Check for updates

Received: 5 December 2023 | Revised: 1 March 2024 | Accepted: 20 May 2024

DOI: 10.1111/btp.13354

bioTROPICA ASSOCIATION FOR TROPICAL BIOLOGY AND CONSERVATION WILEY

ORIGINAL ARTICLE

Seabird presence and seasonality influence nutrient dynamics of atoll habitats

Jennifer Appoo[1,2] | Nancy Bunbury[2,3] | Jake Letori[4] | Aurelie Hector[4] | Annie Gendron[4] | Nicholas A. J. Graham[5] | Gerard Rocamora[4,6] | Matthieu Le Corre[1] | Sébastien Jaquemet[1]

[1]UMR ENTROPIE, Université de La Réunion, 97744 Saint Denis Cedex 9, La Réunion, France

[2]Seychelles Islands Foundation, Victoria, Mahé, Seychelles

[3]Centre for Ecology and Conservation, University of Exeter, Cornwall, UK

[4]Island Conservation Society, Pointe Larue, Mahé, Seychelles

[5]Lancaster Environment Centre, Lancaster University, Lancaster, UK

[6]Island Biodiversity and Conservation Centre, University of Seychelles, Anse Royale, Mahé, Seychelles

Correspondence
Jennifer Appoo, UMR ENTROPIE, Université de La Réunion, 15 Avenue René Cassin, 97744 Saint Denis Cedex 9, La Réunion, France.
Email: jennifer.appoo@univ-reunion.fr

Funding information
Université de La Réunion; Rufford Foundation, Grant/Award Number: 36780-1; Fondation Bertarelli

Associate Editor: Jennifer Powers
Handling Editor: Julio E Campo

Abstract

Marine nutrients underpin productivity and functioning of oceanic island ecosystems. On islands where they nest, seabirds represent a primary source of marine nutrients. In tropical regions, some of the largest seabird populations nest on atolls, yet there is limited information available on seabird contributions to atoll ecosystem nutrient dynamics. To investigate the spatial and seasonal dynamics of seabird contributions, we assessed seabird colonies of different taxa, including red-footed boobies and terns, nesting on separate islands of Farquhar Atoll, Seychelles. We assessed nutrient concentrations of guano, soil, coastal plants, and nearby seagrass in seabird colonies and at a control island with no seabirds, during the wet and dry seasons. Sooty terns contributed the highest quantities of nutrients, estimated at 71.2 N tonne/year and 52.2 P tonne/year. Seabird-derived nutrient transfer occurred year-round from seabird colonies to soil, coastal plants and seagrass. Soil macro- and inorganic nutrients were higher in the high-density tern colony and during the dry season, coinciding with the breeding period of sooty terns. Both red-footed booby and tern colonies maintained high nitrogen levels in coastal plants year-round, while phosphorus levels did not differ between islands or seasons. Seabird-derived nitrogen reversed nitrogen limitation of seagrass during the dry season. We provide the first insights into seabird nutrient contributions to atoll ecosystems in Seychelles, with recommendations for seabird conservation to boost and support atoll and island ecosystem resilience. Our results from a relatively undisturbed atoll serve as a baseline with which more impacted atolls and future changes can be assessed.

KEYWORDS
Indian Ocean, island ecosystems, marine subsidies, red-footed boobies, seagrass, Seychelles, sooty terns, stable isotopes

This is an open access article under the terms of the Creative Commons Attribution-NonCommercial-NoDerivs License, which permits use and distribution in any medium, provided the original work is properly cited, the use is non-commercial and no modifications or adaptations are made.
© 2024 The Author(s). *Biotropica* published by Wiley Periodicals LLC on behalf of Association for Tropical Biology and Conservation.

1 | INTRODUCTION

Resource subsidies are critical in shaping island biodiversity and functioning (Obrist et al., 2020; Polis et al., 1997). Isolated from continental landmasses, oceanic islands receive organisms, detritus, and nutrients mostly from the surrounding marine environment (Polis & Hurd, 1996). Islands are prime nesting and roosting habitats for seabirds, making seabirds a principal source of marine subsidies (Smith et al., 2011). Seabirds act as bio-vectors, transferring and depositing marine nutrients, mainly in the form of guano, from oceanic feeding habitats to their island breeding colonies (Otero et al., 2018). In tropical regions, some of the largest breeding seabird colonies occur on atolls (Berr et al., 2023). On atolls, seabird-derived nutrients sustain terrestrial plant communities (Schmidt et al., 2004; Young et al., 2010) and, when transferred to nearshore reefs via runoff, enhance biomass and growth of corals and fish (Benkwitt et al., 2019; Graham et al., 2018; Savage, 2019). These links have highlighted the major role seabird subsidies play in atoll biodiversity (Benkwitt et al., 2020; Lorrain et al., 2017) and ecosystem services (Plazas-Jiménez & Cianciaruso, 2020), and hence the need to better understand seabird contributions to atoll terrestrial and marine ecosystems (Berr et al., 2023). Despite this importance, studies of seabird effects on atolls remain limited and are often underrepresented in global meta-analyses (Grant et al., 2022; Van Der Vegt & Bokhorst, 2023).

Seabirds are taxonomically diverse, with substantial variation in their spatial and temporal nutrient subsidies (Pascoe et al., 2022). The dynamics of seabird subsidies are therefore governed by species-specific traits related to foraging and breeding. For example, nutrient content of guano depends on diet, nutrient distribution is determined by nesting location and density, and nutrient quantity is influenced by biomass and breeding duration (Smith et al., 2011). Many seabirds are also seasonal breeders, which dictates timing of nutrient deposition. Ultimately, these traits influence ecosystem responses to seabird subsidies, and although these relationships have been explored for temperate or polar seabirds (Zwolicki et al., 2013, 2016), they are relatively unexplored for tropical species. The behavior of tropical seabirds differs markedly from seabirds in temperate or polar regions (Weimerskirch, 2007). For example, tropical seabirds have broader diets and feeding strategies (Catry et al., 2009), and they often have nonseasonal and protracted breeding cycles (Carr et al., 2021; Catry et al., 2013). Investigations of seabird subsidies on atolls have mainly compared seabird effects between high or low seabird densities, regardless of taxonomy (Benkwitt et al., 2021; McCauley et al., 2012). How species-specific seabird foraging and breeding behaviors influence tropical seabird nutrient provisioning, and the broader implications for atoll nutrient dynamics, however, has not yet been studied.

Here, we report on a quantitative and qualitative assessment of seabird-derived nutrients to the terrestrial and marine ecosystems of the relatively undisturbed Farquhar Atoll in Southern Seychelles. We incorporate local weather seasonality since rainfall influences nutrient solubility, as well as nutrient dissipation through runoff and groundwater discharge, and therefore nutrient availability in nearshore environments (McMahon & Santos, 2017; Signa et al., 2021). Specifically, we aimed to (1) assess the nutrient input from seabird colonies of different taxa, (2) determine whether seabird-derived nutrients are transferred to terrestrial and nearshore environments and examine how this varies across taxa and seasons, (3) evaluate how nutrient levels in terrestrial and nearshore habitats differ between seabird colonies and seasons, and (4) determine whether seabird-derived nutrients reverse nutrient limitations and increase growth rates of coastal and marine plants. To address these objectives we sampled guano, soil and coastal plants, representing the main medium and basal components of nutrient transfer from seabird guano to atoll communities, respectively. To assess nutrient provisioning from seabird colonies to the nearshore environment we sampled seagrass, a prominent marine macrophyte of atolls. Seagrasses incorporate nutrients from the surrounding waters over several months, making them ideal indicators of nutrient availability in nearshore environments (Allgeier et al., 2013; Duarte, 1990). We discuss our results in the context of island seabird conservation.

2 | METHODS

2.1 | Study area

Farquhar Atoll (10°11′ S, 51°06′ E) lies in the Western Indian Ocean, ca. 770 km from Mahé, the main island of Seychelles, and 285 km northeast of Madagascar (Figure S1). Farquhar consists of 11 islands (total landmass 8 km^2), the largest three being North Island, South Island and Goëlettes (see also Data S1). Anthropogenic activity on Farquhar is limited to a small settlement on North Island operating an ecotourism establishment, (10 beds, ca. 40 staff, Duvat et al., 2017). On North and South Islands, the beach vegetation consists of native coastal shrubs, which transitions into a mix of indigenous and introduced grasses and trees inland. In contrast, Goëlettes is treeless and covered in a low herb plant community, with coastal shrubs along the shores (Stoddart & Poore, 1970). There are large expanses of seagrass adjacent to the islands in the lagoon and reef flats, dominated by *Thalassodendron ciliatum* (Stokes et al., 2019).

Large breeding colonies of red-footed boobies *Sula sula*, brown noddies *Anous stolidous* and sooty terns *Onychoprion fuscatus*, are found on two separate islands (Duhec et al., 2017). Sooty terns and brown noddies nest on Goëlettes, with estimated population sizes of 208,625 and 19,139 breeding pairs, respectively (Table S1; ICS unpublished data). They form simple nests on the ground, with breeding starting in May and last chicks fledging in October. Two red-footed booby colonies are located along the lagoon coastline and tidal inlets of South Island, estimated at a total of 11,069 breeding pairs (Table S1; ICS unpublished data). Red-footed boobies breed year-round with peaks in March–April and November–December in nests around 1–2 m from the ground. All three species prey mainly on pelagic fish and cephalopods (Catry et al., 2009; Weimerskirch et al., 2005). Other seabirds breed on Farquhar's islets but in smaller

17447429, 2024, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/btp.13354 by INASP/HINARI - SEYCHELLES, Wiley Online Library on [03/07/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

numbers (<100 breeding pairs each), including black-naped terns *Sterna sumatrana*, roseate terns *Sterna dougallii*, lesser noddies *Anous tenuirostris*, greater-crested tern *Thalasseus bergii* and white tern *Gygis alba* (Duhec et al., 2017). North Island, in contrast, has almost no breeding seabirds, attributed to the island's historical use as the main center for human settlement and coconut exploitation (Duhec et al., 2017). Most rain on Farquhar falls between November and April (average total 969.8 mm; ICS, unpublished data) as a result of north-west monsoon winds. Between May and October, trade winds blowing from the south-east result in lower rainfall (average total 399.4 mm; ICS, unpublished data; Piggot, 1961).

