived nutrients were transferred up the food chain to coral-reef fishes, as fish δ^{15}N values were positively related to algal δ^{15}N. As for algal δ^{15}N, fish δ^{15}N values near the recovering motu were more similar to those of the reference motu than the unmanaged motu. Similarly, herbivorous damselfish in the Indian Ocean also show enhanced δ^{15}N around rat-free and rat-eradicated islands than rat-infested islands (Benkwitt et al. 2021a). The weaker effect sizes in fish compared to algae likely reflect that fish were sampled farther offshore, and thus farther away from seabird nutrient inputs, as has been previously observed seen in algae, corals, and herbivorous damselfishes collected at varying distances from shore in other locations (Lorrain et al. 2017; Savage 2019; Benkwitt et al. 2021a). Effect sizes also decreased with increasing trophic level, such that seabird nutrients were most pronounced in herbivorous and omnivorous fishes. Still, this is the first evidence, to our knowledge, that seabird nutrients persist up coral-reef food webs beyond primary consumers. However, the interpretation of δ^{15}N values is more complicated at higher trophic levels, as shifts could indicate not only a change in reliance on seabird-derived nutrients, but also a change in diet or food chain length as δ^{15}N increases with increasing trophic level (Peterson & Fry 1987; Vanderklift & Ponsard 2003). Thus, focusing on primary producers (algae) and primary consumers (herbivores) as proxies for seabird-derived nutrients in coral reef food webs should be prioritized.

4.2. *Microbial taxa respond to seabird nutrients, but their use as indicators may be limited*

With any significant changes in nutrient subsidies to nearshore habitat, we expect to see rapid shifts in microbial dynamics both in the water column (Gast et al. 1999) and in animal-associated microbiomes (Zaneveld et al. 2016; Gantt et al. 2019) as a result of microbial roles in biogeochemical cycling. While seawater bacterial richness was significantly impacted by algal δ^{15}N, only a few dominant water column taxa followed this pattern. For example, the relative abundances of SAR116 (Alphaproteobacteria) and SAR86 (Gammaproteobacteria), which have both previously been shown to associate with N-deficient, oligotrophic surface water (Treusch et al. 2009; West et al. 2016; Li et al. 2018), significantly decreased as algal δ^{15}N increased. Losses of oligotrophic taxa such as these from seawater microbial communities may act as useful indicators of nutrient loading in nearshore habitats. Other relative abundances of dominant microbial taxa, such as the ubiquitous cyanobacterium *Synechococcus*, appeared to be driven by localized conditions. Microbial communities can be fast responders and follow “feast and famine” community dynamics as a result of rapid changes in the availability and limitation of nutrient resources (Teeling et al. 2012; Buchan et al. 2014). However, abundances are likely to be highly ephemeral and communities often exhibit short-term compositional shifts that correspond to processes such as tides (Becker et al. 2020), winds (Iluz et al.

2009), storms and rainfall events (Angly et al. 2016; Ares et al. 2020), and photoperiod or diel periodicity (Jacquet et al. 2001), among others (see Fuhrman et al. 2015), encouraging some caution when relying on these taxa as indicators of long-term impacts.

Conversely, microbes associated with benthic organisms, such as the coral microbiomes examined here, are thought to provide a more time-integrated community to monitor than that of the water column, with the capacity to directly impact the health of the host organisms with which they associate. Overall bacterial richness of coral microbiomes significantly increased with algal δ^{15}N, but none of the dominant microbial taxon abundances reflected nutrient input. However, we also found evidence for localized impacts similar to the water column microbiome. Increased abundances of putatively beneficial coral-associated bacteria, like members of the genus *Endozoicomonas*, were observed in corals from the unrestored motu, particularly on the protected side. Association with this bacterial genus is thought to provide metabolic benefits to the coral host (Bourne et al. 2016; Neave et al. 2017; Tandon et al. 2020) and has recently been suggested to influence coral growth (Wada et al. 2022). Its role in the coral microbiome on unrestored reefs may reflect nutrient limitation resulting from low seabird biomass, where higher abundances of *Endozoicomonas* are maintained to support coral homeostasis under unnatural nutrient regimes. It is clear that seabird-derived nutrients entering the marine ecosystem are impacting coral microbiomes, and monitoring may benefit from targeting the presence or abundance of microbial indicator taxa for coral health.

