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The role of seabirds in nutrient cycling on tropical oceanic islands

Jennifer Appoo

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Jennifer Appoo. The role of seabirds in nutrient cycling on tropical oceanic islands. Animal biology. Université de la Réunion, 2024. English. NNT : 2024LARE0019 . tel-04959935

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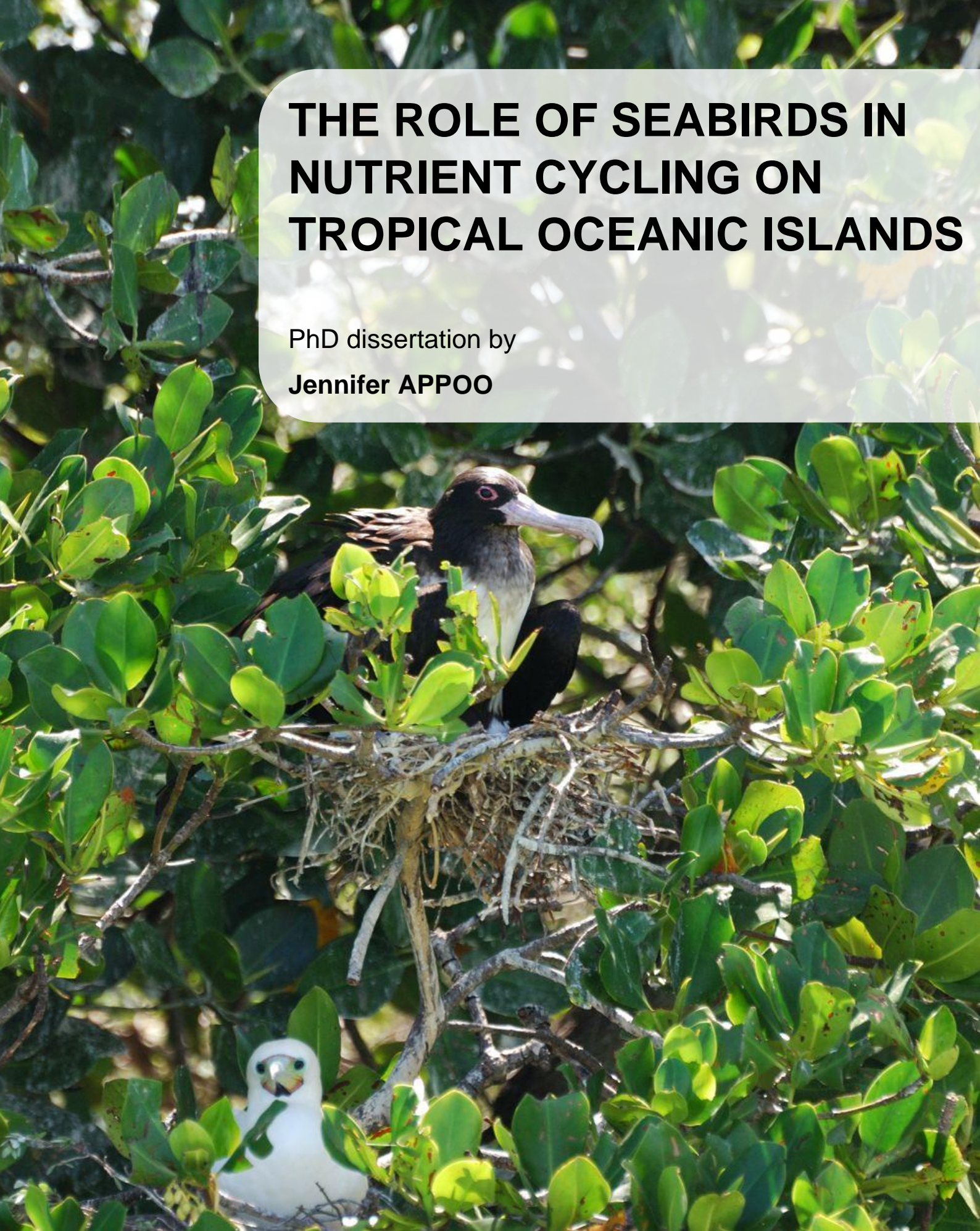
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THE ROLE OF SEABIRDS IN NUTRIENT CYCLING ON TROPICAL OCEANIC ISLANDS

PhD dissertation by
Jennifer APPOO



Thesis submitted for the degree of Doctor of Philosophy
Université de La Réunion, Ecole Doctorale des Sciences, Technologies, Santé
UMR 9220 Ecologie marine tropicale des océans Pacifique et Indien (ENTROPIE)

Discipline: Marine Ecology

The role of seabirds in nutrient cycling on tropical oceanic islands

by Jennifer APPOO

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Defended on 06 September 2024

This thesis received financial support from the Région Réunion and the European Union
(FEDER INTERREG 2021–2027)



Table of Contents

PREFACE	1
ACKNOWLEDGEMENTS	4
ABSTRACT	8
RÉSUMÉ	10
CHAPTER 1: General Introduction	12
1. Nutrient cycling – a key function in ecosystems	12
1.1. Nutrient cycling	12
1.2. Animal-mediated nutrient cycling	13
2. Seabird nutrient cycling	14
2.1. Functional roles of seabirds	14
2.2. Seabirds as nutrient vectors	15
2.3. Impacts of seabird nutrient subsidies	17
3. Research gaps	20
3.1. Tropical seabird islands	20
3.2. Importance of seabird nutrient subsidies on tropical islands	22
3.3. Seabird-derived nutrients in mangrove ecosystems	22
4. Thesis aim and objectives	24
5. Research context	25
5.1. Seabird islands in the tropical Western Indian Ocean	25
5.2. Seychelles archipelago	26
6. Thesis layout	28
CHAPTER 2: Isotopic structure and dynamics of a tropical seabird assemblage	32
ABSTRACT	33
1. INTRODUCTION	34
2. METHODS	36
2.1. Study region	36
2.2. Seabird isotopic compositions	37
2.3. Final dataset	38
2.4. Data analysis	41
3. RESULTS	43
3.1. Structure of seabird isotopic ratios	43
3.2. Drivers of seabird isotopic ratios	46
4. DISCUSSION	47
4.1. Isotopic ratios and niche sizes	48
4.2. Structuring mechanisms	49
4.3. Limitations of the study	52
5. CONCLUSION	53

ACNOWLEDGEMENTS.....	53
AUTHOR CONTRIBUTIONS	54
REFERENCES.....	55
SUPPLEMENTAL INFORMATION	66
CHAPTER 3: Seabird presence and seasonality influence nutrient dynamics of atoll habitats	72
SUPPLEMENTAL INFORMATION	86
CHAPTER 4: Seabird nutrient subsidies enrich mangrove ecosystems and are exported to nearby coastal habitats	97
CHAPTER 5: Seabird nutrient subsidy alters size and resource use of functionally important mangrove macroinvertebrates	118
ABSTRACT	119
1. INTRODUCTION.....	120
2. METHODS	122
2.1. Study area	122
2.2. Field sampling	123
2.3. Sample processing and isotope analysis.....	124
2.4. Data analysis.....	125
3. RESULTS.....	127
3.1. Isotopic and nitrogen composition of food web components	127
3.2. Consumer size	129
3.3. Consumer isotopic niche space	131
3.4. Resource contributions to consumer diet.....	132
4. DISCUSSION	134
5. CONCLUSION	137
ACKNOWLEDGEMENTS	138
AUTHOR CONTRIBUTIONS	138
REFERENCES.....	139
SUPPLEMENTAL INFORMATION	147
CHAPTER 6: General Discussion.....	150
6.1. Overview and key findings	150
6.2. Research contributions, context and implications.....	151
6.2.1. Ecological indicators and references in tropical seabird systems	151
6.2.2. Magnitude and scale of nutrient connectivity in tropical seabird islands	152
6.2.3. Influence of seabird nutrient subsidies on tropical coastal habitats and communities	153
6.2.4. Sooty egg tern harvesting in Seychelles.....	154
6.2.5. Invasive mammal predator eradication on Aldabra	154
6.3. Specific recommendations.....	155
6.4. Concluding remarks: Conserve connectivity.....	164
REFERENCES (for General Introduction and Discussion).....	165

PREFACE

The work contained in this dissertation took place between 1st June 2021 and 30th June 2024. The research was conducted at the laboratory of tropical marine ecology of the Pacific and Indian Oceans (ENTROPIE), at the University of Reunion Island (La Réunion, France), under the main supervision of Prof Sébastien Jaquemet. The research was supervised by Dr Nancy Bunbury from the Seychelles Islands Foundation (Seychelles), and implemented in close collaboration with Prof Nick Graham at Lancaster University (UK). To conduct this work, I obtained a three-year doctoral fellowship in 2020 financed by the Région Réunion and the European Union, through the FEDER INTERREG 2021–2027 operational programme. To implement my project, I was successful in obtaining research grants from the African World Heritage Fund's *Moses Mapesa research grant 2020*, the Rufford Foundation's *Small grants 2022*, the PADI Foundation *Marine research grant 2022* and University of Reunion Island through the *International Relations Department research grant 2022–2024*. I also received substantial financial support from the Bertarelli Foundation's *Marine Science program* through a grant awarded to Prof Nick Graham. For the research, I conducted fieldwork in Chagos, Farquhar and Aldabra (total 8 months), contributing to most of the data in this dissertation.

In addition to this thesis, I participated in the following activities:

Conferences and workshops

1. Virtual World Seabird conference 3, October 2021 (participation).
2. **Thesis presentation: role of seabirds in tropical oceanic islands.** Doctoral seminar (ENTROPIE), La Réunion, November 2021 (oral presentation).
3. **How do seabirds enrich Aldabra's marine ecosystems?** Aldabra Research Station 50th anniversary celebration symposium, London, UK, April 2022 (poster).
4. **Dynamics of seabird nutrient cycling in tropical island ecosystems.** Western Indian Ocean Marine Science Symposium, Port Elizabeth, South Africa, October 2022 (video presentation).
5. **Seabird-derived nutrients in mangroves.** British Ecological Society Aquatic Ecology annual group meeting, Lancaster, UK, September 2023 (lightning talk).
6. Bertarelli Foundation's Indian Ocean Marine Science Symposium, Dhiffushi Island, Maldives, March 2024 (participation).

7. **Impacts of seabirds on mangrove ecosystems.** Seychelles Coastal and Marine Science Symposium, Mahé, Seychelles, May 2024 (oral presentation).
8. **Seabird presence and seasonality influence nutrient dynamics of atoll habitats.** Seychelles Coastal and Marine Science Symposium, Mahé, Seychelles, May 2024 (poster).

Teaching and supervision

1. Animal biology (coursework) – 60 hours. BSc Biology Year 1, University of Reunion Island, Oct–Dec 2021.
2. Elise Wagnier and Maëva Grondin-Bergerat. Laboratory internship: sample preparation for stable isotope analysis, University of Reunion Island, Apr–Jun 2023.
3. Corentin Gstalter and Isabel Xeridat. The trophic niche of tropical seabirds in the Western Indian Ocean. MSc Biology Year 1 dissertation, University of Reunion Island, Apr–Jun 2023.
4. Animal biology (coursework) – 40 hours. BSc Biology Year 1, University of Reunion Island, Oct–Dec 2023.