2.2 | Sampling design

We investigated the influence of seabirds on nutrient dynamics using three separate islands and their breeding seabird species as a treatment group: (a) red-footed boobies on South Island; (b) terns, comprising brown noddies and sooty terns, on Goëlettes; and (c) North Island, with no breeding seabirds, as a control island (except for a few nests and roosting birds at the southern end of the island, JL pers. obs). Because of their relatively low numbers, we did not account for the additional breeding species on Goëlettes and assumed that they make a relatively minor contribution to seabird-derived nutrient dynamics. To account for local seasonality we sampled soil, coastal vegetation and seagrass in both the wet (March 2022) and dry seasons (August 2022). Full details of the sampling and analytical methods are provided in the Data S1.

2.3 | Seabird nutrient input

To determine the quantity of nutrients delivered by seabirds, we collected fresh seabird droppings from the three breeding species within their colonies. Red-footed booby guano was collected on a black plastic sheet (2 × 2 m) pinned to the ground below nesting and roosting individuals in March. Guano was sampled shortly after deposition on the first day, with additional droppings obtained by leaving the plastic sheet overnight and collected in the early morning. For brown noddies and sooty terns, we collected droppings from fresh samples on vegetation near breeding and roosting individuals in April and August, respectively. Droppings were combined to obtain a minimum of 30 g wet weight per species for nutrient analyses (Staunton Smith & Johnson, 1995). Separate individual samples were collected for isotopic analysis (see below). All samples were kept cool in the field and stored frozen until further processing. We determined macro- and micro-nutrient content of fresh guano for each species. Macronutrients consisted of total N, ammonium ($N\text{-}NH_4^+$), nitrate ($N\text{-}N0_3^-$) and total P, while micronutrients comprised of iron (Fe), manganese (Mn), zinc (Zn) and copper (Cu).

We estimated the total annual N and P input from seabird droppings based on the equation by Riddick et al. (2018), and which we adapted following Graham et al. (2018).

$$\text{Nutrient}_{gi} = Q_{gi} \times Dr_i \times \left[\left(Bd_i \times T_i \times f_i \right) + \left(\frac{P_i}{2} \times Bd_i \right) \right]$$

Annual input per nutrient type and species (Nutrient_{gi}, t/year) was obtained from the quantity of N or P measured in seabird droppings for each species (Q_{gi}, mg/g), the species defecation rate (Dr_i, g/bird/day), the number of breeding adults for each species (Bd_i), the length of the breeding period (number of days from courtship to end of chick-rearing, T_i), the proportion of time spent at the colony during breeding (to account for absence of birds during feeding bouts, f_i) and the species productivity (fledged chicks per breeding pair, P_i). The defecation rate for red-footed boobies was from Young et al. (2010). For brown noddies and sooty terns, we estimated excrement rates based on measurements for black noddy *A. minutus* scaled allometrically to body size according to Staunton Smith and Johnson (1995). Values for the length of the breeding period, proportion of time at the colony and productivity for each species were obtained from Riddick et al. (2012). On Farquhar, red-footed booby and brown noddy colonies also contain roosting individuals, while sooty tern colonies do not. We lacked data on non-breeders, so our estimates are for breeding seabirds only.

2.4 | Terrestrial and marine sampling

We sampled soil and terrestrial coastal vegetation in two different habitat types on each island; coastal shrub habitat and low herbaceous habitat. In each habitat type, samples were collected along three randomly placed 50-m transects set a minimum of 100 m apart and parallel to the lagoon shore. As South Island had no low herbaceous habitat, coastal shrub habitat was sampled at each of the two red-footed booby colonies (Figure S1). On the two seabird islands, we sampled within the colonies. Along each transect we collected soil within the uppermost 5 cm at three evenly spaced positions, then homogenized to obtain a composite surface soil sample. Soil was sieved (<2 mm mesh) to remove rocks and debris (Young et al., 2010). A subsample was obtained for isotope analysis, while the remaining was used for nutrient analyses. Along the transect, we collected samples of green leaves in full sun from five individuals of *Heliotropium arboreum* in the coastal shrub habitat and *Achyranthes aspera* in the low herb habitat, reflecting nutrients incorporated over the last 1–2 months (Schmidt et al., 2004; Young et al., 2011). For each transect, we subsampled one leaf from each plant individual for isotope analysis and the remaining leaves were homogenized for nutrient analyses.

For marine sampling, we sampled the seagrass *T. ciliatum* adjacent to each island. Sampling locations were at least 100 m apart and < 300 m from the island. We collected seagrass leaves at six random locations within a 5-m radius. A subsample from each location was obtained for isotope analysis. All samples for isotope analysis were stored frozen upon return from the field until further processing, and the remaining samples were air-dried. We sampled the same locations in both seasons.

17447429, 2024, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/btp.13354 by INASP/HINARI - SEYCHELLES, Wiley Online Library on [03/07/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

2.5 | Nutrient analyses

Nutrient levels and stoichiometric ratios provide useful insights into ecosystem functioning. For soil samples, we characterized their properties including pH, electrical conductivity (EC), total carbon (C), organic carbon (C org) and cationic exchange capacity (CEC), and determined levels of main nutrients required for plant growth in bioavailable and inorganic forms, comprising of $N\text{-}NH_4^+$ and $N\text{-}NO_3^-$, bioavailable phosphorus (P-a) and exchangeable cations (Ca^{2+}, Mg^{2+}, Na^+ and K^+) (Lavelle et al., 2005). For coastal plants and seagrass, we assessed total C and organic C, respectively, and total N and P for both sample types. Levels of limiting nutrients (N and P) determine the quantity of nutrient subsidy and provide information about controls on ecosystem productivity (Polis et al., 1997). We derived stoichiometric ratios for coastal plants and seagrass as indicators of nutrient limitations (Sitters et al., 2015). In plants, reductions in nutrient limitations, determined by low C:nutrient ratios, are diagnostic of high plant nutrient quality (Sitters et al., 2015) and growth rate (Ågren, 2004, 2008). Nutrient analyses were conducted at the CIRAD-Reunion in the laboratory of agronomic analyses.

2.6 | Isotopic analyses

Evidence on nutrient origin can be tracked through nitrogen isotopic ratios ($\delta^{15}N$) (Mizutani & Wada, 1988). Because they feed at high trophic levels in the marine environment, seabirds acquire a high $\delta^{15}N$ signature, making $\delta^{15}N$ a reliable tracer of seabird-derived nutrients (Pascoe et al., 2021). We determined $\delta^{15}N$ on subsamples of seabird guano, soil and plant material. Additionally, we determined carbon isotopic ratios ($\delta^{13}C$) on samples of coastal plants and seagrass. In plants, $\delta^{13}C$ level is an indicator of physiological processes (Marshall et al., 2007), such as high photosynthetic activity or water stress (Mulder et al., 2011). Stable isotope analyses were conducted at Lancaster University, UK. Soil and seagrass samples were run twice, once after repeated acidifications with 1 M HCl to remove carbonates for $\delta^{13}C$ analyses and once without this treatment for $\delta^{15}N$. Accuracy based on internal standards was within 0.2 ‰ SD for $\delta^{15}N$ and 0.1 ‰ SD for $\delta^{13}C$.

2.7 | Data analysis

All analyses were conducted in R version 4.3.0 (R Core Team, 2022). We tested for differences in baseline seabird-derived nutrients entering each colony by comparing guano $\delta^{15}N$ between taxa. Shapiro–Wilk tests revealed non-normality in residuals, therefore we used the Kruskal–Wallis test, followed by Dunn's post hoc tests with Bonferroni correction to identify the taxa. We assessed the transfer of seabird-derived nutrients using linear mixed models (LMMs) for soil, coastal plants and seagrass separately using *lme4* package (Bates et al., 2015). We tested for differences in $\delta^{15}N$ as response variable, between both main and interaction effects of treatments (control, red-footed booby, tern) and seasons (wet, dry) as predictor variables. Sampling location (transect) was included as a random effect to account for repeated sampling. For soil and coastal plants, we pooled measurements of the two habitats (coastal shrub and low herb habitat) since we were interested in the community-level response, and added habitat type as a covariate in the model. Where significant differences were detected, we performed post-hoc tests with Bonferroni adjustment to identify differing groups using the *emmeans* package (Lenth, 2023).

We used principal component analysis (PCA) to explore differences in soil properties and nutrient concentrations between treatment groups and season. PCA was conducted on scaled values and Euclidean distance matrix using the unconstrained redundancy analysis from the *vegan* package (Okanasen et al., 2018). We conducted permutational multivariate analysis of variance (PERMANOVA) based on Euclidean distance matrix to identify differences in soil parameters between treatments, seasons and their interaction. We then performed pairwise comparisons between each level of treatment group with the package *pairwiseAdonis* (Arbizu, 2017), using 10,000 permutations and Bonferroni *p*-value adjustment.