4.3. *Macroalgal community dynamics are indicative of nutrient subsidies*

The strongest evidence of seabird nutrient impact on marine communities was in the community composition of macroalgae close to shorelines, with percent cover, species richness, species evenness, and species diversity all decreasing with seabird-derived nutrients. Interestingly, seabird-derived nutrients have previously been shown to have the opposite effect on temperate macroalgal richness (Rankin & Jones 2021). More broadly, nutrient enrichment in seawater can both increase and decrease macroalgal species richness (reviewed by Zubia et al. 2018), likely dependent on a combination of abiotic and biotic processes. It is also possible that differences in these processes may encourage shifts in macroalgal community composition unrelated to seabird nutrient input. Although not quantified in the present study, there were visual differences in benthic structure among macroalgal survey sites. Previous work has shown that higher reef rugosity can lead to both higher algal biomass and higher species richness (Olsen et al. 2019); however, this may be countered by increased herbivore grazing in structurally complex reef sites (Vergés et al. 2011). While we saw no significant difference in fish biomass by site, herbivorous fishes were more positively correlated with the NMDS axis corresponding to algal δ^{15}N, and in other systems seabird-derived nutrients increase herbivorous fish growth and biomass (Graham et al. 2018; Benkwitt et al. 2021b). Beyond population increases, seabird-derived nutrients may stimulate behavioral responses, as herbivorous reef fishes can target more nutrient-rich algae (Burkepile & Hay 2009; Shantz et al. 2017). Thus, seabird-derived nutrients may lead to increased grazing pressure, which in turn could decrease algal cover and diversity. Overall, the interplay between the impacts of herbivory and seabird nutrient enrichment on macroalgal communities should continue to be investigated.

4.4. *Seabird nutrients do not impact marine macro-community dynamics*

Despite strong patterns in nutrient flow based on island restoration status, we observed few consistent differences in broad benthic and fish communities located greater than 40 m from shore. There are several non-mutually exclusive possibilities for this finding. First, as discussed above, seabird nutrients declined with increasing distance to shore, suggesting they may play a limited role in structuring reef communities farther from shore in this system. Second, other differences among sites, including wave exposure and structural complexity (Graham & Nash 2013; Lange et al. 2021), may be obscuring seabird effects. Still, it seems that seabirds have weaker effects on these communities than other coral-reef metrics. In other locations seabirds similarly had no effect on benthic cover 100–300 m from shore, until seabirds altered recovery trajectories after a major climate disturbance (Benkwitt et al. 2019; Benkwitt et al. 2023). Likewise, even where seabirds enhance fish biomass, the effect sizes are relatively small compared to their effects on fish growth and behavior (Graham et al. 2018; Benkwitt et al. 2021b; Gunn et al. 2023). Thus, seabirds likely have a greater influence on process-based metrics, such as coral and fish growth, than on the resulting community structure, especially as one moves farther offshore, and monitoring efforts may need to be prioritized accordingly.

4.5. *Considerations for monitoring*

(1) Design. This study used a space-for-time substitution (i.e., compared across motu with varying restoration statuses at a single time point). Indeed, most studies do not have a comparative spatial or temporal baseline and, where present, space-for-time substitution is most common. However, this substitution can limit the statistical power necessary for results that contribute to well-informed management decisions, particularly when working in small geographic areas with limited opportunities for adequate replication and when additional covariates (e.g., wind exposure) influence results. Where possible, a before-after-control-impact (BACI) design is the best way to establish whether any differences are being caused by seabirds (or island restoration) while accounting for other confounding variables. This design may further reveal (or rule out) some of the connections that are thus far unresolved between nutrient flow and the broader marine communities (Fig. 8) that may be crucial in developing or managing conservation goals and targets.

(2) Resources. Limited resources are a reality for most monitoring programs, meaning that it will be impossible to monitor all outcomes. Therefore, it is important to prioritize resources to capture the most important outcomes at appropriate time scales, and are efficient in both time and cost. The high correlations among seabird metrics suggest that monitoring either roosting or breeding seabirds should reflect overall seabird use of an area, and the high correlations of seabird estimates across spatial scales indicate that monitoring programs may be able to reduce effort by sub-sampling within islands, as long as habitat (native vegetation versus coconut palms) is accounted for. For marine responses, our results show that algal and fish nutrients, along with microbial and nearshore macroalgal assemblages, are likely to respond relatively quickly to island-based changes, given that the most restoration intervention (eradicating invasive rats) occurred only three years prior to the study. By contrast, broader benthic and fish communities that are farther from shore likely show slower response times. We therefore propose focusing initial monitoring on algal δ^{15}N levels, given that measurement of lower trophic level metrics can be temporally and financially efficient while simultaneously capturing 1) the scale of nutrient impact on nearshore marine habitats and 2) the possible downstream and future impacts on the marine environment. Both can inform or justify whether any further marine monitoring may be appropriate at a restoration site.

(3) Incorporate marine systems into island management. Given that some of the cross-ecosystem effects of island restoration on coral reefs were more nuanced than simple increases in nutrients, building teams with expertise across systems should be a priority. Understanding the interplay between seabirds and marine ecosystem function is critical to benefit innovative restoration

methods, yet relies on in-depth knowledge of multiple systems and species. This, in turn, can lead to further scientific endeavors such as empirical work to find underlying mechanisms across microbes to macrobes.