Outreach and dissemination

1. **Aldabra Atoll, a natural laboratory.** European Researchers Night, La Réunion, September 2021 (oral presentation).
2. **Multi-disciplinary research expedition exploring seabird-island-reef systems in the Chagos archipelago.** Jennifer Appoo, Nia Stephens, Ruth Dunn, Rucha Karkarey, Ines Lange, Eleanor Thomson and Yadvinder Malhi. Indian Ocean Seabird Group newsletter (2022), n°11.
3. **PhD student investigates seabird guano benefits to mangroves.** Seychelles Islands Foundation newsletter, February 2023.
4. **The role of seabirds in nutrient transport and its influence on mangrove forests of Aldabra Atoll.** Jennifer Appoo, Nancy Bunbury, Sébastien Jaquemet and Nick Graham. Indian Ocean Seabird Group newsletter (2024), n°13.
5. **New study reveals positive influence of seabird guano in mangroves.** Seychelles Islands Foundation newsletter, April 2024.
6. **Seabirder spotlight.** The Seabird Group Newsletter n° 156, June 2024.

Other scientific publications outside the scope of this thesis

1. Bunbury *et al.* A conservation success story: A review of 50 years of research and conservation from one of the world's most iconic Marine World Heritage sites. *In prep.*
2. Cheryl L. Sanchez, Nancy Bunbury, Jeanne A Mortimer, Luke A'Bear, **Jennifer Appoo**, Michael Betts, Rainer von Brandis, Lorraine Cook, Janske van de Crommenacker, Jock C Currie, *et al.* (2024). Small-scale movements and site fidelity of two sympatric sea turtle species at a remote atoll. *Marine Biology* 171:91. DOI: <https://doi.org/10.1007/s00227-024-04414-5>
3. Orphéo Ensanya-Volle, **Jennifer Appoo**, Nancy Bunbury, Gemma Clucas, Nasreen Khan, Gerard Rocamora, Cheryl Sanchez and Annette L. Fayet (2023). Differences in foraging range between white-tailed tropicbirds breeding on inner and outer Seychelles Islands. *Marine Ecology Progress Series* 724: 141–154. DOI: <https://doi.org/10.3354/meps14454>
4. Annette L. Fayet, Cheryl Sanchez, **Jennifer Appoo**, Jessica Constance, Gemma Clucas, Lindsay A. Turnbull, and Nancy Bunbury (2023). Marked differences in foraging area use and susceptibility to predation between two closely-related tropical seabirds. *Oecologia* 203: 167–179. DOI: <https://doi.org/10.1007/s00442-023-05459-x>
5. Jeanne A. Mortimer, **Jennifer Appoo**, Bruno Bautil, Michael Betts, April J. Burt, Roselle Chapman, Jock C. Currie *et al.* (2022). Long-term changes in adult size of green turtles at Aldabra Atoll and implications for clutch size, sexual dimorphism and growth rates. *Marine Biology* 169: 123. DOI: <https://doi.org/10.1007/s00227-022-04111-1>

ACKNOWLEDGEMENTS

I am profoundly grateful to my supervisory team who, without their assistance and dedicated involvement in every step of this journey, this thesis would have never been accomplished. A dream like this does not happen over only three years of work. Since the first time I contacted Dr Nancy Bunbury to express my wish of doing a PhD in 2016, she has been my number one supporter. Thank you, Nancy, for supporting my goals from the very beginning, for giving me the opportunity to write my first scientific publication, for your extensive guidance in developing and implementing this project, for the diligent manuscript reviews, for being an excellent mentor and pillar throughout this journey and for your dedication to building capacity in Seychelles. Your kindness and care for students, not only shaped the way I conduct my work but also the way I treat the people around me. It is truly because of you that I am the scientist I am today and have achieved all of this.

From the very beginning, Prof Sebastien Jaquemet showed strong interest in my project and was dedicated to my work until the end. Thank you for your assistance in seeking funding, for the engaging discussions and formulation of ideas, for the quick responses to my queries, for the extensive logistical support for fieldwork and laboratory analyses, and for the time and space you made for me. Your regular follow-ups, updates and feedback was truly key to the successful implementation of this project.

I cannot begin to express my gratitude and appreciation for Prof Nick Graham. Thank you, Nick, for seeing my potential, for your guidance and advice to bring my scientific work to a higher level, for sharing your vast knowledge about tropical marine ecology, for inviting me into the seabird nutrients working group and for extending the support of your research grant and your incredible research lab. During my visit at LEC-REEFs I felt welcomed; I have made lifelong friendships and connections, and it's because you bring amazing people together. Your support and contributions made a daunting thesis project feel more achievable and manageable.

Working with Prof Matthieu Le Corre has been an absolute pleasure. I am extremely grateful for the laughs during fieldwork and for your time and interest in the overall project. I feel very fortunate to have experienced your passion and expertise for the wonderful creatures that are seabirds! I would like to express my gratitude to other members of my thesis committee, Dr Eric Vidal, Dr Anne Lorrain

and Dr Fabien Guerin. Thank you for your words of encouragement and insightful feedback that helped me improve my research. I would also like to thank the reviewers and examiner who accepted to assess my thesis, Prof Heather Koldewey, Prof Hillary Young, Prof Matthieu Le Corre and Prof Nick Graham.

I am forever grateful to the Seychelles Islands Foundation who gave me the incredible opportunity to do my PhD on the magical Aldabra Atoll – I feel extremely privileged. My fieldwork was aided by a hardworking team on Aldabra including Ervin Ally, Elma Balette, Megan O'Brien, Sebastien Cowin, Nikita Pothin, Annabelle Cupidon, Michelle Risi, Alex Rose, Christopher Jones, Guilly Mellie, Werner Bonnelame and Francis Salomon. Thank you all for the long days and extra hours of work you put in to assist me in the field. I received unwavering support from the Head Office team throughout and special thanks goes to Dr Anna Koester, Dr April Burt, Christina Quanz, Dr Annabelle Constance and Dr Frauke Fleischer-Dogley – you have all guided me, encouraged me, and helped me get to where I am professionally, academically, and in life.

My heartfelt thanks go to the Island Conservation Society of Seychelles team for my fieldwork on Farquhar Atoll. The data and sample collection were entirely successful thanks to Jake Letori, Aurelie Hector and Annie Gendron. Your field expertise and assistance were paramount and I am extremely grateful. Thank you, Matthew Morgan, Pierre-Andre Adam and William McNeely, for your assistance with field planning and swift responses to my queries. Rahim Hypolite, Shane Emilie, Keni Mangroo and Norman Webber at the Head Office enabled the smooth implementation of the fieldwork. Thank you to the Island Development Company personnel, especially the Farquhar Island Manager, Mrs Jaqueline, and staff for enabling my field operations.

Dr Gerard Rocamora, thank you for being a diligent collaborator and supporter, for your time in discussing about my project and reviewing manuscript. Thank you to my Green Islands Foundation family who provided stepping stones to this path. Arjan de Groene you were the first to see my potential, encouraged me to do a PhD and guided me towards the correct people. Wilna Accouche, a huge thank you for being supportive of this journey. I can always count on you both to elevate me when I need a boost of confidence.

My fieldwork in the Chagos was made possible by the Bertarelli Foundation through the *Marine Science Program*. Thanks to all who were involved in the planning and implementation of the Reef 1

2022 expedition, notably Rachel Jones, Sharmin Rouff, Prof Chris Perry, Dr Ines Lange and Dr Cassandra Benkwitt. Special thanks go to Nia Stephens for her assistance in sampling seabirds in Chagos and Captain Kilian and the crew of the BPV Grampian Frontier for supporting the expedition.

My laboratory work was successful thanks to numerous lab technicians and interns. Thank you to Dave Hughes at Lancaster University for conducting all the isotope analyses and the team at CIRAD La Bretagne who enabled and conducted the nutrient analyses, namely Dr Marion Collinet, David Diot and Jocelyn Ismond. Thank you to Thiery Cariou at IRD Bretagne for conducting the water sample analyses. Thank you, Jan Bierwirth, Elise Wagnier, Maëva Grondin-Bergerat, Isabel Xeridat and Corentin Gsalter for lab assistance in processing samples. I was also able to access the lab of the Seychelles Fishing Authority to prepare my samples thanks to Rodney Govinden, Marie-Colline and Archille Pascal. My sincere thanks also go to Kelly Anna-Grondin in managing the project finances administered by ENTROPIE research lab.

Thank you to everyone who supported, willingly reviewed and provided constructive feedback on my research proposals and funding applications, or provided recommendation letters whenever I needed; namely Dr Nancy Bunbury, Prof Sébastien Jaquemet, Prof Nick Graham, Prof Matthieu Le Corre, Prof Heather Koldewey, Dr Annette Fayette, Dr Sally Keith, Dr James Robinson, Dr Ruth Dunn, Dr Lila Buckingham, Dr April Burt and Dr Claire-Cecile Juhasz.

During this journey, I had the privilege to meet, discuss and share ideas with some amazing people including Prof Yadvinder Malhi, Dr Eleanor Thomson, Prof Christina Hicks, Dr Rucha Karkarey, Dr Ruth Dunn, Dr Cassandra Benkwitt, Dr Ines Lange, Dr Eva Maire, Sheena Talma, Dr Malcolm Nicol and Dr Shaun Wilson. I am fortunate to have met and learned a great deal from each and every one of you. Throughout the PhD, I also contacted several researchers who provided their experience and advice with field methods, species identification, sampling design and analyses. Thank you for your advice, big and small, to Dr Cassandra Benkwitt, Dr José Paula, Dr Perrine Mangion, Prof Hillary Young, Dr Chris Kaiser-Bunbury, Dr Christina Skinner, Dr Eleanor Thomson, Emmanuel Cordier, Thierry Blasco Prof Mark Carr and Dr Nathalie Bodin.

I would like to acknowledge my incredible lab colleagues for making my time at ENTROPIE feel like home and for their endless support and laughter, namely Margot Thibault, Guillaume Chandelier,

Helena Texeira, Felix Pellerin, Merlene Saunier, Sabine Orłowski, David Ory, Romain Fernandez, Elise Delcour and Ludovic Hoarau – there is no group of people better than you.

Finally, I want to express my gratitude to my family back home, both by blood and by choice. I cannot thank you enough for everything you've done for me, especially to my gecko for accompanying me every step of the way and bringing so much love and joy into my life.

ABSTRACT

Nutrients play a transformative role in shaping ecosystem structure and dynamics. Mobile animals are essential for nutrient cycling processes by facilitating the exchange of nutrients, thereby moderating ecosystem function and biogeochemical cycles. Seabirds play a globally important role in transferring nutrients from oceanic feeding areas to their breeding and roosting islands. However, their role in nutrient cycling on tropical oceanic islands remains less understood compared to islands in temperate and polar areas. This thesis aimed to assess the impacts of seabird nutrient subsidies on tropical oceanic islands by examining various components of the seabird subsidy transfer (nutrient vectors, subsidies, pathways, recipients). We used the Western Indian Ocean (WIO) seabird assemblage and remote seabird islands in Seychelles as study systems. The thesis is divided into the following components:

(i) Nutrient vector: we assessed the structure of seabird tissue nitrogen and carbon isotopic signatures in the tropical WIO. Seabird blood nitrogen isotopes were higher for birds breeding at low latitudes and during the austral winter monsoon, demonstrating their potential as ecological indicators for marine environments in this region.