To examine the influence of seabirds on foliar nutrient levels and ratios of coastal vegetation and seagrass, we ran separate LMMs for each nutrient type (N, P), ratio (C:N, C:P) and $\delta^{13}C$ as response variables. Nutrient ratios were determined on a molar basis, and the log of ratios were used in all analyses and representation to avoid errors and misinterpretation (Isles, 2020). We tested for differences in predictor variables between both main and interaction effects of treatments and seasons, with sampling location as a random effect. Habitat type was included as a covariate for coastal plants, with pooled measurements from the two habitats. We performed post-hoc tests with Bonferroni adjustment between factor levels where significant differences were detected. Lastly, we plotted $\delta^{15}N$ against %N to verify whether seabird subsidies (enrichment in $\delta^{15}N$) resulted in biologically relevant uptake of nitrogen %N in coastal plants and seagrass (Obrist et al., 2022).

For all LMMs, we computed the marginal and conditional R^2 as goodness-of-fit metrics using the *MuMin* package (Barton, 2023). Marginal and conditional R^2 describe the proportion of variance explained by the fixed effects only and fixed and random effects, respectively. For three of 13 models, sampling location (random effect) explained zero variance and led to a singular fit. Removing the random effect led to the same results so we kept it because of our repeated sampling. Model assumptions were verified using the protocol described by Zuur and Ieno (2016).

3 | RESULTS

3.1 | Nutrient input from seabird colonies of different taxa

Breeding sooty terns comprised the highest seabird biomass (496.8 kg/ha) and deposited the highest annual quantities of total N and total P to Farquhar Atoll, estimated at 71.2 (65.7–76.7) tonne/

17447429, 2024, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/btp.13354 by INASP/HINARI - SEYCHELLES, Wiley Online Library on [03/07/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

year and 52.2 (48.2–56.2) tonne/year (min–max, dry weight), respectively. This was followed by red-footed boobies (biomass 22.4 kg/ha) depositing 9.12 (7.74–10.5) N tonne/year and 9.07 (7.70–10.4) P tonne/year and brown noddies (biomass 48.0 kg/ha) contributing 6.30 (5.42–7.17) N tonne/year and 5.90 (5.09–6.72) P tonne/year (Table S1). Total N and P in fresh seabird droppings was similar for the three species, with total N ranging from 10.4% (brown noddy) to 11.1% (sooty tern) and total P ranging from 8.2% (sooty tern) to 10.6% (red-footed booby; Table 1). For micronutrients, brown noddy droppings had the highest quantities of Fe and Cu (330 µg/g and 29.2 µg/g dry weight, respectively), while red-footed booby droppings had the highest Zn and Mg (319 µg/g and 16.8 µg/g dry weight, respectively; Table 1).

3.2 | Seabird-derived nutrient transfer across taxa and seasons

Sooty tern guano $\delta^{15}N$ was higher than for brown noddy (adjusted $p = .04$; Table 2). Soil $\delta^{15}N$ was higher in the red-footed booby and tern colonies compared to the control during both wet and dry seasons (wet: control vs red-footed booby adjusted $p = .04$, control versus tern adjusted $p = .008$; dry: control vs red-footed booby adjusted $p = .04$, control versus tern adjusted $p = .01$; Figure 1a; Table S2). Similarly, seagrass $\delta^{15}N$ was higher in the two seabird colonies compared to the control for both seasons (wet: control vs red-footed booby adjusted $p = .003$, control vs tern adjusted $p = .02$; dry: control vs red-footed booby adjusted $p = .001$, control vs tern adjusted $p = .001$; Figure 1c; Table S2). For coastal plants, $\delta^{15}N$ in the red-footed booby colony was higher than the control during both seasons (wet: adjusted $p = .04$, dry: adjusted $p = .03$), but for the tern colony $\delta^{15}N$ was higher than the control during the wet season only (adjusted $p = .02$; Figure 1b). Coastal vegetation $\delta^{15}N$ in the tern colony was lower during the dry than the wet season (adjusted $p = .002$).

3.3 | Nutrient levels in terrestrial and nearshore habitats

Soil samples all had a pH of 7.0–9.0 (Table S3), with high variation in EC (0.57 ± 0.77, mean ± SD, $n = 36$) and CEC (12.1 ± 10.4, mean ± SD, $n = 36$). Within the cationic exchange complex, Ca^{2+} was the most dominant cation, followed by Mg^{2+}, Na^{+}, and K^{+} (Table S3). The first two axes of the PCA explained 84% of the variance of the whole dataset (Figure 2), with Axis 1 segregating roughly the tern colony from the red-footed booby and control groups, and Axis 2 tending to separate the red-footed booby colony from the control group, especially for dry season samples. Soil physical and chemical parameters differed between groups, with higher nutrient content in the tern colony (PERMANOVA tern vs control: adjusted $p = .05$, tern vs red-footed booby: adjusted $p = .03$). Soil nutrient content was lower in wet season compared to dry season (PERMANOVA $F_{1,35} = 7.01$, $p = .002$; Figure 2). Soil pH was negatively correlated to all other parameters indicating soil acidity increased with increasing nutrients.

For coastal plants, foliar %N was higher in the red-footed booby and tern colonies compared to the control site during the wet and dry seasons (Figure 3a; Table S4). Foliar %N was lower in the dry season than the wet season for the control group (adjusted $p = .01$). Leaf %P did not differ between groups in either season, but each group showed a decrease in %P from the wet to the dry season (control: adjusted $p = .004$, red-footed booby: adjusted $p = .01$, tern: adjusted $p = .003$; Figure 3b).

For seagrass, foliar %N was higher in the red-footed booby and tern colonies compared to the control during the dry season only (Figure 3f). Seagrass %N was higher in the dry season compared to the wet season for the red-footed booby (adjusted $p < .0001$) and tern group (adjusted $p < .0001$). %P in seagrass leaves was lower closer to the tern colony compared to the control site in the dry season (adjusted $p = .01$; Figure 3g). Seagrass %P was higher during the dry season than the wet season for the control group (adjusted $p = .03$; Table S5). There was a linear increase in foliar %N with increasing foliar $\delta^{15}N$ for coastal plants during the wet and dry seasons, and for seagrass during the dry season only (Figure 4).

3.4 | Coastal and marine plant nutrient limitations and growth rates

For coastal plants, log C:P ratios increased from wet to dry seasons for all groups (control: adjusted $p = .0008$, red-footed booby: adjusted $p = .0005$, tern: adjusted $p = .03$; Figure 3d, Table S4). For seagrass, log C:N values differed between all groups during the dry season (Figure 3h; Table S5) and between the wet and dry season

TABLE 1 Nutrient concentrations (total nitrogen [%N], total phosphorus [%P], ammonium [N-NH_4^+], nitrate [N-$N0_3^-$]) and trace elements (iron [Fe], copper [Cu], zinc [Zn], manganese [Mn]) in seabird droppings. Concentrations are given in dry weight.

Species	%N	%P	N-$NH4^+$ mg/g	N-NO_3^- µg/g	Fe	Cu	Zn	Mn
Red-footed booby *Sula sula*	10.7	10.6	16.7	18.0	212	25.1	319	16.8
Brown noddy *Anous stolidous*	10.4	9.8	16.8	29.2	330	29.2	280	15.8
Sooty tern *Onychoprion fuscata*	11.1	8.2	32.2	17.7	295	21.6	171	11.3

17447429, 2024, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/btp.13354 by INASP/HINARI - SEYCHELLES, Wiley Online Library on [03/07/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Component	Species	*n*	Range (min–max, ‰)	Mean ± SE (‰)
Guano	Red-footed booby *Sula sula*	28	6.41–21.9	10.8 ± 0.64
	Brown noddy *Anous stolidous*	25	7.64–15.0	9.77 ± 0.31
	Sooty tern *Onychoprion fuscata*	25	8.76–13.2	10.6 ± 0.22
Soil		36	7.08–20.4	13.3 ± 0.71
Coastal plant	*Heliotropium arboreum*	24	4.31–13.9	9.24 ± 0.59
	Achyranthes aspera	12	7.20–17.6	11.3 ± 1.04
Seagrass	*Thalassodendron ciliatum*	36	0.35–17.0	7.83 ± 0.58

TABLE 2 Overall range, mean ± SE of $\delta^{15}N$ values for each ecosystem component sampled across the study period and sampling locations.

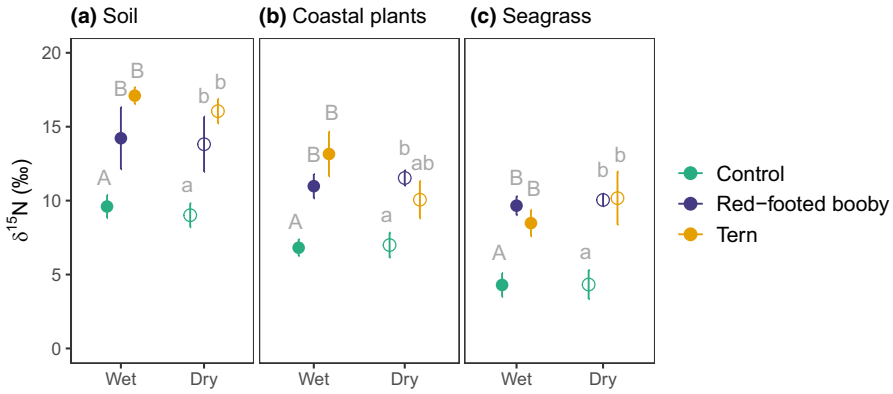


FIGURE 1 $\delta^{15}N$ ‰ (Mean ± *SE*) of each treatment (control, red-footed booby, tern) in wet and dry seasons, for (a) soil, (b) coastal plants and (c) seagrass. Closed and open circles represent the wet and dry season, respectively. Different uppercase and lowercase letters denote significant ($p \leq .05$) differences between means for the wet and dry seasons, respectively.

for all groups (control: adjusted $p = .01$, red-footed booby: adjusted $p = .0001$, tern: adjusted $p = .02$). Log C:P ratios were higher in the tern colony during the dry season (control vs tern: adjusted $p = .005$, tern vs red-footed booby: adjusted $p = .02$; Figure 3i).