5. Conclusions

Globally, the understanding, protection, and restoration of land-sea connectivity is a critical challenge to maintaining healthy and resilient ecological systems (Olds et al. 2018). The importance of these 'ridge-to-reef' linkages have long been recognized in many forms of traditional knowledge, and has underpinned management on many Pacific islands for thousands of years (e.g., Richmond et al. 2007; Fitzpatrick & Giovas 2021; Fache & Pauwels 2022). Thus, it is overdue that we develop the monitoring tools to fully integrate ecosystem connectivity into current management practices. Incorporating land-sea connections is gaining momentum in coral reef conservation, although the focus is typically on limiting negative downstream effects such as reducing pollution and sedimentation (Jupiter et al. 2017; Delevaux et al. 2018b; Delevaux et al., 2018a; Wakwella et al. 2023). Here, we highlight the opposite approach – harnessing positive land-sea connections that can be revitalized with restoration activities, such as removing invasive species from islands. The current UN Decade for Ecosystem Restoration (2021–2030) provides an ideal opportunity to promote restoration efforts that target the recovery of ecosystem function across the land-sea interface and focus on reconnecting the ecological linkages and dependencies of different species across multiple habitats and ecosystems (Wedding et al. 2022; Preston et al., n.d; Wedding et al., n.d). We suggest that restoration initiatives should promote collaboration between terrestrial and marine managers to coordinate monitoring programs. The indicators examined here may be used to begin building a framework for the systematic evaluation and monitoring of island restoration efforts on coral reefs and thus facilitate the development of effective cross-ecosystem monitoring programs.

Permits.

DRM: N°12128-VP.

CITES Export Permit: #FR2198700109-E.

Lancaster University Animal Welfare and Ethical Review Body (AWERB) Permit: A100143.

CRediT authorship contribution statement

Cassandra E. Benkwitt: Writing – review & editing, Writing – original draft, Visualization, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Kalia S.I. Bistolas:** Writing – review & editing, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. **Jayna L. DeVore:** Writing – review & editing, Methodology, Investigation, Funding acquisition, Data curation. **Simon Ducatez:** Writing – review & editing, Methodology, Investigation, Funding acquisition, Data curation. **Jazmín Prado Gómez:** Writing – review & editing, Investigation, Data curation. **Rosalie Wright:** Writing – review & editing, Methodology, Investigation, Funding acquisition, Data curation. **Mayalen Zubia:** Writing – review & editing, Methodology, Data curation. **Pierrick Harnay:** Writing – review & editing, Resources, Project administration, Investigation, Data curation. **Teva Beguet:** Writing – review & editing, Resources, Project administration, Conceptualization. **Lisa M. Wedding:** Writing – review & editing, Supervision, Data curation. **Deron E. Burkepile:** Writing – review & editing, Funding acquisition, Conceptualization. **Frank Murphy:** Writing – review & editing, Resources, Funding acquisition, Conceptualization. **Nicholas A.J. Graham:** Writing – review & editing, Resources, Funding acquisition, Conceptualization. **Rebecca Vega Thurber:** Writing – review & editing, Supervision, Resources, Funding acquisition, Data curation, Conceptualization. **Hannah E. Epstein:** Writing – review & editing, Writing – original draft, Visualization, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

The authors would like to thank the Tetiaroa Society for their financial and logistical support for this project as part of the Tetiaroa Atoll Restoration Program, to Lusiano Kolokilagi, Antonin Fioretti and Carlee Heger for their invaluable field support, to Hinano Murphy for guidance, to Patrick Lyons for lab assistance, and to Dave Hughes for stable isotope preparation and analysis. The authors acknowledge additional financial support for this work from the following awards: National Science Foundation, United States (NSF) PRFB #2006244 (H. E.) and #1907184 (K.B.), Fisheries Society of the British Isles, United Kingdom Postdoctoral International Travelling Fellowship (C.B.), Bertarelli Foundation, Switzerland as part of the Bertarelli Programme in Marine Science (C.B., N.G., L.W., R.W.), Agence nationale de la recherche, France InvEcoF #ANR-22-CE02-0007 (S.D. and J.D.), Fondation Fyssen, France (S.D. and J.D.), University of Oxford, United Kingdom John Fell Fund (L.W., R.W.), and NSF OCE #2023424 and #2023701 (R.V.T. and D.E.B.).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2024.113042.

Data availability

Sequence data will be available on publication under NCBI SRA Accession PRJNA11146751. All other data and code are available via github: github.com/hannaheps/TARP_motu_comparison. Microbial community raw sequence data are available on the NCBI Sequence Read Archive (SRA) under accession PRJNA11146751. All other data and analytical code can be accessed at github.com/hannaheps/TARP_motu_comparison.

References

Álvarez-Romero, J.G., Pressey, R.L., Ban, N.C., Vance-Borland, K., Willer, C., Klein, C.J., Gaines, S.D., 2011. Integrated land-sea conservation planning: the missing links. *Annu. Rev. Ecol. Evol. Syst.* 42, 381–409.