(ii) Nutrient subsidy: we determined guano isotopic and nutrient concentrations of breeding seabirds on Farquhar and Aldabra atolls, and estimated their annual nutrient deposition rates. Seabird colonies contributed a total of 86.6 N tonne.yr⁻¹ and 67.2 P tonne.yr⁻¹ on Farquhar and 41.9 N tonne.yr⁻¹ and 40.9 P tonne.yr⁻¹ on Aldabra, confirming seabirds as key nutrient providers in their tropical breeding islands.

(iii) Nutrient pathways: we traced seabird-derived nutrient transfer across the land-sea interface on Farquhar and in Aldabra's mangroves. Nutrient transfer from seabird colonies to island and nearshore seagrass habitats on Farquhar occurred during both wet and dry seasons, and in Aldabra's mangroves, seabird-derived nutrients were transferred trophically to invertebrate fauna and horizontally from mangroves to adjacent coastal habitats through tidal flow. These results demonstrate the spatial scale of seabird nutrient connectivity in ocean-atoll-coastal ecosystems.

(iv) Nutrient recipients: we compared sites with and without seabirds to evaluate the impacts of seabird-derived nutrients on island and coastal habitats and communities. On Farquhar, seabird-derived

nutrients maintained high foliar nitrogen levels in coastal plants year-round, indicating persistent enrichment of island habitats by tropical seabird colonies. On Aldabra, seabird-derived nutrients enriched mangroves and alleviated their nutrient limitations, and enriched the mangrove macroinvertebrate food web. These findings confirm seabirds as drivers of productivity of atoll habitats and communities. Seabird-derived nutrient enrichment of basal food sources led to larger sizes of mangrove crabs, suggesting seabird nutrient subsidies could benefit mangrove fisheries.

The results of the thesis further our understanding of the ecological and socio-economic importance of seabirds in tropical oceanic islands and highlight the importance of incorporating nutrient connectivity linkages into seabird island management practices to maintain healthy socio-ecological systems and boost tropical island resilience to climate change.

Keywords: Atoll, Indian Ocean, macroinvertebrates, mangroves, marine subsidies, nutrient connectivity, Seychelles, stable isotopes, trophic ecology.

RÉSUMÉ

Les nutriments jouent un rôle primordial dans le fonctionnement et la dynamique des écosystèmes. En facilitant leurs échanges entre écosystèmes, les animaux mobiles sont essentiels dans la dynamique des nutriments et les cycles biogéochimiques. Globalement, les oiseaux marins jouent un rôle important dans le transfert de nutriments des zones d'alimentation en mer vers des colonies de reproduction ou de repos à terre, sur des îles océaniques. Néanmoins, leur rôle dans le cycle des nutriments sur les îles océaniques tropicales reste moins étudié par rapport aux zones tempérées et polaires. Cette thèse a évalué les impacts des apports en nutriments des oiseaux marins sur les îles océaniques tropicales en examinant les différentes composantes de ce processus (le vecteur, les apports, le transfert, les impacts). Pour atteindre cet objectif, nous sommes focalisés sur les oiseaux marins de l'océan Indien occidental et les îles aux Seychelles comme sites d'études.

(i) Vecteur de nutriments : nous avons mesuré les valeurs isotopiques en azote et en carbone des tissus des oiseaux marins dans l'océan Indien occidental. Pour l'azote du sang, les valeurs étaient plus élevées pour les colonies situées à basses latitudes et pour les individus se reproduisant pendant la mousson d'hiver austral. Cela suggère le potentiel d'utiliser les isotopes de l'azote du sang des oiseaux marins en tant qu'indicateurs écologiques des environnements marins dans cette région.

(ii) Apport en nutriments : nous avons déterminé les concentrations isotopiques et en nutriments du guano des oiseaux marins nichant sur les atolls de Farquhar et d'Aldabra, et estimé les taux annuels de dépôt en nutriments. Les colonies d'oiseaux marins déposent annuellement au moins 86,6 tonnes d'azote et 67,2 tonnes de phosphate sur Farquhar, et 41,9 tonnes d'azote et 40,9 tonnes phosphate sur Aldabra. Cela confirme que les oiseaux marins sont des fournisseurs clés de nutriments sur leurs îles de reproduction.

(iii) Transfert de nutriments : nous avons tracé le transfert de nutriments des oiseaux marins à l'interface terre-mer sur Farquhar et dans les mangroves d'Aldabra. Le transfert de nutriments des colonies vers les habitats insulaires et les herbiers marins sur Farquhar a lieu toute l'année. Dans les mangroves d'Aldabra, les nutriments ont été transférés dans la chaîne trophique des macro-invertébrées, et de la mangrove vers les habitats côtiers adjacents par la marée. Ces résultats démontrent l'échelle spatiale de la connectivité maintenue par les oiseaux marins.

(iv) Impacts des nutriments : nous avons comparé des sites avec et sans oiseaux marins pour évaluer les impacts des nutriments des oiseaux marins sur les habitats insulaires et côtiers et les communautés associées. Sur Farquhar, les nutriments des oiseaux marins ont des niveaux élevés d'azote dans les plantes côtières toute l'année, ce qui indique un enrichissement persistant des habitats insulaires par les colonies d'oiseaux marins. À Aldabra, les nutriments des oiseaux marins ont enrichi les mangroves et réduit leurs limitations en nutriments, et ont enrichi le réseau trophique des macro-invertébrés de la mangrove. Ces résultats confirment que les oiseaux marins sont des moteurs de la productivité des habitats et communautés des atolls. L'enrichissement en nutriments des oiseaux marins a conduit à des tailles plus grandes de crabes de mangrove, ce qui pourrait être bénéfiques pour les pêcheries de mangrove.

Cette thèse permet de mieux comprendre l'importance écologique et socio-économique des oiseaux marins sur les îles océaniques tropicales. Elle souligne l'importance d'incorporer la connectivité biologique dans la gestion des îles avec des colonies oiseaux marins pour maintenir des systèmes socio-écologiques en bon état et renforcer la résilience des îles tropicales face au changement climatique.

Mots-clés : Atoll, océan Indien, connectivité biologique, macro-invertébrés, mangroves, Seychelles, isotopes stables, écologie trophique.

CHAPTER 1

General Introduction

1. Nutrient cycling – a key function in ecosystems

1.1. Nutrient cycling

Nutrient cycling is a fundamental function of ecosystems. It underpins all ecosystems and sustains all life on earth (Vanni, 2002). Nutrient cycling consists of “the transformation and movement of elements within and between various biotic or abiotic components of the Earth” (Lavelle et al., 2005; Vanni, 2002). Nutrient cycling processes make available essential macro-elements (e.g. carbon, oxygen, nitrogen, phosphorus, sulphur) and micro-elements (e.g. iron, manganese, zinc, silicon) needed for organisms to grow (Lavelle et al., 2005). These elements move through the atmosphere, hydrosphere, lithosphere and biosphere, referred to as biogeochemical cycle, which may occur at local and global scales (Kumar and Mina, 2018).

Multiple passive or active processes are involved in the movement of elements (Polis et al., 1997). Nutrient cycling is considered passive when matter is distributed by environmental or physical factors such as wind, current, tides, gravity and erosion. For example, wind or waves depositing macroalgae on shores (Hyndes et al., 2022). Alternatively, nutrient cycling is active when biotic vectors are involved in the distribution or uptake of matter (McInturf et al., 2019). For example, mycorrhizal fungi facilitate the absorption of water and nutrients from the soil by plants (Huey et al., 2020), or aquatic insects that emerge from lakes as adults and occupy nearby terrestrial habitats for foraging and mating (Dreyer et al., 2015). Both active and passive processes can therefore result in nutrient inputs originating from outside ecosystem boundaries, referred to as ‘allochthonous nutrient inputs’ (Huxel et al., 2002). Recent estimates suggest nutrient cycling by both passive and active processes to be of the same magnitude, highlighting the importance of biodiversity in nutrient cycling (McInturf et al., 2019).

1.2. Animal-mediated nutrient cycling

Animals are prime nutrient cycling agents. This is mainly associated with animals' functional roles in food webs and ecosystems, and occurs in two main ways. First, animals mediate nutrient cycling directly by storing and transforming nutrients within their bodies. Nutrients are ingested and assimilated in body tissues. Nutrients are either used for growth or are released through excretion (urine production). Nutrients not assimilated in the body are released through egestion (faeces production). In addition, nutrients stored in body tissues as biomass become available when organisms die, through decomposition and remineralization by micro-organisms (bacteria and fungi). Second, animals influence nutrient cycling indirectly by impacting their prey population (predation) and on the physical properties of their habitat, which results in cascading effects throughout food webs. For example, predatory fishes reduce biomass and alter species composition of their herbivore prey, leading to increased biomass and altered species composition of primary producers through trophic cascades (Polis et al., 1997; Vanni, 2002; Schmitz et al., 2010). Carbon (C), nitrogen (N) and phosphorus (P) are the main macro-elements transformed and distributed by animals. Carbon is usually stored and transferred in organic forms by consumption of biomass (Lavelle et al., 2005). Nitrogen and phosphorus are typically provided as biologically available compounds through excretion e.g., ammonium (NH_4^+) and phosphate (PO_4^-), as well as in less bioavailable compounds in a variety of forms through egestion (Allgeier et al., 2017).

The movement of animals between habitats and ecosystems is a distinct feature of animal-mediated nutrient cycling, giving rise to the term 'mobile link' (Lundberg and Moberg, 2003). Through their movement patterns, animals can displace resources against natural energy gradients at multiple spatial and temporal scales (McInturf et al., 2019; Subalusky and Post, 2019), providing 'spatial subsidies' between 'donor' and 'recipient' entities (Polis et al., 1997; Allgeier et al., 2017). A spatial subsidy is a donor-controlled resource transferred to a recipient system, with subsequent effects on the recipient system (Lundberg and Moberg, 2003; Polis et al., 1997). Because they are rich in nutrients that are limiting to primary producers, such as nitrogen and phosphorus (Elser et al., 2007), the movement of resources by animals has a profound influence on ecosystem structure and dynamics. However, the magnitude of impacts of animal-mediated subsidies is highly context dependent, shaped by characteristics of the donor system, the resource flow, and the recipient system (Allgeier et al., 2017;

Subalusky and Post, 2019). In donor systems, properties of the animal vector e.g., mass, physiology, population size, life history and behaviour, as well as abiotic features of the donor system e.g., size, seasonality and productivity, determine the quantity, quality, timing and duration of the resource flow (subsidy). In addition, characteristics of the recipient system e.g., location, geomorphological features, resource demand, and the type of primary and secondary producers present, influence the subsidy impact (Subalusky and Post, 2019).

Animal-mediated nutrient cycling occurs in almost every ecosystem and involves a wide range of taxa. For example, in terrestrial habitats, Serengeti wildebeests *Connochaetes* spp. undergo annual migration between grasslands and woodlands in East Africa, in the wet and dry season, respectively. Movement of the herds alters nutrients, productivity and trophic relationships through their role as herbivores but also as prey for resident predators (Bauer and Hoyer, 2014). In the sea, whales move large quantities of nutrients through their excretion, laterally between their polar feeding locations and temperate or tropical breeding areas, as well as vertically between deep and surface waters, boosting marine primary productivity (Doughty et al., 2016). Mobile animals also connect marine and terrestrial systems, for example the Pacific salmon *Oncorhynchus* spp. migrates to the North Pacific Ocean as smolt and returns to rivers to spawn as adults, altering food webs, energy and productivity of ocean, rivers and land (Bauer and Hoyer, 2014). Overall, through their multiple functional roles, animals act as sinks, sources and mediators of nutrients within global nutrient cycles (Polis et al., 1997).