Leaf $\delta^{13}C$ in coastal vegetation did not differ between groups in either season, but rather increased from the wet to the dry season for all groups (Figure 3e; Table S4). For seagrass, $\delta^{13}C$ was higher near the red-footed booby colony compared to the tern colony during the wet season (adjusted $p = .002$) and higher near the red-footed booby colony than the control during the dry season (adjusted $p = .02$; Figure 3j). Furthermore, $\delta^{13}C$ in seagrass decreased from the wet to the dry season near the control (adjusted $p = .0006$) and red-footed booby colony (adjusted $p = .003$).

4 | DISCUSSION

We estimated substantial seabird nutrient contributions on Farquhar Atoll, with a combined total from all three seabird species of 86.6 N tonne/year and 67.2 P tonne/year. Breeding sooty terns contributed the highest quantities of nutrients. We detected persistent seabird-derived nutrient transfer from red-footed booby and tern colonies to soil, coastal plants and seagrass. Soil macro- and inorganic nutrient levels were higher in the tern colony during the dry season, coinciding with the breeding period of sooty terns, while foliar nitrogen in coastal plants was higher in both seabird colonies year-round. Seabird-derived nutrients reversed nitrogen limitation of seagrass during the dry season.

4.1 | Seabird nutrient contributions across taxa

Population size is a key driver in nutrient quantity since it dictates the number of individuals acting as nutrient vectors (Subalusky & Post, 2019). In our study, sooty terns comprised the largest population and contributed the highest quantities of nutrients. While brown noddies were more abundant and had higher biomass compared to red-footed boobies, their nutrient quantity contribution was lower than that of red-footed boobies. This suggests that the year-round breeding of red-footed boobies supported an overall higher nutrient input. Our estimated nutrient inputs, ranged from 23.1 N kg/ha/year and 23.0 P kg/ha/year on South Island to 2421.6 N kg/ha/year and 1815.3 P kg/ha/year on Goëlettes. Nutrient inputs on Goëlettes exceeded those of agriculture practices (60–400 N kg/ha/year, Young et al., 2010; 156 N kg/ha/year and 30 kg P kg/ha/year, McFadden et al., 2016), and other tropical seabird islands (e.g., Heron Island, Australia: 587.5 N kg/ha/year, 118.8 P kg/ha/year [Staunton Smith & Johnson, 1995]; Guarita, Brazil: 1950.5 N kg/ha/year, Redonda, Antigua and Barbuda: 173. 4 N kg/ha/year, Siriba, Brazil: 221.08 N kg/ha/year [Linhares & Bugoni, 2023]). Our estimates do not account for nutrient contributions from non-breeding seabirds, which can constitute a large proportion of total populations

17447429, 2024, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/btp.13354 by INASP/HINARI - SEYCHELLES, Wiley Online Library on [03/07/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

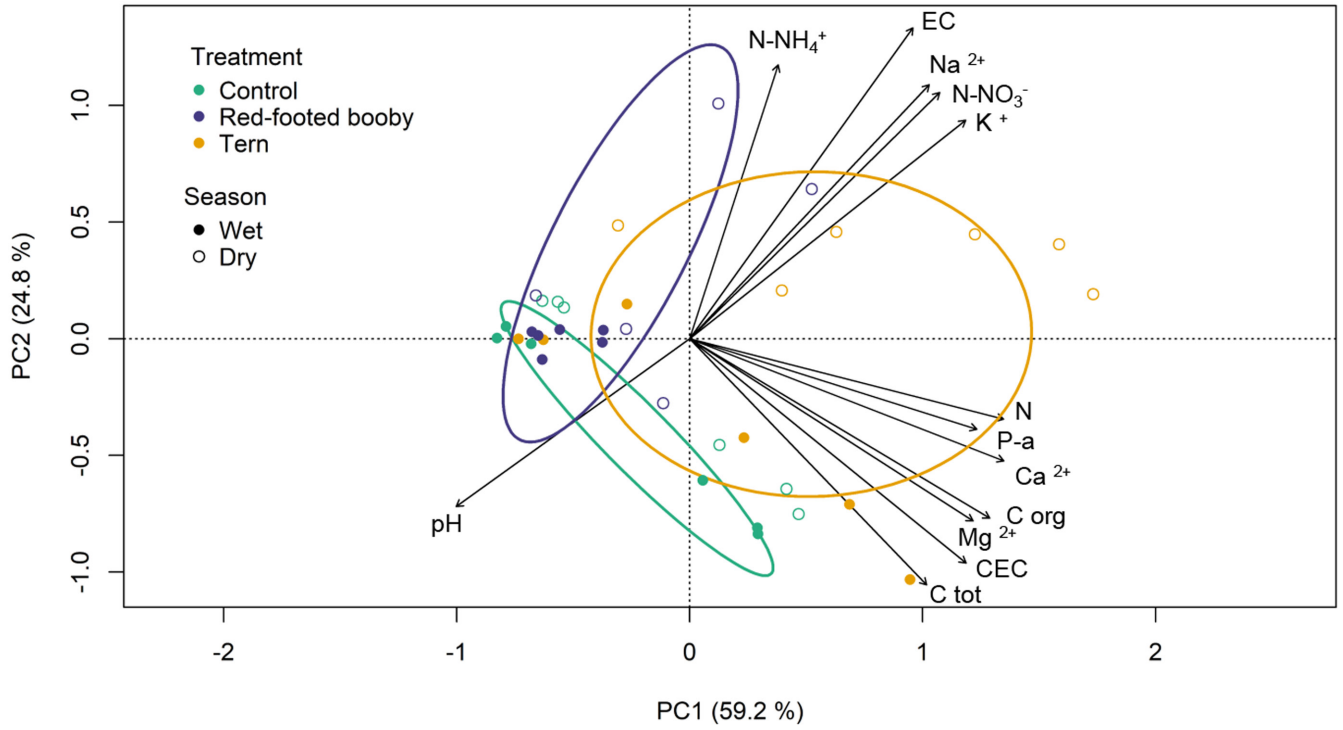


FIGURE 2 Results from principal component analysis (PCA) on the relationships between soil physical and chemical parameters across treatment and season. Points represent transect observations, with color depicting the treatment group and shape depicting the season. Black arrows represent the strength (arrow length) and direction of soil variable gradients. Ellipses represent 1 *SD* from the centroid of each treatment group.

(Schreiber & Chovan, 1986); for example, non-breeders can comprise 33% of breeding populations and spend 50% less time than breeders in their colony in temperate areas (Riddick et al., 2012). Quantification of non-breeding individuals year-round and their diurnal movement patterns would refine our estimates.

Tropical seabirds exhibit overlapping diets with a large diversity of prey items (Catry et al., 2009; Cherel et al., 2008). Consequently, guano macronutrient levels were similar for our three study species. Micronutrient content in guano concurs with that of their prey, comprising small pelagic fish and cephalopods rich in iron and zinc (Sabino et al., 2022). These concentrations are consistent with results of recent reviews and meta-analyses, for example, Suliforme droppings contain the highest levels of phosphorus and zinc compared to other seabird orders (De La Peña-Lastra, 2021; Grant et al., 2022). With similar guano nutrient content, differences in nutrient provisioning between the three seabird species in our study were therefore mainly driven by their biomass and breeding traits, that is, breeding duration. Guano $\delta^{15}N$ for sooty terns was slightly higher than for brown noddies, which may be due to differences in metabolism and the main fish species consumed (De La Peña-Lastra, 2021). In the Western Indian Ocean, sooty terns and brown noddies diet includes post-larval goatfish, anchovies and flying fish (Catry et al., 2009; Jaquemet et al., 2008). Here, sooty terns and brown noddies nested on the same island and their guano $\delta^{15}N$ did not differ from that of red-footed boobies, indicating similar nutrient isotopic baselines for these two seabird islands.