Angly, F.E., Heath, C., Morgan, T.C., Tonin, H., Rich, V., Schaffelke, B., Bourne, D.G., Tyson, G.W., 2016. Marine microbial communities of the Great Barrier Reef lagoon are influenced by riverine floodwaters and seasonal weather events. *PeerJ* 4, e1511.

Ares, Á., Brisbin, M.M., Sato, K.N., Martín, J.P., Iinuma, Y., Mitarai, S., 2020. Extreme storms cause rapid but short-lived shifts in nearshore subtropical bacterial communities. *Environ. Microbiol.* 22, 4571–4588.

Becker, C.C., Weber, L., Suca, J.J., Llopiz, J.K., Mooney, T.A., Apprill, A., 2020. Microbial and nutrient dynamics in mangrove, reef, and seagrass waters over tidal and diurnal time scales. *Aquat. Microb. Ecol.* 85, 101–119.

Benkwitt, C.E., Wilson, S.K., 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., Wilson, S.K., Graham, N.A.J., 2020. Biodiversity increases ecosystem functions despite multiple stressors on coral reefs. *Nat. Ecol. Evol.* 4, 919–926.

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

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

Benkwitt, C.E., Carr, P., Wilson, S.K., Graham, N.A.J., 2022. Seabird diversity and biomass enhance cross-ecosystem nutrient subsidies. *Proc. r. Soc. B* 289, 20220195.

Benkwitt, C.E., D'Angelo, C., Dunn, R.E., Gunn, R.L., Healing, S., Mardones, M.L., Wiedenmann, J., Wilson, S.K., Graham, N.A.J., 2023. Seabirds boost coral reef resilience. *Sci. Adv.* 9, eadj0390.

Bourne, D.G., Morrow, K.M., Webster, N.S., 2016. Insights into the coral microbiome: Underpinning the health and resilience of reef ecosystems. *Annu. Rev. Microbiol.* 70, 317–340.

Brooke, M. de L., Bonnaud, E., Dilley, B.J., Flint, E.N., Holmes, N.D., Jones, H.P., Provost, P., Rocamora, G., Ryan, P.G., Surman, C., Buxton, P.T., 2017. Seabird population changes following mammal eradications on islands. *Anim. Conserv.* 21, 3–12.

Buchan, A., LeCleir, G.R., Gulvik, C.A., González, J.M., 2014. Master recyclers: features and functions of bacteria associated with phytoplankton blooms. *Nat Rev Microbiol* 12, 686–698.

Bullock, J.M., Fuentes-Montemayor, E., McCarthy, B., Park, K., Hails, R.S., Woodcock, B. A., Watts, K., Corstanje, R., Harris, J., 2022. Future restoration should enhance ecological complexity and emergent properties at multiple scales. *Ecography* 2022, e05780.

Burkepile, D.E., Hay, M.E., 2009. Nutrient versus herbivore control of macroalgal community development and coral growth on a Caribbean reef. *Mar. Ecol. Prog. Ser.* 389, 71–84.

Carlson, R.R., Evans, L.J., Foo, S.A., Grady, B.W., Li, J., Seeley, M., Xu, Y., Asner, G.P., 2021. Synergistic benefits of conserving land-sea ecosystems. *Global Ecol. Conserv.* 28, e01684.

Darling, E.S., Graham, N.A.J., Januchowski-Hartley, F.A., Nash, K.L., Pratchett, M.S., Wilson, S.K., 2017. Relationships between structural complexity, coral traits, and reef fish assemblages. *Coral Reefs* 36, 561–575.

Delevaux, J.M.S., Whittier, R., Stamoulis, K.A., Bremer, L.L., Jupiter, S., Friedlander, A. M., Poti, M., Guannel, G., Kurashima, N., Winter, K.B., Toonen, R., Conklin, E., Wiggins, C., Knudby, A., Goodell, W., Burnett, K., Yee, S., Htun, H., Oleson, K.L.L., Wiegner, T., Ticktin, T., 2018a. A linked land-sea modeling framework to inform ridge-to-reef management in high oceanic islands. *PLOS ONE* 13, e0193230.

Delevaux, J.M.S., Winter, K.B., Jupiter, S.D., Blaich-Vaughan, M., Stamoulis, K.A., Bremer, L.L., Burnett, K., Garrod, P., Troller, J.L., Ticktin, T., 2018b. Linking land and sea through collaborative research to inform contemporary applications of traditional resource management in Hawai'i. *Sustainability* 10, 3147.

Donovan, M.K., Adam, T.C., Shantz, A.A., Speare, K.E., Munsterman, K.S., Rice, M.M., Schmitt, R.J., Holbrook, S.J., Burkepile, D.E., 2020. Nitrogen pollution interacts with heat stress to increase coral bleaching across the seascape. *PNAS* 117, 5351–5357.