2. Seabird nutrient cycling

2.1. Functional roles of seabirds

The term 'connector species' describes animals involved in cross-boundary exchange of resources to recognize the unique role they play in maintaining connectivity. A prime example of connector species is seabirds; a group of birds that are mostly or entirely dependent on the marine environment for foraging and the terrestrial environment for breeding (Young and VanderWerf, 2023). Seabirds represent one of the most biologically diverse avian groups, comprising ca. 350 species and representing 3.5% of all extant bird species (Croxall et al., 2012). Broadly, seabirds include birds from the Orders Sphenisciformes (penguins), Procellariiformes (petrels, shearwaters, albatrosses), Pelecaniformes (pelicans, boobies, frigatebirds, cormorants), and Charadriiformes (terns, gulls, auks) (Schreiber and

Burger, 2001). Seabird life history characteristics are typified by long life span, late reproductive maturity and reproduction, small clutch size and extended breeding periods. Another key attribute is colonial living, when individuals aggregate in often large numbers on land to breed (Young and VanderWerf, 2023).

Seabirds play key functional roles in both marine and terrestrial environments (Sekercioglu, 2006). As marine high trophic level predators, seabirds exert considerable control through trophic processes. Trophic effects of seabirds occur via two main pathways, as consumers of marine prey (top-down control) and as nutrient vectors (bottom-up control). Top-down control occurs at sea, where seabirds feed over varying distances and across multiple trophic levels, consuming important quantities of prey. Fish consumption by seabirds is estimated at 70 million tonnes globally, an amount close to annual fishing catches (ca. 80 million tonnes; Brooke, 2004). Seabirds return to their breeding colonies on land, where they transport and deposit nutrients of marine origin through multiple forms, such as dropping of whole prey or through stomach oils, loss of feathers, adult and chick carcasses, egg remains (hatched, abandoned or destroyed), and through excretion and egestion (Smith et al., 2011). Because of their colonial and often philopatric behaviour, seabirds transport and accumulate substantial quantities of marine-derived nutrients on land. The magnitude of nutrient flow between marine and terrestrial environments by breeding seabirds worldwide is estimated at 0.59×10^3 Gg N y^{-1} and 0.10×10^3 Gg P y^{-1} , which are the same order of magnitude of the sea-to-land transfer, through annual catches by commercial fisheries (3.7×10^3 Gg N y^{-1} and 0.32×10^3 Gg P y^{-1} ; Otero *et al.*, 2018). Seabird-derived nutrients affect primary producers and largely shape food webs around breeding colonies (Sekercioglu, 2006). As mobile links, seabirds also contribute to the dispersal of genetic material such as seeds, parasites and pathogens (Signa et al., 2021); with the former being particularly important in the colonization of remote oceanic islands (Aoyama et al., 2012). Seabirds also have non-trophic effects and act as ecosystem engineers by physically altering their environment through nest construction, with consequences on soil and vegetation structure at their breeding colonies (Smith et al., 2011).

2.2. Seabirds as nutrient vectors

Nutrient cycling is one of the most important ecological functions of seabirds (Signa et al., 2021). Seabird droppings, commonly referred to as 'guano', represent the main form of seabird-derived nutrient

inputs on land (Smith et al., 2011). Guano is a mix of undigested food residues and metabolic waste products (Bird et al., 2008). Because of seabirds' diet rich in protein, the two principal elements in guano are nitrogen and phosphorus (Hutchinson, 1950). These elements occur mainly in mobile and bioavailable forms, facilitating their assimilation and dispersal. In fresh guano, nitrogen occurs as uric acid (50–80%), followed by ammonium (NH_4^+ , 8–40%), and amino acids and proteins (ca. 8%), while phosphorus occurs mainly as phosphate (PO_4^- , approx. 54%) (Lindeboom, 1984; Staunton Smith and Johnson, 1995; De La Peña-Lastra, 2021a). When deposited, nitrogen as uric acid is transformed by bacteria in soil into ammonium and subsequently to nitrate (NO_3^-). Part of the ammonium is volatilized and lost to the atmosphere as ammonia gas (NH_3), while the remaining forms are accumulated or transferred to other ecosystem compartments through runoff and/or leaching (Figure 1.1). Some of the atmospheric ammonia is returned back to the surrounding environment via rainfall. Eventually, the remaining nitrate that is not leached or assimilated, are lost to the atmosphere as nitrous (N_2O) and nitrogen (N_2) gases (Lindeboom, 1984; Kazama, 2019). In contrast, phosphorus is less mobile and is adsorbed into the soil when deposited, however, a fraction can be transferred and assimilated in ecosystems as orthophosphate (HPO_4^{2-}) (Otero et al., 2015, 2018). Seabird guano also contains various micro-elements, for example zinc (Zn), cadmium (Cd) copper (Cu), lead (Pb), arsenic (As), manganese (Mn) and Nickel (Ni) (De La Peña-Lastra, 2021a).

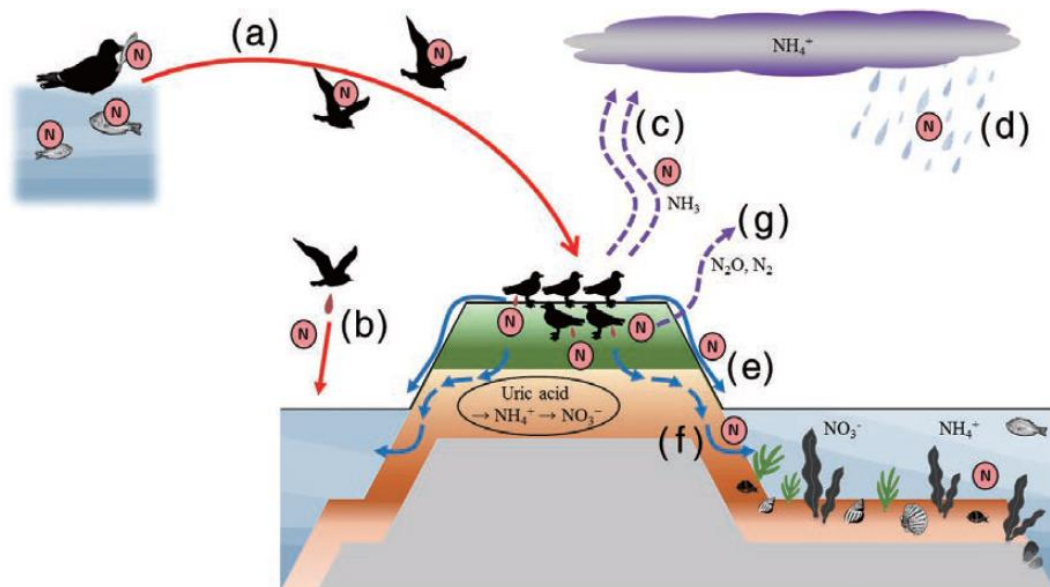


Figure 1.1. Flow and transformation of seabird-derived nitrogen at a breeding colony. (a) Seabirds feed on nitrogen-rich prey in the open ocean and return to their colonies where they excrete large quantities of guano. (b) Guano can be deposited directly in the surrounding nearshore habitat by overflying birds. Seabird-derived nitrogen

deposited mainly as uric acid is rapidly mineralized into NH_4^+ and NO_3^- in colony soils. (c) A part of the mineralized seabird-derived nitrogen volatilizes into NH_3 gas. (d) Some of the NH_3 gas is returned back to the colony and surrounding area via rainfall. (e) The remaining NH_4^+ and NO_3^- accumulated in soils runs off to the nearshore environment with rainfall and flood tides, (f) through leaching by groundwater, or (g) volatilized as N_2O and N_2 gases (Kazama, 2019).

Guano production varies among species. Multiple factors, including physiology, metabolism, individual age, stage of the annual cycle and diet, determine guano nutrient composition and quantity (Michelutti et al., 2010; Smith et al., 2011). Among these, the main determinant of guano nutrient concentration is diet. For example, birds that forage at higher trophic levels have higher guano nitrogen content compared to birds that consume prey at lower trophic levels (Bird et al., 2008). Meta-analyses reveal total nitrogen content is highest in Procellariiformes (19%) and lowest in Charadriiformes (7%), while total phosphorus content is highest in Suliformes (15%) and lowest in Procellariiformes (1%; Grant et al., 2022). Micro-nutrient concentrations also vary, with highest levels of zinc and cadmium observed in Suliformes, and highest levels of lead and arsenic recorded in Charadriiformes (De La Peña-Lastra, 2021a; Grant et al., 2022). On the other hand, the quantity of guano deposited is mainly determined by population and body sizes, as well as duration of island occupation (breeding period). The quantities of nitrogen and phosphorus deposited by breeding seabirds worldwide are estimated at 591 Gg N y^{-1} and 99 Gg P y^{-1} . Seabird nutrient fluxes are globally significant, positioning seabirds as important drivers in global nutrient cycles (Otero et al., 2018).

2.3. Impacts of seabird nutrient subsidies

Nitrogen and phosphorus are essential for all life forms (Elser et al., 2007). Since these nutrients regulate primary production, seabird-derived nitrogen and phosphorus subsidies have considerable impacts when deposited at breeding colonies. These impacts influence terrestrial and aquatic environments, as well as the atmosphere, and can extend at global scales (De La Peña-Lastra, 2021a). The effects of seabird nutrient subsidies occur through a variety of pathways and responses vary widely, depending on ecosystem context, with impacts generally more pronounced in nutrient-limited environments (Subalusky and Post, 2019). In terrestrial environments, seabird-derived nutrients alter soil physical and chemical properties (García et al., 2002; Otero et al., 2015; De La Peña-Lastra et al., 2021b; Mutillod et al., 2023), plant chemical and physiological traits (Mulder and Keall, 2001; Mulder et al., 2009; Clyde et al., 2021), and plant community composition, diversity, biomass and productivity

(Anderson and Polis, 1999; Ellis, 2005; Fukami et al., 2006; Wardle et al., 2009; Lameris et al., 2016; Duda et al., 2020). These effects amplify up food chains, leading to increases in abundance of invertebrates (Sanchez-Pinero and Polis, 2000; Towns et al., 2009), rodents (Stapp and Polis, 2003) and landbirds (Hentati-Sundberg et al., 2020), larger sizes of reptiles (Richardson et al., 2019), and increase survival of marsupials (Wolfe et al., 2004) and reproductive success of mammals (Iason et al., 1986).