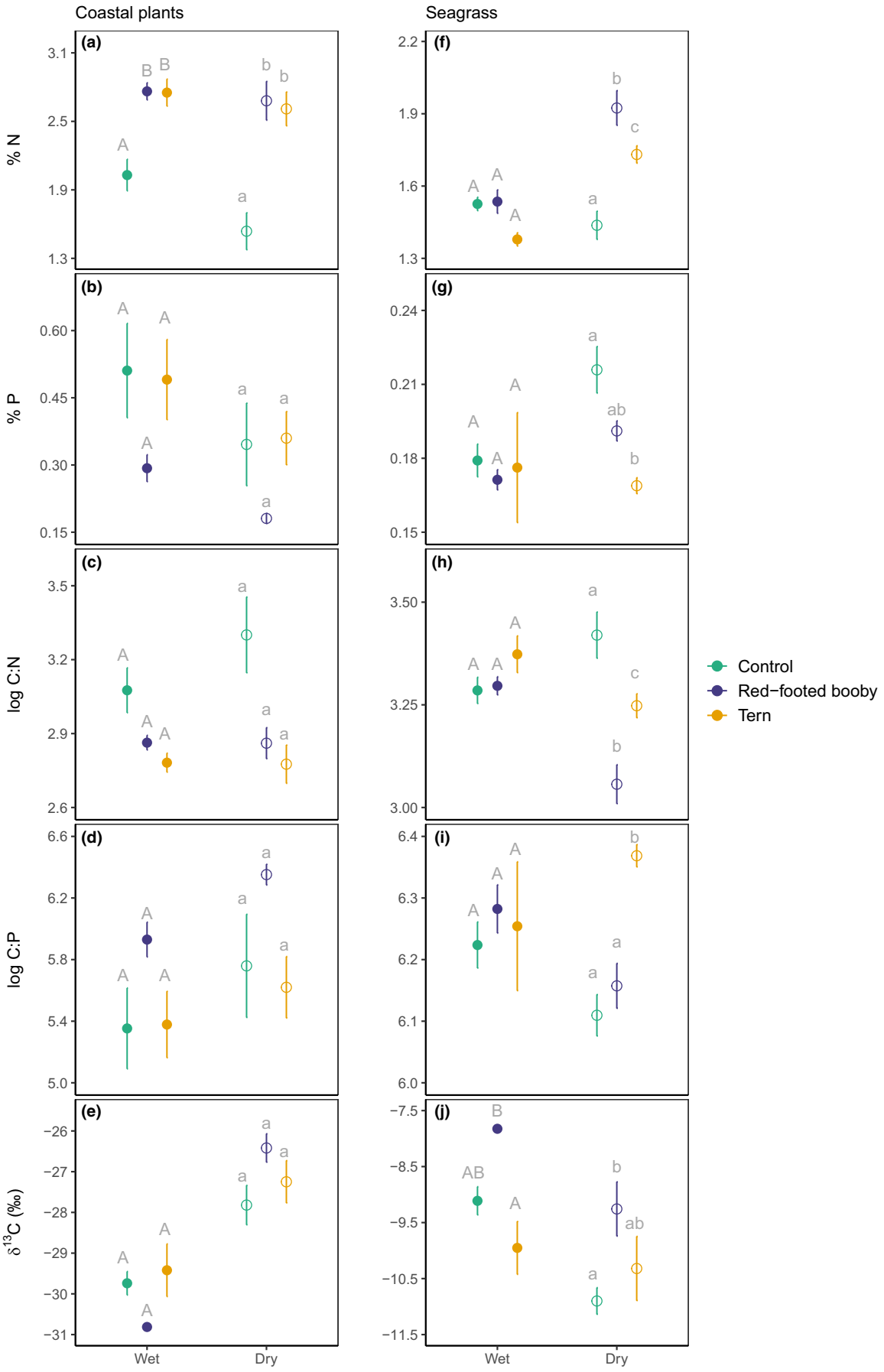
4.2 | Seabird-derived nutrient transfer

In the red-footed booby colony, the high $\delta^{15}N$ in both seasons indicated persistent transfer of seabird-derived nutrients to terrestrial and nearshore marine habitats linked to their year-round breeding patterns. In contrast, despite the breeding of the tern colony coinciding only with the dry season, we also detected high $\delta^{15}N$ during the wet season in terrestrial and nearshore ecosystems. This is presumably linked partly to brown noddies breeding in much smaller numbers during the wet season (ICS, unpublished data) and individuals which can remain at their breeding grounds year-round (Bailey, 1968; Lebarbenchon et al., 2023). However, because of isotopic fractionation of guano, nutrient input during the breeding season can maintain isotope levels throughout the non-breeding season (Pascoe et al., 2022). High $\delta^{15}N$ values in sediment have also played an important role in identifying abandoned seabird colonies (Mizutani et al., 1991) and tracking seabird activity over centuries from sediment cores (Michelutti et al., 2009).

4.3 | Nutrient levels in terrestrial and nearshore habitats

Although both seabird colonies had higher soil nutrient concentrations than the control site, soil macro- and inorganic nutrient levels were higher in the tern colony than in the red-footed booby

17447429, 2024, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/btp.13354 by INASP/HINARI - SEYCHELLES, Wiley Online Library on [03/07/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License



17447429, 2024, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/btp.13354 by INASP/HINARI - SEYCHELLES, Wiley Online Library on [03/07/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

FIGURE 3 Mean (± SE) of nutrient levels (expressed in % dry weight), log nutrient ratios and $\delta^{13}C$ ‰ of each group (control, red-footed booby, tern) in wet and dry seasons, for (a–e) coastal plants and (f–j) seagrass. Closed and open circles represent the wet and dry season, respectively. Different uppercase and lowercase letters denote significant ($p \leq .05$) differences between means for the wet and dry seasons, respectively. Note differences in y-axis scales. Error bars absent in some cases due to scaling.

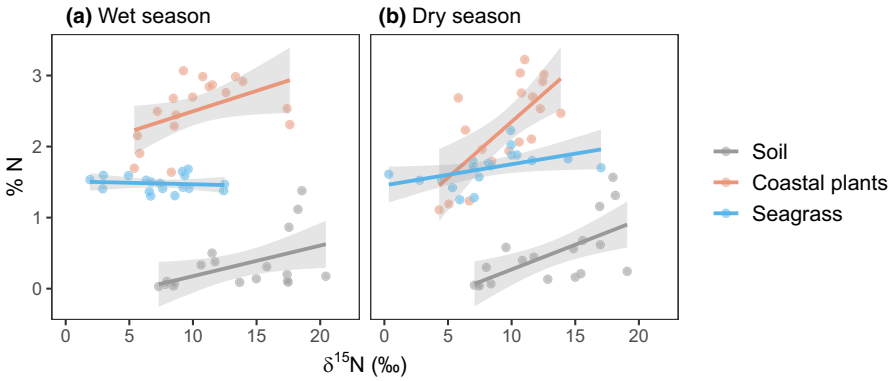


FIGURE 4 Relationships between $\delta^{15}N$ and %N during the (a) wet and (b) dry season for soil, coastal plants and seagrass. Shaded areas represent 95% CI.

colony. This is linked to the higher nest density of terns (Table S1) but it may also be influenced by the terns being ground-nesters, in contrast to the tree-nesting habits of red-footed boobies (Gaiotto et al., 2022). Furthermore, the red-footed booby colony's presence on South Island is relatively recent (ICS, unpublished data), in contrast to the long-established tern colony, where nutrients have accumulated over several decades. However, observed patterns may also be due to island size since the tern colony is on the smallest island of the study. On small islands, subsidy impacts are more pronounced since they have a greater perimeter-to-area ratio which enable greater per-unit-area effects (Obrist et al., 2022; Pascoe et al., 2021). Furthermore, soil nutrient levels were lower during the wet season, likely due to rainfall which increases solubility and loss of soil nutrients, either by plant uptake, or through leaching and surface run-off (De La Peña-Lastra, 2021). However, in the tern colony, higher nutrients during the dry season are almost certainly related to breeding seasonality. The relatively short occurrence of very high numbers of breeding sooty terns and brown noddies leads to an annual pulse in nutrient resources. Year-round sampling would elucidate the duration of effects and nutrient dynamics of this resource pulse. Additional studies can also assess intra-island nutrient variations, by documenting nest densities at sampling sites for within-colony comparisons, or at multiple distances outside the colony (Pascoe et al., 2022).

The persistent $\delta^{15}N$ enrichment in the seabird colonies led to year-round biologically relevant uptake of nitrogen (%N) in coastal vegetation. Average foliar %N was 1.4–1.7 times higher in both seabird colonies than the control site in both seasons. In contrast, foliar %P showed no response to seabird contributions, which has been observed elsewhere (Mulder et al., 2011). Phosphorus is less soluble than nitrogen and strongly adsorbed in soils, especially the calcareous soils of atolls which precipitate phosphorus as calcium phosphate (Otero et al., 2015). Phosphorus stability in soils can be long-lasting, even reflecting seabird-derived phosphorus from extinct colonies (De La Peña-Lastra et al., 2021; Mutillod et al., 2023; Wardle et al., 2009). Although a few red-footed boobies have recently started nesting at the southern tip of the control island, historically they used to occur in larger numbers on the control island (Feare, 1978), suggesting coastal plants on this island may derive phosphorus from long-term reserves (Mulder et al., 2011). Moreover, lower rainfall facilitates phosphorus retention in soil (De La Peña-Lastra, 2021), explaining the marked decrease in foliar %P during the dry season in all groups.

Despite the year-round transfer of seabird-derived nutrients to seagrass in the nearshore environment, $\delta^{15}N$ enrichment resulted in biologically relevant nitrogen uptake (seagrass foliar %N) at the seabird colonies only during the dry season. This was contrary to our expectations, since higher rainfall increases nutrient loadings in nearshore environments through surface run-off or leaching (Rankin & Jones, 2021). The higher biomass of seabirds, coinciding with the dry season, suggests that a critical threshold in seabird density is needed to generate responses in seagrass foliar nitrogen. Similar results were shown in Baltic Sea islands, with high nitrogen values in marine algae were detected only at islands with high seabird nesting densities (Kolb et al., 2010).

The carbonate substrate of tropical seagrass binds strongly with phosphorus, maintaining phosphorus levels in seagrass, even after many decades of discontinued seabird contributions (Herbert & Fourqurean, 2008), allowing us to make similar conclusions as with coastal plants. The dry season decrease in seagrass phosphorus levels near the tern colony is likely related to seagrass location and local oceanographic conditions. Seagrass near the tern colony is less sheltered than seagrass growing in the lagoon near the other two treatment groups. Exposed areas have lower rates of sediment oxygen uptake and consequently, lower rates of sediment phosphorus release compared to sheltered sites (Fourqurean & Zieman, 2002; Jensen et al., 1998). During the dry season, increased wave activity by the south-east monsoon winds may further reduce this process in seagrass at the tern colony, leading to decreased phosphorus availability.