Dunn, R.E., Benkwitt, C.E., Maury, O., Barrier, N., Carr, P., Graham, N.A.J., 2024. Island restoration to rebuild seabird populations and amplify coral reef functioning. *Conservation Biology* e14313.

Fache, E., Pauwels, S., 2022. The ridge-to-reef approach on Cicia Island, Fiji. *Ambio* 51, 2376–2388.

Fitzpatrick, S.M., Giovas, C.M., 2021. Tropical islands of the Anthropocene: Deep histories of anthropogenic terrestrial–marine entanglement in the Pacific and Caribbean. *PNAS* 118, e2022209118.

Fuhrman, J.A., Cram, J.A., Needham, D.M., 2015. Marine microbial community dynamics and their ecological interpretation. *Nat. Rev. Microbiol.* 13, 133–146.

Gann, G.D., McDonald, T., Walder, B., Aronson, J., Nelson, C.R., Jonson, J., Hallett, J.G., Eisenberg, C., Guariguata, M.R., Liu, J., Hua, F., Echeverría, C., Gonzales, E., Shaw, N., Decleer, K., Dixon, K.W., 2019. International principles and standards for the practice of ecological restoration. Second Edition. *Restor. Ecol.* 27, S1–S46.

Gantt, S.E., McMurray, S.E., Stubler, A.D., Finelli, C.M., Pawlik, J.R., Erwin, P.M., 2019. Testing the relationship between microbiome composition and flux of carbon and nutrients in Caribbean coral reef sponges. *Microbiome* 7, 124.

Gast, G.J., Jonkers, P.J., van Duyl, F.C., Bak, R.P.M., 1999. Bacteria, flagellates and nutrients in island fringing coral reef waters: Influence of the ocean, the reef and eutrophication. *Bull. Mar. Sci.* 65, 523–538.

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

Graham, N.A.J., Nash, K.L., 2013. The importance of structural complexity in coral reef ecosystems. *Coral Reefs* 32, 315–326.

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

Gunn, R.L., Benkwitt, C.E., Graham, N.A.J., Hartley, I.R., Algar, A.C., Keith, S.A., 2023. Terrestrial invasive species alter marine vertebrate behaviour. *Nat. Ecol. Evol.* 7, 82–91.

Hjältén, J., Nilsson, C., Jørgensen, D., Bell, D., 2016. Forest–Stream Links, Anthropogenic Stressors, and Climate Change: Implications for Restoration Planning. *BioScience* 66, 646–654.

Iluz, D., Dishon, G., Capuzzo, E., Meeder, E., Astoreca, R., Montecino, V., Znachor, P., Ediger, D., Marra, J., 2009. Short-term variability in primary productivity during a wind-driven diatom bloom in the Gulf of Eilat (Aqaba). *Aquat. Microb. Ecol.* 56, 205–215.

Jacquet, S., Partensky, F., Lennon, J.-F., Vaulot, D., 2001. Diel Patterns of Growth and Division in Marine Picoplankton in Culture. *J. Phycol.* 37, 357–369.

Jones, H.P., 2010. Seabird islands take mere decades to recover following rat eradication. *Ecol. Appl.* 20, 2075–2080.

Jones, H.P., Tershy, B.R., Zavaleta, E.S., Croll, D.A., Keitt, B.S., Finkelstein, M.E., Howald, G.R., 2008. Severity of the effects of invasive rats on seabirds: a global review. *Conserv. Biol.* 22, 16–26.

Jones, H.P., Holmes, N.D., Butchart, S.H.M., Tershy, B.R., Kappes, P.J., Corkery, I., Aguirre-Muñoz, A., Armstrong, D.P., Bonnaud, E., Burbidge, A.A., Campbell, K., Courchamp, F., Cowan, P.E., Cuthbert, R.J., Ebbert, S., Genovesi, P., Howald, G.R., Keitt, B.S., Kress, S.W., Miskelly, C.M., Oppel, S., Poncet, S., Rauzon, M.J., Rocamora, G., Russell, J.C., Samaniego-Herrera, A., Seddon, P.J., Spatz, D.R., Towns, D.R., Croll, D.A., 2016. Invasive mammal eradication on islands results in substantial conservation gains. *PNAS* 113, 4033–4038.

Jupiter, S.D., Wenger, A., Klein, C.J., Albert, S., Mangubhai, S., Nelson, J., Teneva, L., Tulloch, V.J., White, A.T., Watson, J.E.M., 2017. Opportunities and constraints for implementing integrated land–sea management on islands. *Environ. Conserv.* 44, 254–266.

Kappes, P.J., Jones, H.P., 2014. Integrating seabird restoration and mammal eradication programs on islands to maximize conservation gains. *Biodivers Conserv* 23, 503–509.

Kier, G., Kreft, H., Lee, T.M., Jetz, W., Ibisch, P.L., Nowicki, C., Mutke, J., Barthlott, W., 2009. A global assessment of endemism and species richness across island and mainland regions. *PNAS* 106, 9322–9327.