Seabird-derived nutrients can also enter freshwater and marine environments around breeding colonies. This occurs through four main pathways; direct guano deposition by overflying birds, surface run-off, leaching into ground water followed by dispersal during tidal oscillations, and the return of atmospheric ammonia volatilized from colonies by way of rainfall (Young et al., 2011a). Rivers and lakes near seabird colonies have elevated water, algal and invertebrate nutrient concentrations (Harding et al., 2004; Finne et al., 2022) and higher biomass of plankton, microbial and algal communities (Klimaszuk et al., 2015; González-Bergonzoni et al., 2017), than water bodies not near seabird colonies. In nearshore marine environments adjacent to seabird colonies, seabird-derived nutrients enrich food webs (Wainright et al., 1998; Gagnon et al., 2013; Zmudczyńska-Skarbek et al., 2015; Vizzini et al., 2016; Andrades et al., 2024). Such nutrient enrichment promotes high marine phytoplankton biomass (Shatova et al., 2016; Petkuvienė et al., 2019; Browning et al., 2023), increasing macroalgal abundance and diversity (Wootton, 1991; Benkwitt et al., 2019; Rankin and Jones, 2021), and abundance of zooplankton (McCauley et al., 2012) and marine invertebrates (Bosman and Hockey, 1986; Kolb et al., 2010). Seabird nutrient subsidies also impact the atmosphere. Seabird colonies are major point sources of ammonia emissions (Riddick et al., 2014). Globally, ammonia emissions by breeding seabirds is estimated at 270 Gg NH₃ y⁻¹, with the highest amounts emitted from polar seabird colonies (Riddick et al., 2012). Through the release of ammonia, as well as other greenhouse gases such as nitrous oxide, methane and carbon dioxide (Zhu et al., 2009), seabirds influence the regulation of the Earth's climate (De La Peña-Lastra, 2021a). For example, ammonia emissions from Arctic seabird colonies seed clouds which promotes cooling of these polar areas (Croft et al., 2016).

While the impacts of seabird nutrient subsidies are mostly considered beneficial in ecosystems, they can also be detrimental. In nutrient-rich environments or through excessive guano deposition in high density colonies, eutrophication can occur in water bodies, leading to mortality of marine organisms

(Signa et al., 2015; Saifutdinov and Korobushkin, 2020). On land, high guano loading destroys plant communities (Gillham, 1961). Due to their high position in marine food webs and long-life span, seabirds magnify and accumulate pollutants (Signa et al., 2021). Seabirds introduce persistent organic pollutants (Blais et al., 2005; Foster et al., 2011; Gilmour et al., 2019) and toxic metallic trace elements (Michelutti et al., 2010; Santamans et al., 2017; De La Peña-Lastra et al., 2022) to their breeding areas, presenting ecotoxicological risks to recipient communities. Physical pollutants such as plastic particles are also transported by seabirds through ingestion or as nest material (Grant et al., 2022). Seabird colonies can pose a threat to ecosystems through their ammonia emissions. Ammonia is a reactive gas that is readily incorporated into local environments (Riddick et al., 2018). Excess ammonia can adversely affect plant growth and reduce plant tolerance to diseases, pests and environmental stressors (Riddick et al., 2014). Overall, through their nutrient subsidies, seabirds act as keystone species, profoundly shaping the structure and dynamics of entire communities, food webs and ecosystems in the vicinity of their colonies.

Despite their ecological significance, seabirds remain one of the most threatened group of birds (Croxall et al., 2012; Paleczny et al., 2015). Because they interact with the sea and the land, seabirds face threats in both realms. On land, seabirds are particularly threatened by invasive alien species which predate on eggs, chicks and adult birds (Towns et al., 2011). Other land-based threats include hunting/trapping, colony disturbance, light pollution and diseases. At sea, seabirds are notably affected by fisheries either through bycatch or overfishing. Human-induced climate change also impacts seabirds, through increased frequency in extreme weather events, changes in oceanographic conditions which lead to declines in food availability, and sea level rise which results in inundation of colonies (Croxall et al., 2012; Dias et al., 2019). These threats impact seabird nutrient uptake, transfer and delivery, directly and indirectly (Table 1.1; Buckner et al., 2017). Reductions in seabird nutrient subsidies ramify throughout food webs around their breeding colonies and have far-reaching consequences (Şekercioğlu et al., 2004). The presence of invasive foxes decimated seabird populations in the Aleutian archipelago, resulting in the transition of several islands from grassland to dwarf shrub-dominated landscapes (Maron et al., 2006). Impacts of seabird population loss also extend to nearshore environments. Seabird decline caused by invasive rats in the Chagos archipelago, led to reductions in the growth and biomass of herbivorous reef fish. This resulted in reductions in their grazing and bioerosion rates, both of which are critical functions for maintaining healthy coral reefs (Graham et

al., 2018). Assessing the impacts of seabird nutrient subsidies in ecosystems is therefore critical to acknowledge, understand and reverse ecosystem breakdown caused by decimation of seabird colonies.

Table 1.1. Examples of top-down and bottom-up mediated impacts of human activities on seabird nutrient subsidies (adapted from Buckner et al., 2017).

	Human activities	Consequence
Donor system		
Top-down	Seabird exploitation or accidental mortality (vessel collision, entanglement, bycatch)	Loss of nutrient vector
Bottom-up	Commercial fisheries (prey competition and depletion)	Decline in nutrient subsidy
Transfer pathway		
Bottom-up	Light pollution, loss of nesting habitat	Blocking nutrient transfer
Recipient system		
Top-down	Guano mining, nest exploitation	Loss of nutrient vector
Bottom-up	Invasive alien species (introduced predators or vegetation)	Loss of nutrient vector

3. Research gaps

3.1. Tropical seabird islands

Because of their dependence on the marine environment, seabirds usually breed in coastal areas, such as cliffs and headlands, but predominantly on uninhabited islands. Seabird colonies represent a key source of allochthonous nutrients to their breeding islands (Polis and Hurd, 1996). On some islands, seabird nutrient subsidies are substantial and seabirds become integral to maintaining island ecosystem functioning, giving rise to the term ‘seabird islands’ (Anderson and Mulder, 2011). Despite the global distribution of seabird islands, research on the impacts of seabird nutrient subsidies is primarily concentrated in temperate and polar regions because of the higher concentrations of seabirds found in these areas (Otero et al., 2018). Nevertheless, tropical islands also host large seabird colonies (Berr et al., 2023) and global reviews and meta-analyses reveal important gaps in seabird nutrient subsidy research in the tropics (Grant et al., 2022; Van Der Vegt and Bokhorst, 2023).

The dynamics of seabird nutrient fluxes differ substantially between temperate or polar areas and tropical regions. A key difference is linked to the foraging and breeding behaviour of tropical seabirds. At higher latitudes, distinct seasonal shifts in marine productivity and prey governs the breeding schedules of seabirds and their presence on land (Young and VanderWerf, 2023). In oligotrophic surface tropical waters, seasonality in marine productivity is less conspicuous, and food resources are localised, ephemeral and unpredictable, but also influenced by seasonal changes in wind and currents (Jaquemet et al., 2007; Weimerskirch, 2007; Soanes et al., 2021). With this variability in food supply, tropical seabird communities exhibit a range of breeding behaviours, including seasonal and non-seasonal breeding cycles, multiple breeding peaks annually, and with synchronous and asynchronous breeding. Furthermore, some tropical seabird populations have non-breeding individuals that maintain constant presence on land in communal roosting colonies, during and outside the breeding period (Schreiber and Chovan, 1986; Weimerskirch et al., 2017). Guano deposition can therefore be continuous in tropical seabird colonies, regulated by diurnal foraging forays (Staunton Smith and Johnson, 1995; Jones et al., 2005). Overall, this results in both intermittent pulses and sustained nutrient inputs at tropical seabird colonies (Signa et al., 2021). Moreover, climatic conditions such as temperature and rainfall fundamentally influence the dispersal and assimilation of components of seabird guano (De La Peña-Lastra, 2021a). For example, due to higher temperatures, ammonia emissions from tropical seabird colonies are much higher than from colonies in colder climates (Riddick et al., 2014). In addition to nutrients, temperature and light limit primary production. Temperature affects the rate of metabolism and all biological activity (Brown, 2014), causing tropical biological communities to respond differently to seabird nutrient subsidies.

Many tropical islands are found within biodiversity hotspots, and are critical for regional and global conservation (Myers et al., 2000). Additionally, tropical coastal zones harbour some of the most biodiverse and productive marine ecosystems on the planet, including coral reefs, mangroves and seagrass. However, biological communities in the tropics face higher extinction risks than in temperate zones (Clarke et al., 2017). This concern is particularly acute for island biota, which are disproportionately vulnerable to anthropogenic impacts, such as invasive species, habitat loss, overexploitation and climate change (Fernández-Palacios et al., 2021). An increased understanding of the role of seabird populations in the functioning of tropical island and coastal ecosystems is therefore

urgent to advance management and conservation efforts of tropical seabird islands (Benkwitt et al., 2020).

3.2. Importance of seabird nutrient subsidies on tropical islands

Research on seabird nutrient subsidies on tropical islands has characterised tropical seabird guano input (Staunton Smith and Johnson, 1995; Liu et al., 2006), and demonstrated how seabird-derived nutrients alter soil, plants and food webs on tropical islands in various regions, including the Gulf of California (Wait et al., 2005; Wilder et al., 2022), Brazil (Gaiotto et al., 2022), South China Sea (Wu et al., 2018), Great Barrier Reef (Schmidt et al., 2004) and Pacific Ocean (Young et al., 2010; 2011b; Caut et al., 2012; Rowe et al., 2017). However, some geographical locations such as seabird islands in the Indian Ocean are underrepresented in these studies. More recently, investigations in nearshore environments shows that corals adjacent to seabird colonies incorporate seabird-derived nitrogen (Lorrain et al., 2017; Linhares and Bugoni, 2023; Choisnard et al., 2024), altering coral feeding strategies (Thibault et al., 2022), promoting faster coral growth rates (Savage, 2019) and higher coral cover, consequently leading to faster recovery rates after bleaching events (Benkwitt et al., 2019, 2023). Seabird nutrient subsidies also impact tropical fish communities. Seabird-derived nutrients enhance biomass and growth rates, and alter behaviour and functions of herbivorous reef fishes (Graham et al., 2018; Benkwitt et al., 2021; Gunn et al., 2023), and increase occurrence and abundance of sharks and rays (McCauley et al., 2012; Schiele et al., 2023). By boosting ecosystem productivity of tropical coastal zones, seabirds contribute to the livelihoods of coastal inhabitants. The ecosystem services of seabird nutrient subsidies on tourism and coral reef fisheries is estimated at US\$ 650 million annually (Plazas-Jiménez and Cianciaruso, 2020). These studies underscore the importance of land-sea linkages in coastal ecosystem functioning and have shed light on the ecological connection facilitated by seabirds in nearshore tropical environments. The term 'island-ocean connection' is increasingly used, highlighting the marine co-benefits of seabird island management (Sandin et al., 2022).