17447429, 2024, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/btp.13354 by INASP/HINARI - SEYCHELLES, Wiley Online Library on [03/07/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

4.4 | Coastal and marine plant nutrient limitation and growth rates

Although seabird-derived nutrients increased foliar %N in coastal plants, we did not detect any reductions in nutrient limitation (log C:N, log C:P) to growth. This implies that other factors limit coastal plants in their responses to seabird contributions on atolls, such as limited availability of other essential macro- and micro-nutrients (Lavelle et al., 2005). Additionally, we did not find differences in foliar $\delta^{13}C$. In temperate locations, positive correlations between higher foliar seabird-derived nutrient levels and $\delta^{13}C$ enrichment have been documented, suggesting faster plant growth (Wainright et al., 1998). The lack of response in our study could be due to low sample sizes. We did detect increases in foliar $\delta^{13}C$ from the wet to the dry season, confirming water stress in the latter. To reduce water loss, plants reduce stomatal conductance, leading to reduced discrimination of ^{13}C isotopes and causing $\delta^{13}C$ to increase (Mulder et al., 2011).

In nearshore environments, response to seabird-derived nutrients is also governed by local geomorphological and oceanographic features, such as bottom topography, wave action, currents, distance to shore, and depth (Kazama, 2020; Signa et al., 2021). For seagrass, other factors such as epiphyte load, light availability and grazing pressure all interact to influence their functioning (Anderson & Fourqurean, 2003; Frankovich & Fourqurean, 1997). In our study, the transfer and uptake of seabird-derived nitrogen in seagrass during the dry season led to reduced nitrogen limitation (log C:N), coinciding with the higher biomass of breeding seabirds during this season. However, a larger sample size and quantification of seagrass physical parameters is needed to clarify the response of seagrass to seabird contributions.

4.5 | Conservation implications

From our results we can draw recommendations for management of tropical seabird populations. Nutrient input was driven by sooty terns in our study because of their higher biomass. Sooty terns are the most abundant tropical seabird (Hughes et al., 2017), therefore maintaining or restoring their populations and other highly-abundant species should be prioritized, because they have the greatest potential for supporting and boosting resilience of tropical island ecosystems (Berr et al., 2023). In Seychelles, sooty tern eggs have been exploited commercially since the beginning of the 20th century (Feare, 1976a; Hutchinson, 1950). Managed by local authorities, harvesting strategies are largely based on population demographic parameters (Feare, 1976b; Feare & Doherty, 2004, 2011). Based on our nutrient input estimations of an unharvested colony on Farquhar Atoll, we recommend phasing out egg exploitation, and replacing harvesting with sustainable ecotourism practices as income generating activities to reduce disturbance and rebuild sooty tern populations and their nutrient inputs.

Our results also show that other tropical seabirds, for example, red-footed boobies, supply nutrients continuously because of their lengthy breeding and roosting patterns, which helps maintain nutrient status of soil, plants and nearshore marine communities. Seabird conservation efforts should therefore also target species that breed year-round. Ultimately restoring, and supporting breeding populations of a range of seabirds on islands is likely to provide the widest range of nutrients throughout the year and contribute the most to atoll ecosystem functioning (Benkwitt et al., 2022).

4.6 | Conclusion

We present the first research on seabird nutrient contributions to atoll ecosystems in Seychelles, showing the spatial and temporal influences that tropical seabird subsidies have on soil and plants, and seagrass growing adjacent to atolls. Our study builds on research showing that response to seabird contributions is influenced by seabird biomass, breeding and foraging behaviors, seasonality and solubility of nutrients (Smith et al., 2011). Seabird-subsidized atolls play substantial roles in maintaining biodiversity and marine connectivity. Our research provides insights into a relatively undisturbed system which can be used as a benchmark site with which to compare more directly impacted atolls and future changes.

AUTHOR CONTRIBUTIONS

Conceptualization: Jennifer Appoo, Nancy Bunbury, Sébastien Jaquemet. *Investigation and data curation*: Jennifer Appoo, Jake Letori, Aurelie Hector, Annie Gendron. *Methodology, formal analysis, writing–original draft*: Jennifer Appoo. *Writing–review and editing*: Nancy Bunbury, Jake Letori, Aurelie Hector, Nicholas A.J. Graham, Gerard Rocamora, Matthieu Le Corre, Sébastien Jaquemet.

ACKNOWLEDGMENTS

We thank Island Conservation Society for providing logistical support during the fieldwork, and Islands Development Company for travel and permission to work on Farquhar Atoll. Special thanks go to ICS Heads of Conservation and Science, Pierre-André Adam, Matthew Morgan, and William McNeely and the rest of the Farquhar team for facilitating information. Funding was provided by the Rufford Foundation, the University of Reunion Island International Relations Department and the Bertarelli Foundation through the Marine Science Program. JA was supported by a doctoral fellowship from the Reunion Island Regional Council. Fieldwork was conducted under permit number A0157 by Seychelles Bureau of Standards.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Dryad Digital Repository at https://doi.org/10.5061/dryad.b8gtht7m4

ORCID

Jennifer Appoo https://orcid.org/0000-0002-3980-9435

17447429, 2024, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/btp.13354 by INASP/HINARI - SEYCHELLES, Wiley Online Library on [03/07/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

REFERENCES

Ågren, G. I. (2004). The C: N: P stoichiometry of autotrophs–theory and observations: The C: N: P stoichiometry of autotrophs. *Ecology Letters*, *7*(3), 185–191. https://doi.org/10.1111/j.1461-0248.2004.00567.x

Ågren, G. I. (2008). Stoichiometry and nutrition of plant growth in natural communities. *Annual Review of Ecology, Evolution, and Systematics*, *39*(1), 153–170. https://doi.org/10.1146/annurev.ecolsys.39.110707.173515

Allgeier, J. E., Yeager, L. A., & Layman, C. A. (2013). Consumers regulate nutrient limitation regimes and primary production in seagrass ecosystems. *Ecology*, *94*(2), 521–529. https://doi.org/10.1890/12-1122.1

Anderson, W. T., & Fourqurean, J. W. (2003). Intra- and interannual variability in seagrass carbon and nitrogen stable isotopes from south Florida, a preliminary study. *Organic Geochemistry*, *34*(2), 185–194. https://doi.org/10.1016/S0146-6380(02)00161-4

Arbizu, P. M. (2017). pairwiseAdonis: Pairwise multilevel comparison using Adonis. R 531 package version 0.4.

Bailey, R. S. (1968). The pelagic distributions of seabirds in the Western Indian Ocean. *IBIS*, *110*(4), 493–519. https://doi.org/10.1111/j.1474-919X.1968.tb00060.x

Barton, K. (2023). *MuMIn: Multi-Model Inference* (1.47.5).

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using **lme4**. *Journal of Statistical Software*, *67*(1), 1–48. https://doi.org/10.18637/jss.v067.i01

Benkwitt, C. E., Carr, P., Wilson, S. K., & Graham, N. A. J. (2022). Seabird diversity and biomass enhance cross-ecosystem nutrient subsidies. *Proceedings of the Royal Society B: Biological Sciences*, *289*(1974), 20220195. https://doi.org/10.1098/rspb.2022.0195

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

Benkwitt, C. E., 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 Biology*, *25*(8), 2619–2632. https://doi.org/10.1111/gcb.14643

Benkwitt, C. E., Wilson, S. K., & Graham, N. A. J. (2020). Biodiversity increases ecosystem functions despite multiple stressors on coral reefs. *Nature Ecology & Evolution*, *4*(7), 919–926. https://doi.org/10.1038/s41559-020-1203-9

Berr, T., Dias, M. P., Andréfouët, S., Davies, T., Handley, J., Le Corre, M., Millon, A., & Vidal, É. (2023). Seabird and reef conservation must include coral islands. *Trends in Ecology & Evolution*, *38*(6), 490–494. https://doi.org/10.1016/j.tree.2023.02.004

Carr, P., Votier, S., Koldewey, H., Godley, B., Wood, H., & Nicoll, M. A. C. (2021). Status and phenology of breeding seabirds and a review of important bird and biodiversity areas in the British Indian Ocean Territory. *Bird Conservation International*, *31*(1), 14–34. https://doi.org/10.1017/S0959270920000295

Catry, T., Ramos, J., Jaquemet, S., Faulquier, L., Berlincourt, M., Hauselmann, A., Pinet, P., & Le Corre, M. (2009). Comparative foraging ecology of a tropical seabird community of the Seychelles, western Indian Ocean. *Marine Ecology Progress Series*, *374*, 259–272. https://doi.org/10.3354/meps07713

Catry, T., Ramos, J. A., Catry, I., Monticelli, D., & Granadeiro, J. P. (2013). Inter-annual variability in the breeding performance of six tropical seabird species: Influence of life-history traits and relationship with oceanographic parameters. *Marine Biology*, *160*(5), 1189–1201. https://doi.org/10.1007/s00227-013-2171-2

Cherel, Y., Corre, M., Jaquemet, S., Ménard, F., Richard, P., & Weimerskirch, H. (2008). Resource partitioning within a tropical seabird community: New information from stable isotopes. *Marine Ecology Progress Series*, *366*, 281–291. https://doi.org/10.3354/meps07587

De La Peña-Lastra, S. (2021). Seabird droppings: Effects on a global and local level. *Science of the Total Environment*, *754*, 142148. https://doi.org/10.1016/j.scitotenv.2020.142148

De La Peña-Lastra, S., Gómez-Rodríguez, C., Pérez-Alberti, A., Torre, F., & Otero, X. L. (2021). Effects of a yellow legged gull (Larus michahellis) colony on soils and cliff vegetation in the Atlantic Islands of Galicia National Park (NW Spain). *Catena*, *199*, 105115. https://doi.org/10.1016/j.catena.2020.105115

Duarte, C. (1990). Seagrass nutrient content. *Marine Ecology Progress Series*, *67*, 201–207. https://doi.org/10.3354/meps067201

Duhec, A., Jeanne, R., & Skerrett, A. (2017). Breeding seabirds of Farquhar atoll, Seychelles including the return of two species: Red-footed booby Sula sula and Greater-crested tern Thalasseus bergii. *Sea Swallows*, *66*, 3–14.