Lange, I.D., Benkwitt, C.E., McDevitt-Irwin, J.M., Tietjen, K.L., Taylor, B., Chinkin, M., Gunn, R.L., Palmisciano, M., Steyaert, M., Wilson, B., East, H.K., Turner, J., Graham, N.A.J., Perry, C.T., 2021. Wave exposure shapes reef community composition and recovery trajectories at a remote coral atoll. *Coral Reefs* 40, 1819–1829.

Le Corre, M., Danckwerts, D.K., Ringler, D., Bastien, M., Orlowski, S., Morey Rubio, C., Pinaud, D., Micol, T., 2015. Seabird recovery and vegetation dynamics after Norway rat eradication at Tromelin Island, western Indian Ocean. *Biol. Conserv.* 185, 85–94.

Leichter, J.J., Stewart, H.L., Miller, S.L., 2003. Episodic nutrient transport to Florida coral reefs. *Limnol. Oceanogr.* 48, 1394–1407.

Li, Y.-Y., Chen, X.-H., Xie, Z.-X., Li, D.-X., Wu, P.-F., Kong, L.-F., Lin, L., Kao, S.-J. & Wang, D.-Z. (2018). Bacterial diversity and nitrogen utilization strategies in the upper layer of the northwestern Pacific Ocean. *Front. Microbiol.*, 9.

Loreau, M., Mouquet, N., Holt, R.D., 2003. Meta-ecosystems: a theoretical framework for a spatial ecosystem ecology. *Ecol. Lett.* 6, 673–679.

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

Mulder, C.P., Anderson, W.B., Towns, D.R., Bellingham, P.J. (Eds.), 2011. *Seabird Islands: Ecology, Invasion, and Restoration.* Oxford University Press, New York.

Neave, M.J., Michell, C.T., Apprill, A., Voolstra, C.R., 2017. *Endozoicomonas* genomes reveal functional adaptation and plasticity in bacterial strains symbiotically associated with diverse marine hosts. *Sci. Rep.* 7, 40579.

Olds, A.D., Nagelkerken, I., Huijbers, C.M., Gilby, B.L., Pittman, S.J. & Schlacher, T.A. (2018). Connectivity in coastal seascapes. In: *Seascape Ecology* (ed. Pittman, S.J.). John Wiley & Sons Ltd, pp. 261–292.

Olsen, Y.S., Mattio, L., Zavala Perez, A., Babcock, R.C., Thompson, D., Haywood, M.D.E., Keesing, J., Kendrick, G.A., 2019. Drivers of species richness and abundance of marine macrophytes on shallow tropical reefs of north-western Australia. *J. Biogeogr.* 46, 170–184.

Perring, M.P., Standish, R.J., Price, J.N., Craig, M.D., Erickson, T.E., Ruthrof, K.X., Whiteley, A.S., Valentine, L.E., Hobbs, R.J., 2015. Advances in restoration ecology: rising to the challenges of the coming decades. *Ecosphere* 6, art131.

Peterson, B.J., Fry, B., 1987. Stable isotopes in ecosystem studies. *Annu. Rev. Ecol. Syst.* 18, 293–320.

Polis, G.A., Anderson, W.B., 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.

Polunin, N.V.C., Roberts, C.M., 1993. Greater biomass and value of target coral-reef fishes in two small Caribbean marine reserves. Marine Ecology Progress Series 100, 167–176.

Prach, K., Durigan, G., Fennessy, S., Overbeck, G.E., Torezan, J.M., Murphy, S.D., 2019. A primer on choosing goals and indicators to evaluate ecological restoration success. *Restor. Ecol.* 27, 917–923.

Preston, J., Debney, A., Gamble, C., Underwood, G.J.C., Garbutt, A., Harley, J., Baker, R., Dunk, R., Grigg, M., Hancock, B., Hendy, I., La Marca, E.C., Murray, J., Reeves, S.E., Robertson, M., Sturrock, A.M., Thurstand, R.H., Unsworth, R.K.F., Ward, E.A., Ward, S.L., Watson, G.L., Watson, S.C.L., Wedding, L.M., Worthington, T.A., Wright, R.A., Yesson, C. & zu Ermgassen, P.S.E. (In review). Seascape connectivity: evidence, knowledge gaps and implications for coastal ecosystem restoration practice and policy.

R Core Team. (2022). R: A language and environment for statistical computing.

Rankin, L.L., Jones, H.P., 2021. Nearshore ecosystems on seabird islands are potentially influenced by invasive predator eradications and environmental conditions: a case study at the Mercury Islands, New Zealand. *Mar. Ecol. Prog. Ser.* 661, 83–96.

Richmond, R.H., Rongo, T., Golbuu, Y., Victor, S., Idechong, N., Davis, G., Kostka, W., Neth, L., Hamnett, M., Wolanski, E., 2007. Watersheds and coral reefs: Conservation science, policy, and implementation. *BioScience* 57, 598–607.