3.3. Seabird-derived nutrients in mangrove ecosystems

Seabird nutrient subsidies also influence other tropical coastal habitats such as mangroves and seagrass, which are used by seabirds worldwide as breeding, roosting and foraging sites (Buelow and Sheaves, 2015; Unsworth and Butterworth, 2021). Mangroves are highly productive and are rich in

carbon, despite occurring mostly in nutrient-poor tidal environments (Alongi, 2018). This is largely possible due to the evolution of multiple adaptations for retaining and recycling nutrients (Reef et al., 2010). For example, mangrove leaves have long lifespan to limit nutrient investment in new leaves and reduce nutrient loss, resulting in them being evergreen (Aerts, 1995), and they can exhibit high resorption of nutrients from senescent leaves prior to leaf fall (Lin et al., 2010). Mangroves are highly sensitive to variations in nutrient availability, responding through changes in leaf traits and nutrient conservation strategies (Feller et al., 1999; Lovelock et al., 2004). Nutrient enrichment influences mangrove productivity (Feller, 1995) and ecological functions such as carbon sequestration and water filtration (Feller et al., 2010; Hayes et al., 2017). The responses of mangroves to nutrient additions are governed by complex interacting factors such as forest species composition, age, forest development stage and intertidal position, as well as abiotic properties such as soil type, redox status, and salinity (Alongi, 2020a). Studies on the influence of seabird nutrient subsidies document an enrichment of mangroves, but they solely focus on mangrove trees and are restricted in geographical range (Onuf et al., 1977; Adame et al., 2015; Irick et al., 2015; McFadden et al., 2016; Simpson et al., 2021). Given the diversity of mangrove species and the large range in mangrove forest properties, there is a pressing need for research into how seabird nutrient subsidies influence mangroves and associated communities.

Mangrove forests have experienced substantial degradation and deforestation, with a loss of 20–35% of their global extent since 1980 (Goldberg et al., 2020). Mangroves provide numerous benefits and support the livelihoods and cultural values of millions of coastal inhabitants worldwide (Worthington et al., 2020). Mangrove forests shape and maintain intertidal areas, accumulate and recycle sediment and associated elements, and support coral reefs and seagrass beds. In doing so, mangroves provide coastal protection, pollution control, and products such as timber, fuelwood and fisheries resources for coastal inhabitants. Within the tropical marine area, mangroves sequester among the largest quantities of carbon per unit area, estimated at 15 Tg C_{org} a⁻¹ globally, representing a vital blue carbon ecosystem (Alongi, 2020b). Evaluating the impact of seabird nutrient subsidies on mangrove ecosystems also facilitates an understanding of the influence of seabirds on mangrove ecosystem service delivery.

Mangrove forests are important habitats for a myriad of invertebrate taxa, providing shelter, food and nursery grounds (Nagelkerken et al., 2008). Macrofaunal invertebrate communities including

polychaetes, molluscs and crustaceans, play major ecological roles in shaping the structure and functioning of mangrove forests (Cannicci et al., 2008). Through their bioturbating and feeding activities, mangrove macroinvertebrates influence sediment biogeochemistry, promote recycling of organic matter and nutrients, and regulate mangrove growth (Lee, 2008). Furthermore, they are food sources for numerous vertebrates such as fishes and birds (Nagelkerken et al., 2008; Sandoval, 2023). Ultimately, invertebrate assemblages substantially influence mangrove ecosystem functioning (Cannicci et al., 2021). Despite this, the impact of seabird nutrient subsidies on mangrove invertebrate groups remains largely unexplored.

4. Thesis aim and objectives

A challenge of maintaining healthy socio-ecological systems relies on understanding, protecting, and restoring island-ocean connections. Investigations on the cross-ecosystem nutrient transfer by breeding seabirds are disproportionately focussed on temperate and polar regions, which means that the functional role of seabirds in tropical island-ocean ecosystems remains largely underestimated. The primary goal of this thesis is **to assess the impacts of seabird nutrient subsidies on tropical oceanic islands**. Seabird populations have faced and continue to face significant threats, compromising island-ocean nutrient linkages. Consequently, this research is needed to inform management strategies aimed at restoring seabird populations and preserving their functional roles, which are vital for sustaining the livelihoods of tropical coastal inhabitants.

To achieve this overarching aim, I explore the nutrient dynamics of various components of the seabird subsidy transfer through four main objectives. The components include the nutrient vector (seabirds), the nutrient subsidy (guano), the nutrient pathways (flow) and the nutrient recipients (impacts). Specifically, the objectives are to:

1. Characterize isotopic signatures of tropical seabirds (nutrient vector);
2. Characterize seabird guano contributions quantitatively and qualitatively (nutrient subsidy);
3. Assess pathways of seabird-derived nutrient transfer across the land-sea interface of tropical seabird islands (nutrient pathways);
4. Evaluate the impacts of seabird-derived nutrients on tropical island and coastal habitats and communities (nutrient recipients).

To meet these objectives, I focus on the tropical Western Indian Ocean (WIO) seabird assemblage and use remote seabird islands in the Seychelles archipelago as case studies, where the influence of seabirds is isolated from direct local human influence. Seychelles seabird islands harbour large seabird colonies and diverse coastal habitats, providing opportunities to explore the effects of seabird nutrient subsidies on overlooked coastal ecosystems, such as seagrass beds and mangrove forests. I integrate frameworks from trophic and functional ecology to advance our understanding of tropical seabird nutrient cycling from the organismic to the ecosystem level. I combine ecological monitoring, field sampling and laboratory analysis and use biogeochemical assays to investigate nutrient dynamics in tropical seabird communities, and to explore the magnitude and extent of seabird nutrient impacts in tropical island-ocean ecosystems.

5. Research context

5.1. Seabird islands in the tropical Western Indian Ocean

The tropical WIO is a global biodiversity hotspot, boasting exceptional biological diversity, yet facing high anthropogenic pressures (Myers et al., 2000). Although the tropical Indian Ocean is characterised by low marine productivity in surface waters, there are numerous large oceanographic and climatic features that govern productivity patterns, such as the seasonal Somalia upwelling, seasonal monsoon and the Indian Ocean Dipole (Schott et al., 2009). As a result, the region supports large concentrations of marine megafauna such as cetaceans, sea turtles, elasmobranchs and seabirds (Laran et al., 2017). The tropical WIO has numerous islands, many of which are uninhabited and support native and threatened biological communities. These islands and associated coastal ecosystems, whose functioning is little known, therefore have a major role in the conservation of regional biodiversity and represent priority targets for research.

Seabirds are highly abundant in the WIO. The WIO islands host breeding habitats for 30 species and 7.4 million breeding pairs of seabirds. The largest seabird colonies in the region are found on islands away from high human population densities and with some level of protection. These are mainly found in the Seychelles archipelago, the Mozambique Channel, and the Mascarene region (Le Corre et al., 2012). The most abundant seabird is the sooty tern *Onychoprion fuscata*, which constitutes 85% of the total seabird numbers. This is followed by the lesser noddy *Anous tenuirostris*, wedge-tailed

shearwater *Ardenna pacifica* and brown noddy *Anous stolidus*, collectively comprising 11% of the total population (Danckwerts et al., 2014). Some of the seabird populations are regionally or globally significant, with their breeding sites designated as 'Important Bird and Biodiversity Areas' (IBAs) by BirdLife International (Fishpool and Evans, 2001; Carr et al., 2021b).

Despite the high abundance estimates, seabird populations in the tropical WIO are a fraction of what they used to be. Reductions in seabird populations have been observed since the 18th century, with several documented extinct colonies and species (Feare, 1978; Feare et al., 2007). Seabirds in this region face a multitude of threats by human activities. At sea, seabirds are threatened by overfishing of predatory fishes such as tuna by industrial fishing practices. Many tropical seabirds are near-obligate commensals, meaning they are dependent on predatory fish to drive prey to the surface, making them available for seabirds (Danckwerts et al., 2014). Industrial tuna fishing areas substantially overlap with seabird foraging locations and have increased 30-fold since 1950 (Le Corre et al., 2012). On multiple islands, native habitats were destroyed by guano exploitation or converted into coconut plantations in the 19th century. This and the subsequent abandonment of the plantations, has greatly reduced breeding habitat for seabirds (Feare et al., 2007; Carr et al., 2021a). Furthermore, mammalian predators such as rats and cats were introduced to the majority of islands by the arrival of humans, presenting a particularly acute threat to seabird populations (Russell et al., 2016). Seabirds and their eggs, especially sooty terns, are also exploited for food, both legally and illegally, causing multiple population declines and local extinctions (Feare, 1976; Le Corre and Bemanaja, 2009). Climate change and severe weather events also impact colonies. High category tropical cyclones in 2006 and 2016 devastated entire seabird communities in the southern Seychelles (Skerrett, 2016; Duvat et al., 2017). Some low-lying coral islands have also been progressively lost by erosion and are no longer occupied by nesting seabirds (Feare et al., 2007). Climate change can also amplify El Niño Southern Oscillation events, which impact oceanographic conditions and results in low breeding productivity and high chick mortality (Ramos et al., 2002, 2006).

5.2. Seychelles archipelago

The islands of the Seychelles archipelago lie between 04–10 °S and 46–56 °E (Figure 1.2). Seychelles consists of 115 islands, with a land surface area of 455 km², scattered over a total sea area of 1.37 million km². The central archipelago lies on the Mahé Plateau, a submarine continental shelf, where

most of the islands are of granitic origin (landmass 244 km², referred to as the 'Inner Islands'). Outside of this plateau, the islands are all of coral origin (landmass 211 km², referred to as the 'Outer Islands'), consisting of atolls, coral cays and sandbanks. There are three main groups of coral islands; the Amirantes group (29 islands), Farquhar group (13 islands), the Aldabra group (67 islands). 98% of Seychelles human population, estimated at 98,000 in 2020, is based in the Inner Islands (Etongo and Arrisol, 2021). Seychelles has a tropical climate governed by seasonal changes in monsoon winds. Winds blowing from the south-east between April and October bring dry and rough sea conditions, while from November to March, north-westerly winds bring rain and calm seas (Rocamora and Skerrett, 2001). The average annual temperature is 26 °C and the Outer Islands are generally drier than Inner Islands, with annual rainfall ranging from 1000 mm on Aldabra to over 2400 mm on Mahé.

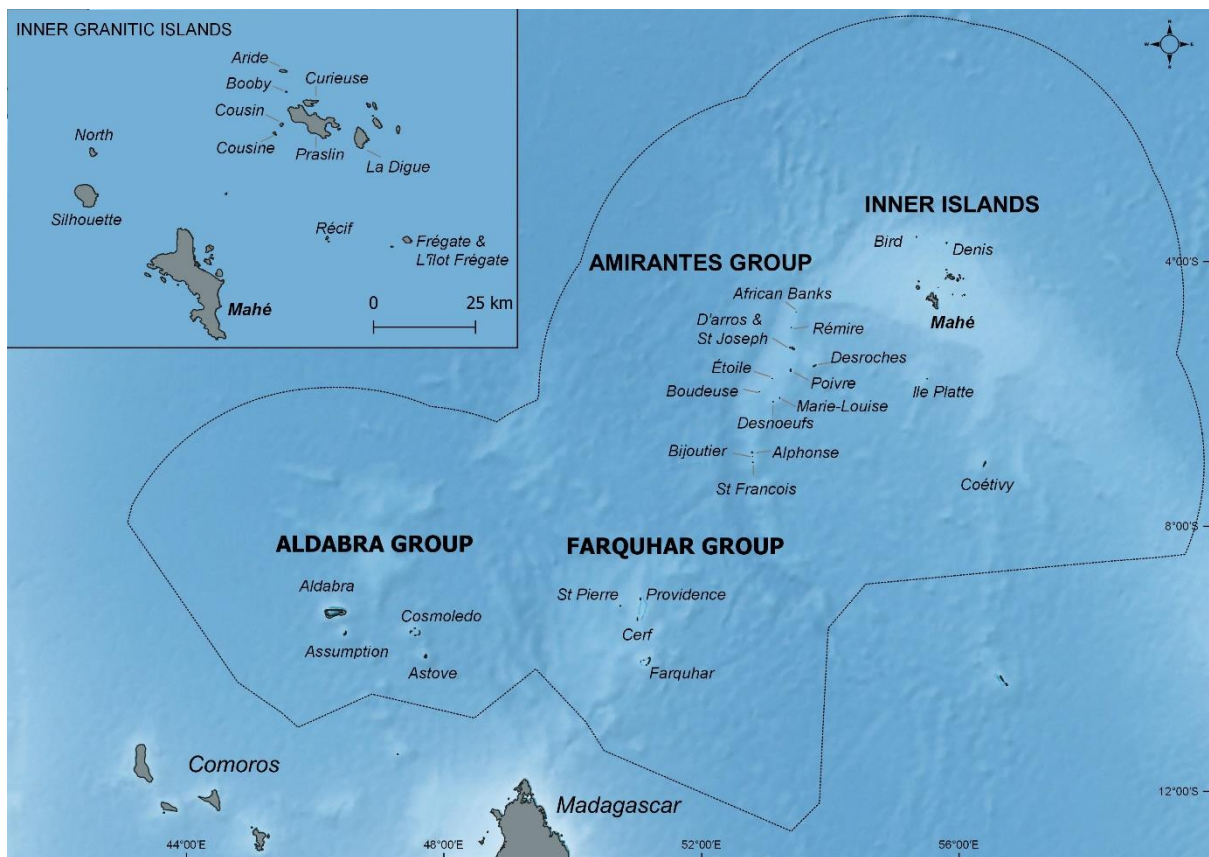


Figure 1.2. Seychelles archipelago and extent of economic exclusive zone (dotted line).