Duvat, V. K. E., Volto, N., & Salmon, C. (2017). Impacts of category 5 tropical cyclone Fantala (April 2016) on Farquhar atoll, Seychelles Islands, Indian Ocean. *Geomorphology*, *298*, 41–62. https://doi.org/10.1016/j.geomorph.2017.09.022

Feare, C. J. (1976a). The breeding of the sooty tern *Sterna fuscata* in the Seychelles and the effects of experimental removal of its eggs. *Journal of Zoology*, *179*(3), 317–360. https://doi.org/10.1111/j.1469-7998.1976.tb02299.x

Feare, C. J. (1976b). The exploitation of sooty tern eggs in the Seychelles. *Biological Conservation*, *10*(3), 169–181. https://doi.org/10.1016/0006-3207(76)90033-1

Feare, C. J. (1978). The decline of booby (Sulidae) populations in the western Indian Ocean. *Biological Conservation*, *14*(4), 295–305. https://doi.org/10.1016/0006-3207(78)90046-0

Feare, C. J., & Doherty, P. F. (2004). Survival estimates of adult sooty terns Sterna fuscata from Bird Island, Seychelles: Survival estimates of adult sooty terns. *IBIS*, *146*(3), 475–480. https://doi.org/10.1111/j.1474-919x.2004.00288.x

Feare, C. J., & Doherty, P. F. (2011). Age at first breeding and pre-breeding survival in 600 Seychelles sooty terns Onychoprion fuscatus. *Marine Ornithology*, *39*, 221–226.

Fourqurean, J. W., & Zieman, J. C. (2002). Nutrient content of the seagrass Thalassia testudinum reveals regional patterns of relative availability of nitrogen and phosphorus in the Florida keys USA. *Biogeochemistry*, *61*, 229–245.

Frankovich, T., & Fourqurean, J. (1997). Seagrass epiphyte loads along a nutrient availability gradient, Florida bay, USA. *Marine Ecology Progress Series*, *159*, 37–50. https://doi.org/10.3354/meps159037

Gaiotto, J. V., Nunes, G. T., & Bugoni, L. (2022). Dissipation of seabird-derived nutrients in a terrestrial insular trophic web. *Austral Ecology*, *47*(5), 1037–1048. https://doi.org/10.1111/aec.13196

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

Grant, M. L., Bond, A. L., & Lavers, J. L. (2022). The influence of seabirds on their breeding, roosting and nesting grounds: A systematic review and meta-analysis. *Journal of Animal Ecology*, *91*(6), 1266–1289. https://doi.org/10.1111/1365-2656.13699

Herbert, D. A., & Fourqurean, J. W. (2008). Ecosystem structure and function still altered two decades after short-term fertilization of a seagrass meadow. *Ecosystems*, *11*(5), 688–700. https://doi.org/10.1007/s10021-008-9151-2

Hughes, B. J., Martin, G. R., Giles, A. D., & Reynolds, S. J. (2017). Long-term population trends of sooty terns Onychoprion fuscatus: Implications for conservation status. *Population Ecology*, *59*(3), 213–224. https://doi.org/10.1007/s10144-017-0588-z

Hutchinson, G. (1950). Survey of existing knowledge of biogeochemistry. 3, the biogeochemistry of vertebrate excretion. *Bulletin of the American Museum of Natural History*, *96*, 288–311.

Isles, P. D. F. (2020). The misuse of ratios in ecological stoichiometry. *Ecology*, *101*(11), e03153. https://doi.org/10.1002/ecy.3153

17447429, 2024, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/btp.13354 by INASP/HINARI - SEYCHELLES, Wiley Online Library on [03/07/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Jaquemet, S., Potier, M., Cherel, Y., Kojadinovic, J., Bustamante, P., Richard, P., Catry, T., Ramos, J. A., & Le Corre, M. (2008). Comparative foraging ecology and ecological niche of a superabundant tropical seabird: The sooty tern Sterna fuscata in the southwest Indian Ocean. *Marine Biology*, *155*(5), 505–520. https://doi.org/10.1007/s00227-008-1049-1

Jensen, H. S., McGlathery, K. J., Marino, R., & Howarth, R. W. (1998). Forms and availability of sediment phosphorus in carbonate sand of Bermuda seagrass beds. *Limnology and Oceanography*, *43*(5), 799–810. https://doi.org/10.4319/lo.1998.43.5.0799

Kazama, K. (2020). Bottom-up effects on coastal marine ecosystems due to nitrogen input from seabird feces. *Ornithological Science*, *18*(2), 117. https://doi.org/10.2326/osj.18.126

Kolb, G., Ekholm, J., & Hambäck, P. (2010). Effects of seabird nesting colonies on algae and aquatic invertebrates in coastal waters. *Marine Ecology Progress Series*, *417*, 287–300. https://doi.org/10.3354/meps08791

Lavelle, P., Dugdale, R., Scholes, R., Berhe, A. A., Carpenter, E., Codispoti, L., Izac, A.-M., Lemoalle, J., Luizao, F., Scholes, M., Treguer, P., & Ward, B. (2005). Nutrient cycling. In *Ecosystems and human well-being: Current state and trends: Findings of the condition and trends working group*. Island Press.

Lebarbenchon, C., Boucher, S., Feare, C., Dietrich, M., Larose, C., Humeau, L., Le Corre, M., & Jaeger, A. (2023). Migratory patterns of two major influenza virus host species on tropical islands. *Royal Society Open Science*, *10*(10), 230600. https://doi.org/10.1098/rsos.230600

Lenth, R. V. (2023). Emmeans: Estimated Marginal Means, aka Least-Squares Means. *R Package Version* 1(8):6.

Linhares, B. D. A., & Bugoni, L. (2023). Seabirds subsidize terrestrial food webs and coral reefs in a tropical rat-invaded archipelago. *Ecological Applications*, *33*(2), e2733. https://doi.org/10.1002/eap.2733

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. *Scientific Reports*, *7*(1), 3721. https://doi.org/10.1038/s41598-017-03781-y

Marshall John, D., Brooks, J. R., & Lajtha, K. (2007). Sources of variation in the stable isotopic composition of plants. In R. Michener & K. Lajtha (Eds.), *Stable isotopes in ecology and environmental science* (Second ed., pp. 22–60). Blackwell Publishing.

McCauley, D. J., DeSalles, P. A., Young, H. S., Dunbar, R. B., Dirzo, R., Mills, M. M., & Micheli, F. (2012). From wing to wing: The persistence of long ecological interaction chains in less-disturbed ecosystems. *Scientific Reports*, *2*(1), 409. https://doi.org/10.1038/srep00409

McFadden, T. N., Kauffman, J. B., & Bhomia, R. K. (2016). Effects of nesting waterbirds on nutrient levels in mangroves, gulf of Fonseca, Honduras. *Wetlands Ecology and Management*, *24*(2), 217–229. https://doi.org/10.1007/s11273-016-9480-4

McMahon, A., & Santos, I. R. (2017). Nitrogen enrichment and speciation in a coral reef lagoon driven by groundwater inputs of bird guano. *Journal of Geophysical Research: Oceans*, *122*(9), 7218–7236. https://doi.org/10.1002/2017JC012929

Michelutti, N., Keatley, B. E., Brimble, S., Blais, J. M., Liu, H., Douglas, M. S. V., Mallory, M. L., Macdonald, R. W., & Smol, J. P. (2009). Seabird-driven shifts in Arctic pond ecosystems. *Proceedings of the Royal Society B: Biological Sciences*, *276*(1656), 591–596. https://doi.org/10.1098/rspb.2008.1103

Mizutani, H., Kabaya, Y., Moors, P. J., Speir, T. W., & Lyon, G. L. (1991). Nitrogen isotope ratios identify deserted seabird colonies. *Auk*, *108*, 960–964.

Mizutani, H., & Wada, E. (1988). Nitrogen and carbon isotope ratios in seabird rookeries and their ecological implications. *Ecology*, *69*(2), 340–349. https://doi.org/10.2307/1940432

Mulder, C. P. H., Jones, H. P., Kameda, K., Palmborg, C., Schmidt, S., Ellis, J. C., Orrock, J. L., Wait, A., Wardle, D. A., Yang, L., Young, H., Croll, D. A., & Vidal, E. (2011). Impacts of seabirds on plant and soil properties. In C. P. H. Mulder, W. B. Anderson, D. R. Towns, & P. J. Bellingham (Eds.), *Seabird Islands* (pp. 135–176). Oxford University Press. https://doi.org/10.1093/acprof:osobl/9780199735693.003.0005

Mutillod, C., Baumberger, T., Prudent, P., Saatkamp, A., Vidal, E., Le-Mire-Pecheux, L., & Affre, L. (2023). Yellow-legged gull populations (Larus michahellis) link the history of landfills to soil eutrophication and time-related vegetation changes on small Mediterranean islands. *Science of the Total Environment*, *878*, 162948. https://doi.org/10.1016/j.scitotenv.2023.162948

Obrist, D. S., Hanly, P. J., Brown, N. E. M., Ernst, C. M., Wickham, S. B., Fitzpatrick, O. T., Kennedy, J. C., Nijland, W., Reshitnyk, L. Y., Darimont, C. T., Starzomski, B. M., & Reynolds, J. D. (2022). Biogeographic features mediate marine subsidies to Island food webs. *Ecosphere*, *13*(7), e4171. https://doi.org/10.1002/ecs2.4171

Obrist, D. S., Hanly, P. J., Kennedy, J. C., Fitzpatrick, O. T., Wickham, S. B., Ernst, C. M., Nijland, W., Reshitnyk, L. Y., Darimont, C. T., Starzomski, B. M., & Reynolds, J. D. (2020). Marine subsidies mediate patterns in avian Island biogeography. *Proceedings of the Royal Society B: Biological Sciences*, *287*(1922), 20200108. https://doi.org/10.1098/rspb.2020.0108

Okanasen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. M., Szoecs, E., & Wagner, H. (2018). *vegan: Community Ecology Package* (2.5-3).