Russell, J.C., Faulquier, L., Tonione, M.A., 2011. Rat invasion of Tetiaroa Atoll, French Polynesia. In: Veitch, C.R., Clout, M.N., Towns, D.R. (Eds.), *Island Invasives: Eradication and Management.* IUCN, Gland, Switzerland, pp. 118–123.

Russell, J.C., Kueffer, C., 2019. Island biodiversity in the Anthropocene. *Annu. Rev. Environ. Resour.* 44, 31–60.

Sandin, S.A., Becker, P.A., Becker, C., Brown, K., Erazo, N.G., Figuerola, C., Fisher, R.N., Friedlander, A.M., Fukami, T., Graham, N.A.J., Gruner, D.S., Holmes, N.D., Holthuijzen, W.A., Jones, H.P., Rios, M., Samaniego, A., Sechrest, W., Semmens, B. X., Thornton, H.E., Vega Thurber, R., Wails, C.N., Wolf, C.A., Zgliczynski, B.J., 2022. Harnessing island–ocean connections to maximize marine benefits of island conservation. *PNAS* 119, e2122354119.

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

Schiesari, L., Matias, M.G., Prado, P.I., Leibold, M.A., Albert, C.H., Howeth, J.G., Leroux, S.J., Pardini, R., Siqueira, T., Brancalion, P.H.S., Cabeza, M., Coutinho, R.M., Diniz-Filho, J.A.F., Fournier, B., Lahr, D.J.G., Lewinsohn, T.M., Martins, A., Morsello, C., Peres-Neto, P.R., Pillar, V.D., Vázquez, D.P., 2019. Towards an applied metaecology. *Perspect. Ecol. Conserv.* 17, 172–181.

Shantz, A.A., Ladd, M.C., Burkepile, D.E., 2017. Algal nitrogen and phosphorus content drive inter- and intraspecific differences in herbivore grazing on a Caribbean reef. *J. Exp. Mar. Biol. Ecol.* 497, 164–171.

Spatz, D.R., Holmes, N.D., Will, D.J., Hein, S., Carter, Z.T., Fewster, R.M., Keitt, B., Genovesi, P., Samaniego, A., Croll, D.A., Tershy, B.R., Russell, J.C., 2022. The global contribution of invasive vertebrate eradication as a key island restoration tool. *Sci. Rep.* 12, 13391.

Steibl, S., Steiger, S., Wegmann, A.S., Holmes, N.D., Young, H.S., Carr, P., Russell, J.C., 2024. Atolls are globally important sites for tropical seabirds. *Nat. Ecol. Evol.* 1–9.

Steven, A.D.L., Atkinson, M.J., 2003. Nutrient uptake by coral-reef microatolls. *Coral Reefs.* 22, 197–204.

Tandon, K., Lu, C.-Y., Chiang, P.-W., Wada, N., Yang, S.-H., Chan, Y.-F., Chen, P.-Y., Chang, H.-Y., Chiou, Y.-J., Chou, M.-S., Chen, W.-M., Tang, S.-L., 2020. Comparative genomics: Dominant coral-bacterium *Endozoicomonas acroporae* metabolizes dimethylsulfoniopropionate (DMSP). *ISME J.* 14, 1290–1303.

Teeling, H., Fuchs, B.M., Becher, D., Klockow, C., Gardebrecht, A., Bennke, C.M., Kassabgy, M., Huang, S., Mann, A.J., Waldmann, J., Weber, M., Klindworth, A., Otto, A., Lange, J., Bernhardt, J., Reinsch, C., Hecker, M., Peplies, J., Bockelmann, F. D., Callies, U., Gerdts, G., Wichels, A., Wiltshire, K.H., Glöckner, F.O., Schweder, T., Amann, R., 2012. Substrate-controlled succession of marine bacterioplankton populations induced by a phytoplankton bloom. *Science* 336, 608–611.

Tershy, B.R., Shen, K.-W., Newton, K.M., Holmes, N.D., Croll, D.A., 2015. The importance of islands for the protection of biological and linguistic diversity. *BioScience* 65, 592–597.

Treusch, A.H., Vergin, K.L., Finlay, L.A., Donatz, M.G., Burton, R.M., Carlson, C.A., Giovannoni, S.J., 2009. Seasonality and vertical structure of microbial communities in an ocean gyre. *ISME J.* 3, 1148–1163.

Tulloch, V.J.D., Atkinson, S., Possingham, H.P., Peterson, N., Linke, S., Allan, J.R., Kaiye, A., Keako, M., Sabi, J., Suruman, B., Adams, V.M., 2021. Minimizing cross-realm threats from land-use change: A national-scale conservation framework connecting land, freshwater and marine systems. *Biol. Cons.* 254, 108954.

United Nations Environment Agency. (2019). Resolution 73/284: United Nations Decade on Ecosystem Restoration (2021–2030) [WWW Document]. *https://undocs.org/A/RES/73/284*. URL https://undocs.org/A/RES/73/284.