Seychelles' islands have high levels of endemism; endemic species include 14 birds, five bats, 16 reptiles, 12 amphibians, two freshwater fishes, and 20% of native plants (Rocamora and Henriette, 2015). Moreover, some of the coral islands of Seychelles maintain intact ecosystems and abundant

native species due to their isolation from dense human populations, with some islands remaining uninhabited. Seychelles supports the highest abundance of breeding seabirds in the tropical WIO, representing 51% of all breeding seabirds in the region (Danckwerts et al., 2014). Nineteen breeding seabird species have been recorded, including 10 species of tern, two tropicbirds, two shearwaters, three boobies and two frigatebirds. Seabird species richness is highest on the granitic islands as well as on the coral islands belonging to Farquhar and Aldabra groups. Breeding colonies of larger seabirds such as boobies *Sula* spp. and frigatebirds *Fregata* spp. occur exclusively on the coral islands. 13 out of 20 IBAs in Seychelles are based on seabird populations, with three further considered as potential seabird IBAs (Rocamora and Skerrett, 2001).

The Seychelles economy is heavily dependent on the marine environment, with fisheries and tourism representing the main economic pillars. Fisheries contributes to 20% of the employment sector and 15% of the country's gross domestic product (GDP) (Philpot et al., 2015). Small-scale fishery, comprised of artisanal and semi-industrial fishing, targets mainly demersal and pelagic fish, sea cucumber, lobster and octopus, are an important food source for Seychelles' population (Etongo and Arrisol, 2021; Sabino et al., 2022). Industrial large-scale fishing of mainly tuna and tuna-like species occurs in pelagic waters. Tuna comprises 68% of the country's export (Christ et al., 2020). Tourism contributes to 21% of employment and 25% of Seychelles GDP (Philpot et al., 2015). Tourism in Seychelles relies on the exceptional natural beauty and biological diversity of its islands and marine areas. Sustainable use and protection of Seychelles biodiversity and marine areas is therefore vital for the socioeconomic development and food security of the country. Biodiversity conservation is a national priority in Seychelles, with 47% of the land and 26% of territorial waters currently designated as protected areas. In addition, multiple successful conservation and restoration initiatives have contributed to the safeguarding and rebounding of numerous endemic and threatened species (Rocamora and Henriette, 2015; Bunbury et al., 2019; Feare et al., 2021; Pritchard et al., 2022).

6. Thesis layout

I explore the dynamics of tropical seabird nutrient cycling in four data chapters (Chapters 2–5). Each chapter addresses one or multiple thesis objectives which are aimed at examining different components of the seabird subsidy transfer (Figure 1.3). These chapters were written as manuscripts for peer-

reviewed journals, and are published (Chapters 3 and 4), in review (Chapter 5) or in preparation (Chapter 2) at the time of thesis submission.

I start my thesis by examining the nutrient dynamics of nutrient vectors i.e., seabirds in **Chapter 2**, by asking **How are seabird isotopic signatures ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) structured across the WIO?** I address this question by compiling seabird isotopic values collected in the WIO over the last two decades. The results reveal how biological, ecological, spatial, and temporal variables influence the isotopic compositions of tropical seabirds in this region. The implications of seabirds as marine environmental indicators and baseline references for the region are discussed.

In **Chapter 3**, I evaluate **How do spatial and seasonal dynamics of seabird nutrient contributions impact atoll habitats?** I quantify guano contributions and compare seabird colonies of different taxa nesting on separate islands of Farquhar Atoll, Seychelles, taking into account local weather seasonality. The results reveal the dominant traits influencing tropical seabird nutrient contributions and the consequent impacts on island and seagrass habitats. The findings are used to provide recommendations relevant for tropical seabird conservation.

In **Chapter 4**, I examine **How do seabird-derived nutrients influence mangroves, and to what extent they are transferred within the mangrove ecosystem?** I quantify guano contributions, and trace the transfer and uptake of seabird-derived nutrients in multiple mangrove ecosystem components, at sites with and without nesting seabirds on Aldabra Atoll, Seychelles. The results show the extent of nutrient connectivity facilitated by seabirds, vertically and horizontally, within the coastal seascape. The implications on the health of mangrove forests are discussed.

Building on the previous chapter, **Chapter 5** explores **What are the impact of seabird nutrient subsidies on the mangrove macroinvertebrate food web?** I examine the nutrient status of basal resources, the nutrient status and morphology of macroinvertebrate consumers, and the contribution of basal resources to consumer diet, at mangrove sites with and without seabirds on Aldabra Atoll. The results show how seabird nutrient subsidies alter the size and resource use of macroinvertebrate fauna, with implications for mangrove ecosystem processes and service delivery.

I summarize the key findings of the thesis in **Chapter 6** to highlight the role of seabird populations in tropical oceanic islands. I present the contributions of this thesis to island-ocean

connectivity science and the practical implications of my research. I close my thesis by providing recommendations for policy, monitoring, research and conservation of tropical seabird islands.

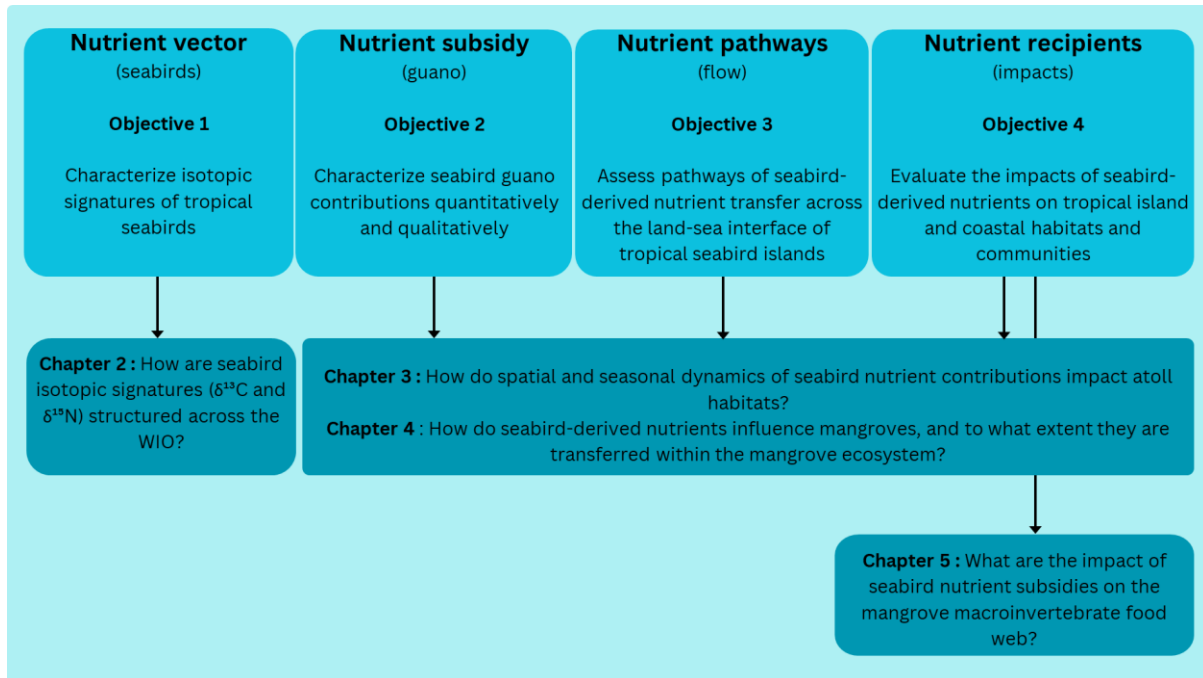


Figure 1.3. Conceptual diagram of thesis structure, showing the links between thesis objectives and data chapters. The thesis objectives address different components of the seabird subsidy transfer.