Otero, X. L., De La Peña-Lastra, S., Pérez-Alberti, A., Ferreira, T. O., & Huerta-Diaz, M. A. (2018). Seabird colonies as important global drivers in the nitrogen and phosphorus cycles. *Nature Communications*, *9*(1), 246. https://doi.org/10.1038/s41467-017-02446-8

Otero, X. L., Tejada, O., Martín-Pastor, M., De La Peña, S., Ferreira, T. O., & Pérez-Alberti, A. (2015). Phosphorus in seagull colonies and the effect on the habitats. The case of yellow-legged gulls (Larus michahellis) in the Atlantic Islands National Park (Galicia-NW Spain). *Science of the Total Environment*, *532*, 383–397. https://doi.org/10.1016/j.scitotenv.2015.06.013

Pascoe, P., Shaw, J., Trebilco, R., Kong, S., & Jones, H. (2021). Island characteristics and sampling methodologies influence the use of stable isotopes as an ecosystem function assessment tool. *Ecological Solutions and Evidence*, *2*(3), e12082. https://doi.org/10.1002/2688-8319.12082

Pascoe, P., Shaw, J., Trebilco, R., Weldrick, C., Hindell, M. A., & Jones, H. (2022). Temporal and spatial variability in stable isotope values on seabird islands: What, where and when to sample. *Ecological Indicators*, *143*, 109344. https://doi.org/10.1016/j.ecolind.2022.109344

Piggot, C. J. (1961). Notes on some of the Seychelles Islands, Indian Ocean.Pdf. *Atoll Research Bulletin*, *83*, 1–10.

Plazas-Jiménez, D., & Cianciaruso, M. V. (2020). Valuing ecosystem services can help to save seabirds. *Trends in Ecology & Evolution*, *35*(9), 757–762. https://doi.org/10.1016/j.tree.2020.06.008

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. *Annual Review of Ecology and Systematics*, *28*(1), 289–316. https://doi.org/10.1146/annurev.ecolsys.28.1.289

Polis, G. A., & Hurd, S. D. (1996). Linking marine and terrestrial food webs: Allochthonous input from the ocean supports high secondary productivity on small islands and coastal land communities. *The American Naturalist*, *147*(3), 396–423.

R Core Team. (2022). *R: A language and environment for statistical language and environment for statistical computing*. R Foundation for Statistical Computing.

Rankin, L., & Jones, H. (2021). Nearshore ecosystems on seabird islands are potentially influenced by invasive predator eradications and environmental conditions: A case study at the Mercury Islands, New

17447429, 2024, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/btp.13354 by INASP/HINARI - SEYCHELLES, Wiley Online Library on [03/07/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Zealand. *Marine Ecology Progress Series*, *661*, 83–96. https://doi.org/10.3354/meps13590

Riddick, S. N., Dragosits, U., Blackall, T. D., Daunt, F., Wanless, S., & Sutton, M. A. (2012). The global distribution of ammonia emissions from seabird colonies. *Atmospheric Environment*, *55*, 319–327. https://doi.org/10.1016/j.atmosenv.2012.02.052

Riddick, S. N., Dragosits, U., Blackall, T. D., Tomlinson, S. J., Daunt, F., Wanless, S., Hallsworth, S., Braban, C. F., Tang, Y. S., & Sutton, M. A. (2018). Global assessment of the effect of climate change on ammonia emissions from seabirds. *Atmospheric Environment*, *184*, 212–223. https://doi.org/10.1016/j.atmosenv.2018.04.038

Sabino, M. A., Bodin, N., Govinden, R., Arrisol, R., Churlaud, C., Pethybridge, H., & Bustamante, P. (2022). The role of tropical small-scale fisheries in trace element delivery for a Small Island developing state community, the Seychelles. *Marine Pollution Bulletin*, *181*, 113870. https://doi.org/10.1016/j.marpolbul.2022.113870

Savage, C. (2019). Seabird nutrients are assimilated by corals and enhance coral growth rates. *Scientific Reports*, *9*(1), 4284. https://doi.org/10.1038/s41598-019-41030-6

Schmidt, S., Dennison, W. C., Moss, G. J., & Stewart, G. R. (2004). Nitrogen ecophysiology of Heron Island, a subtropical coral cay of the great barrier reef, Australia. *Functional Plant Biology*, *31*(5), 517–528. https://doi.org/10.1071/FP04024

Schreiber, R. W., & Chovan, J. L. (1986). Roosting by pelagic seabirds: Energetic, Populational, and social considerations. *The Condor*, *88*(4), 487–492. https://doi.org/10.2307/1368276

Signa, G., Mazzola, A., & Vizzini, S. (2021). Seabird influence on ecological processes in coastal marine ecosystems: An overlooked role? A critical review. *Estuarine, Coastal and Shelf Science*, *250*, 107164. https://doi.org/10.1016/j.ecss.2020.107164

Sitters, J., Atkinson, C. L., Guelzow, N., Kelly, P., & Sullivan, L. L. (2015). Spatial stoichiometry: Cross-ecosystem material flows and their impact on recipient ecosystems and organisms. *Oikos*, *124*(7), 920–930. https://doi.org/10.1111/oik.02392

Smith, J. L., Mulder, C. P. H., & Ellis, J. C. (2011). Seabirds as ecosystem engineers: Nutrient inputs and physical disturbance. In C. P. H. Mulder, W. B. Anderson, D. R. Towns, & P. J. Bellingham (Eds.), *Seabird Islands* (pp. 27–55). Oxford University Press.

Staunton Smith, J., & Johnson, C. (1995). Nutrient inputs from seabirds and humans on a populated coral cay. *Marine Ecology Progress Series*, *124*, 189–200. https://doi.org/10.3354/meps124189

Stoddart, D. R., & Poore, M. E. D. (1970). Geography and ecology of Farquhar atoll. *Atoll Research Bulletin*, *136*, 7–36.

Stokes, H. J., Mortimer, J. A., Hays, G. C., Unsworth, R. K. F., Laloë, J.-O., & Esteban, N. (2019). Green turtle diet is dominated by seagrass in the Western Indian Ocean except amongst gravid females. *Marine Biology*, *166*(10), 135. https://doi.org/10.1007/s00227-019-3584-3

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

Van Der Vegt, W., & Bokhorst, S. (2023). Bird traits and their nutrient impact on terrestrial invertebrate populations. *Polar Biology*, 1–12. https://doi.org/10.1007/s00300-023-03161-5

Wainright, S. C., Haney, J. C., Kerr, C., Golovkin, A. N., & Flint, M. V. (1998). Utilization of nitrogen derived from seabird guano by terrestrial and marine plants at St. Paul, Pribilof Islands, Bering Sea, Alaska. *Marine Biology*, *131*(1), 63–71. https://doi.org/10.1007/s002270050297

Wardle, D. A., Bellingham, P. J., Bonner, K. I., & Mulder, C. P. H. (2009). Indirect effects of invasive predators on litter decomposition and nutrient resorption on seabird-dominated islands. *Ecology*, *90*(2), 452–464. https://doi.org/10.1890/08-0097.1

Weimerskirch, H. (2007). Are seabirds foraging for unpredictable resources? *Deep Sea Research Part II: Topical Studies in Oceanography*, *54*(3–4), 211–223. https://doi.org/10.1016/j.dsr2.2006.11.013

Weimerskirch, H., Le Corre, M., Jaquemet, S., & Marsac, F. (2005). Foraging strategy of a tropical seabird, the red-footed booby, in a dynamic marine environment. *Marine Ecology Progress Series*, *288*, 251–261. https://doi.org/10.3354/meps288251

Young, H. S., McCauley, D. J., & Dirzo, R. (2011). Differential responses to guano fertilization among tropical tree species with varying functional traits. *American Journal of Botany*, *98*(2), 207–214. https://doi.org/10.3732/ajb.1000159

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. *Proceedings of the National Academy of Sciences*, *107*(5), 2072–2077. https://doi.org/10.1073/pnas.0914169107

Zuur, A. F., & Ieno, E. N. (2016). A protocol for conducting and presenting results of regression-type analyses. *Methods in Ecology and Evolution*, *7*(6), 636–645. https://doi.org/10.1111/2041-210X.12577

Zwolicki, A., Zmudczyńska-Skarbek, K., Matuła, J., Wojtuń, B., & Stempniewicz, L. (2016). Differential responses of Arctic vegetation to nutrient enrichment by plankton- and fish-eating colonial seabirds in Spitsbergen. *Frontiers in Plant Science*, *07*, 1959. https://doi.org/10.3389/fpls.2016.01959

Zwolicki, A., Zmudczyńska-Skarbek, K. M., Iliszko, L., & Stempniewicz, L. (2013). Guano deposition and nutrient enrichment in the vicinity of planktivorous and piscivorous seabird colonies in Spitsbergen. *Polar Biology*, *36*(3), 363–372. https://doi.org/10.1007/s00300-012-1265-5

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Appoo, J., Bunbury, N., Letori, J., Hector, A., Gendron, A., Graham, N. A. J., Rocamora, G., Le Corre, M., & Jaquemet, S. (2024). Seabird presence and seasonality influence nutrient dynamics of atoll habitats. *Biotropica*, *56*, e13354. https://doi.org/10.1111/btp.13354

17447429, 2024, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/btp.13354 by INASP/HINARI - SEYCHELLES, Wiley Online Library on [03/07/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License