Vander Zanden, M.J., Clayton, M.K., Moody, E.K., Solomon, C.T., Weidel, B.C., 2015. Stable isotope turnover and half-life in animal tissues: A literature synthesis. *PLOS ONE* 10, e0116182.

Vanderklift, M.A., Ponsard, S., 2003. Sources of variation in consumer-diet δ15N enrichment: a meta-analysis. *Oecologia* 136, 169–182.

Vergés, A., Vanderklift, M.A., Doropoulos, C., Hyndes, G.A., 2011. Spatial patterns in herbivory on a coral reef are influenced by structural complexity but not by algal traits. *PLOS ONE* 6, e17115.

Vozzo, M.L., Doropoulos, C., Silliman, B.R., Steven, A., Reeves, S.E., ter Hofstede, R., van Koningsveld, M., van de Koppel, J., McPherson, T., Ronan, M., Saunders, M.I., 2023. To restore coastal marine areas, we need to work across multiple habitats simultaneously. *PNAS* 120, e2300546120.

Wada, N., Hsu, M.-T., Tandon, K., Hsiao, S.-S.-Y., Chen, H.-J., Chen, Y.-H., Chiang, P.-W., Yu, S.-P., Lu, C.-Y., Chiou, Y.-J., Tu, Y.-C., Tian, X., Chen, B.-C., Lee, D.-C., Yamashiro, H., Bourne, D.G., Tang, S.-L., 2022. High-resolution spatial and genomic characterization of coral-associated microbial aggregates in the coral *Stylophora pistillata*. *Sci. Adv.* 8, eabo2431.

Wakwella, A., Wenger, A., Jenkins, A., Lamb, J., Kuempel, C.D., Claar, D., Corbin, C., Falinski, K., Rivera, A., Grantham, H.S., Jupiter, S.D., 2023. Integrated watershed management solutions for healthy coastal ecosystems and people. *Cambridge Prisms: Coastal Futures* 1, e27.

Wedding, L.M. et al. (In review). Global sustainability requires synergies between planning and restoration to benefit ocean-human health.

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., Micheli, F., 2022. Linking multiple stressor science to policy opportunities through network modeling. *Marine Policy* 146, 105307.

West, N.J., Lepère, C., Manes, C.-L. de O., Catala, P., Scanlan, D.J., Lebaron, P., 2016. Distinct spatial patterns of SAR11, SAR86, and Actinobacteria diversity along a transect in the ultra-oligotrophic South Pacific Ocean. *Front. Microbiol.* 7, 234.

Williams, G.J., Sandin, S.A., Zgliczynski, B.J., Fox, M.D., Gove, J.M., Rogers, J.S., Furby, K.A., Hartmann, A.C., Caldwell, Z.R., Price, N.N., Smith, J.E., 2018. Biophysical drivers of coral trophic depth zonation. *Mar. Biol.* 165, 60.

Wilson, S.K., Graham, N.A.J., Polunin, N.V.C., 2007. Appraisal of visual assessments of habitat complexity and benthic composition on coral reefs. *Mar. Biol.* 151, 1069–1076.

Wood, J.R., Alcover, J.A., Blackburn, T.M., Bover, P., Duncan, R.P., Hume, J.P., Louys, J., Meijer, H.J.M., Rando, J.C., Wilmshurst, J.M., 2017. Island extinctions: processes, patterns, and potential for ecosystem restoration. *Environ. Conserv.* 44, 348–358.

Wortley, L., Hero, J.-M., Howes, M., 2013. Evaluating ecological restoration success: A review of the literature. *Restor. Ecol.* 21, 537–543.

Young, H.S., McCauley, D.J., Dunbar, R.B., Dirzo, R., 2010. Plants cause ecosystem nutrient depletion via the interruption of bird-derived spatial subsidies. *PNAS* 107, 2072–2077.

Young, H.S., Miller-ter Kuile, A., McCauley, D.J., Dirzo, R., 2017. Cascading community and ecosystem consequences of introduced coconut palms (*Cocos nucifera*) in tropical islands. *Can. J. Zool.* 95, 139–148.

Zaneveld, J.R., Burkepile, D.E., Shantz, A.A., Pritchard, C.E., McMinds, R., Payet, J.P., Welsh, R., Correa, A.M.S., Lemoine, N.P., Rosales, S., Fuchs, C., Maynard, J.A., Thurber, R.V., 2016. Overfishing and nutrient pollution interact with temperature to disrupt coral reefs down to microbial scales. *Nat. Commun.* 7, 11833.

Zubia, M., Depetris, M., Flores, O., Turquet, J., Cuet, P., 2018. Macroalgae as a tool for assessing the ecological status of coral reefs under the Water Framework Directive: A case study on the reef flats of La Réunion (Indian Ocean). *Mar. Pollut. Bull.* 137, 339–351.