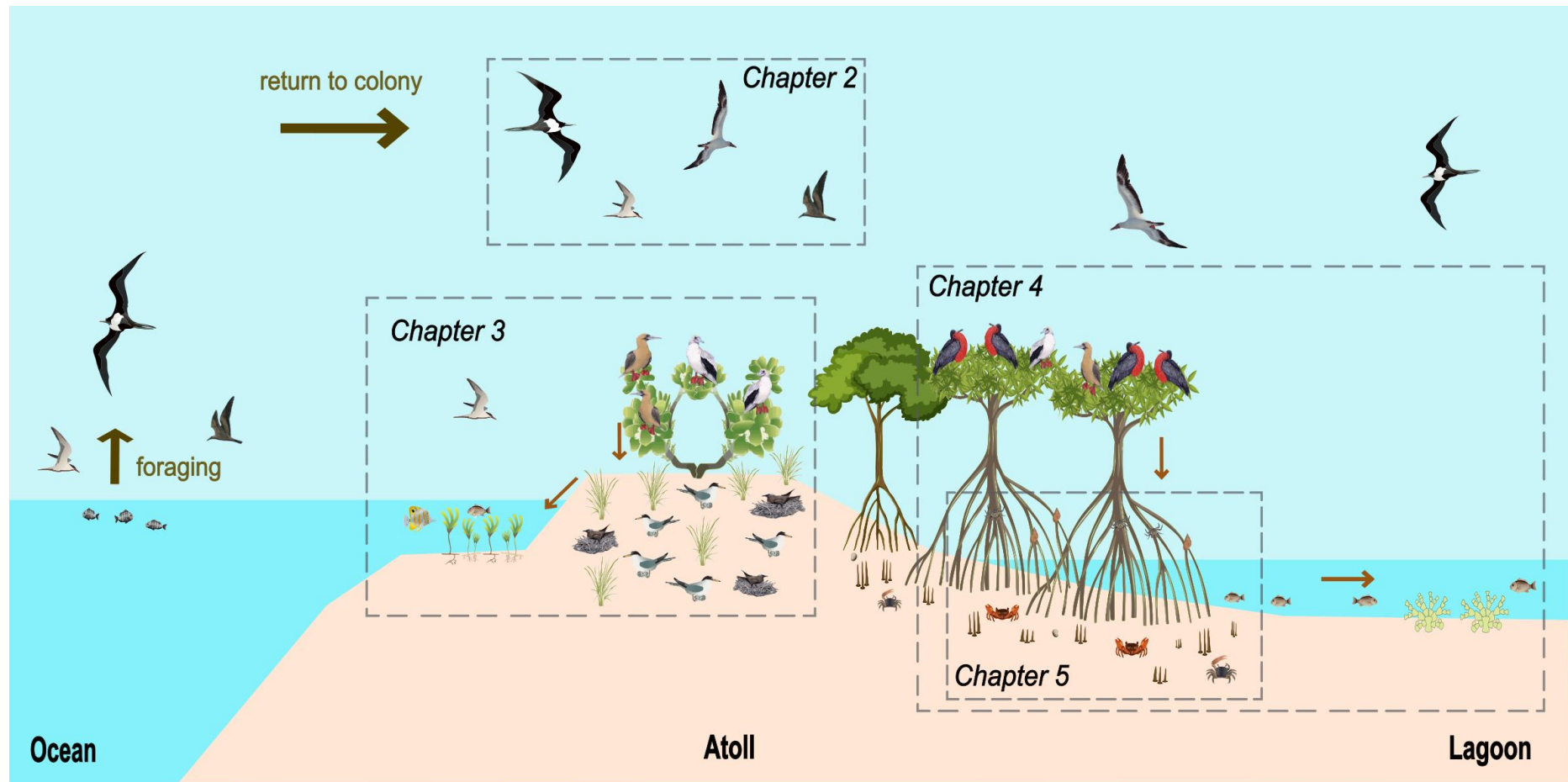


Figure 1.4. Schematic diagram of seabird nutrient transport from the open ocean to tropical breeding colonies. Dashed boxes indicate the focus for each data chapter and orange arrows depicts seabird-derived nutrient flow in recipient ecosystems.

CHAPTER 2

Isotopic structure and dynamics of a tropical seabird assemblage

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ABSTRACT

Climatic and anthropogenic impacts are profoundly altering marine ecosystem structure and functioning, increasing the urgency for understanding the mechanisms that shape marine communities. Here, we use nitrogen ($\delta^{15}\text{N}$) and carbon ($\delta^{13}\text{C}$) stable isotopes as biochemical markers of food web structure, to examine how biological, ecological, spatial and temporal variables influence the isotopic composition of a tropical seabird assemblage. We combine isotopic ratios of seabird blood and feathers, representing the breeding and non-breeding periods, respectively, collected from seabird populations across the tropical Western Indian Ocean between 2003 and 2023. Seabird isotopic ratios were structured by biological factors such as taxonomic group and body mass. Charadriiformes had lower $\delta^{15}\text{N}$ values than Procellariiformes and Pelecaniformes during the breeding period, indicating that they fed at lower trophic levels. Seabird $\delta^{15}\text{N}$ values and body mass were positively correlated for Charadriiformes but negatively correlated for Pelecaniformes. Ecological traits also influenced isotopic ratios, with nearshore-foraging birds occurring at lower trophic levels (lower blood $\delta^{15}\text{N}$ values) than offshore-foraging birds. Seasonal comparisons showed that blood and feather $\delta^{15}\text{N}$ values were more enriched during the austral winter monsoon than the austral summer monsoon. Moreover, we observed a spatial trend, with seabird blood $\delta^{15}\text{N}$ values decreasing at higher latitudes. The best predictors of seabird blood $\delta^{15}\text{N}$ were biological (species), spatial (colony location) and environmental (sea surface temperature, chlorophyll-a concentration) variables, while for seabird blood $\delta^{13}\text{C}$ values, the best predictors were biological, spatial and temporal (year) variables. Modelled relationships showed higher seabird blood $\delta^{15}\text{N}$ values at low sea surface temperatures and high chlorophyll-a concentrations, and a decline in seabird blood $\delta^{13}\text{C}$ over the last two decades. Our study provides important isotopic baselines and offers preliminary insights on the potential of seabird blood $\delta^{15}\text{N}$ as indicator of marine environmental conditions in the tropical Western Indian Ocean.

Keywords: body size, biomonitoring, foraging range, Western Indian Ocean, latitudinal gradient, seasonal variations, stable isotopes, marine predators.

1. INTRODUCTION

Understanding the mechanisms that shape communities is increasingly urgent, particularly in light of the impacts of climate change and anthropogenic activities on ecosystem structure and function (Rogers et al., 2020; Priya et al., 2023). Marine environments are complex and dynamic, presenting challenges for research, but biochemical techniques offer advantages by enabling integrated measurements of food web structure across space and time (Young et al., 2015). Nitrogen ($\delta^{15}\text{N}$) and carbon ($\delta^{13}\text{C}$) stable isotopes are key biochemical tracers providing insights on trophic relationships and pathways of nutrient cycling and energy flow within food webs (Peterson & Fry, 1987; Post, 2002). $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ ratios integrate source and process information and are sensitive to changes (Layman et al., 2007a), thereby facilitating information on the drivers structuring marine communities (Layman et al., 2007b; Cherel & Carrouée, 2022).

At large spatial scales, variations in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ ratios in marine communities reflect natural biogeochemical cycle processes impacting primary producers at the base of the food web (McMahon et al., 2013). These variations are heavily influenced by biological and physical fractionation events, which exhibit spatial and temporal variability (Pethybridge et al., 2015). Variations in $\delta^{15}\text{N}$ of marine primary producers are driven by nitrogen fixation, water column denitrification and nitrogen use by primary producers (Lorrain et al., 2015; Espinasse et al., 2019). Variations in phytoplankton $\delta^{13}\text{C}$ are determined by the quantity of dissolved carbon dioxide and phytoplankton community dynamics, which are both dependent on sea surface temperatures (Magozzi et al., 2017). The resulting spatiotemporal variations in isotopic baselines delineate distinct geographic regions and ocean basins, and are propagated up food webs (Graham et al., 2010; Magozzi et al., 2017). At local scales within food webs, $\delta^{15}\text{N}$ increases at each trophic level, providing information on trophic position, while $\delta^{13}\text{C}$ remains relatively constant across trophic levels, offering insights on the source of primary production (i.e., benthic or pelagic and nearshore or offshore; Hobson et al., 1994; Cherel & Hobson, 2007). Together, $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ ratios in food webs characterize the isotopic niche space, enabling inferences on resource and habitat use, respectively (Newsome et al., 2007).

Marine top predators are prime indicators of marine environmental conditions since they integrate information from the bottom to the top of the food web and exhibit clear responses to environmental variability or change (Sergio et al., 2008; Hazen et al., 2019). Seabirds excel in this

capacity since they respond to environmental change in a timely and detectable manner (Frederiksen et al., 2007; Bertrand et al., 2012) and are accessible for monitoring during their reproductive aggregations on land. This facilitates observations on multiple coexisting species at various trophic levels simultaneously (Piatt & Sydeman, 2007). Isotopic compositions of seabirds reflect their diet, which can both vary due to a range of factors, such as species identity, size, sex (Käkelä et al., 2007; Austin et al., 2021; Cannell et al., 2022), colony location and oceanographic conditions that affect their prey (Jaquemet et al., 2008; Jacoby et al., 2023). Studies from temperate and polar regions have documented the biological, spatial, temporal, and environmental factors driving variations in seabird isotopic ratios (Ceia et al., 2018; Will & Kitaysky, 2018; Ramírez et al., 2021; Atkins et al., 2023), but investigations in tropical regions are limited.

The Western Indian Ocean (WIO) is a seabird hotspot, hosting globally and regionally important breeding seabird populations (Fishpool & Evans, 2001; Carr et al., 2021). The largest seabird concentrations are found on isolated and protected islands and atolls (Le Corre et al., 2012), where they fulfil a vital role in enriching island and coastal habitats with marine nutrients transported from their oceanic feeding grounds (Graham et al., 2018; Benkwitt et al., 2021; Appoo et al., 2024). Studies on stable isotopes in this region have examined differences in seabird isotopic compositions within and between colonies (Cherel et al., 2008; Jaquemet et al., 2008; Catry et al., 2008), but not yet for the regional seabird assemblage. In particular, there has been no quantitative assessment regarding the structure of seabird isotopic ratios and niche in relation to species biological and ecological traits, during the breeding and non-breeding periods, which represent distinct foraging conditions (Cherel et al., 2014). During breeding, seabirds are constrained to their colonies for egg incubation or chick rearing, thus behaving as central-place foragers. This reduces their foraging opportunities compared to the non-breeding period, when seabirds can access more foraging areas and resources (Shealer, 2001). Furthermore, while spatial and seasonal patterns in isotopic compositions have been detected in predatory fishes in this region (Ménard et al., 2007; Dhurmeea et al., 2020), this has not yet been examined for seabirds. As a result, the primary drivers of tropical seabird isotopic compositions remain unknown.

Here, we investigate how biological, ecological, spatial, and temporal variables influence isotopic compositions of a tropical seabird assemblage. We do this using seabird $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of seabird populations across the tropical WIO. Specifically, we examine the influences of biological,

ecological, spatial and temporal variables on the structure of seabird isotopic ratios and niche. Subsequently, we evaluate the main drivers influencing seabird isotopic compositions. Our study provides broad insights into isotopic variability within a tropical seabird hotspot and presents important baselines for monitoring changes in marine environmental conditions.

2. METHODS

2.1. Study region

The tropical WIO, here defined as the area between 4 and 22 °S, and between 40 and 74 °E (Figure 1), hosts a diverse seabird community, consisting of up to 30 breeding species and totalling approx. seven million breeding pairs (Le Corre et al., 2012). The biggest seabird concentrations occur in the Seychelles archipelago and on islands in the Mozambique Channel (Le Corre et al., 2012). Breeding phenologies vary greatly, comprising of species with seasonal and non-seasonal cycles, as well as synchronous and asynchronous breeding (Feare, 1981; Carr et al., 2021). Seabirds in this region are mainly surface foragers and a few are shallow divers (Ballance & Pitman, 1999), feeding largely on squid and diverse fish species (Diamond, 1971; Cherel et al., 2008; Catry et al., 2009).

Oceanographic conditions around the islands and atolls in the tropical WIO are generally nutrient-poor. However, seasonally predictable phytoplankton blooms occur in response to shifts in monsoon winds that cause horizontal advection and vertical nutrient upwelling (Schott & McCreary, 2001). During the austral winter monsoon (May–Oct), winds blow from the southwest across the region, promoting cooler and more productive waters compared to the austral summer monsoon (Nov–Apr), with productivity peaks occurring in the Somali region and the Mozambique Channel. During the austral summer monsoon, winds blow from the northeast across the region and lower intensity blooms occur in mid-ocean areas (Tomczak & Godfrey, 2003; Lévy et al., 2007). In addition, oceanographic features such as ocean fronts, eddies and seamounts can mix, advect and entrain nutrients, leading to smaller-scale spatial variations in locally enhanced primary productivity (Tew-Kai & Marsac, 2009; Jaquemet et al., 2014).

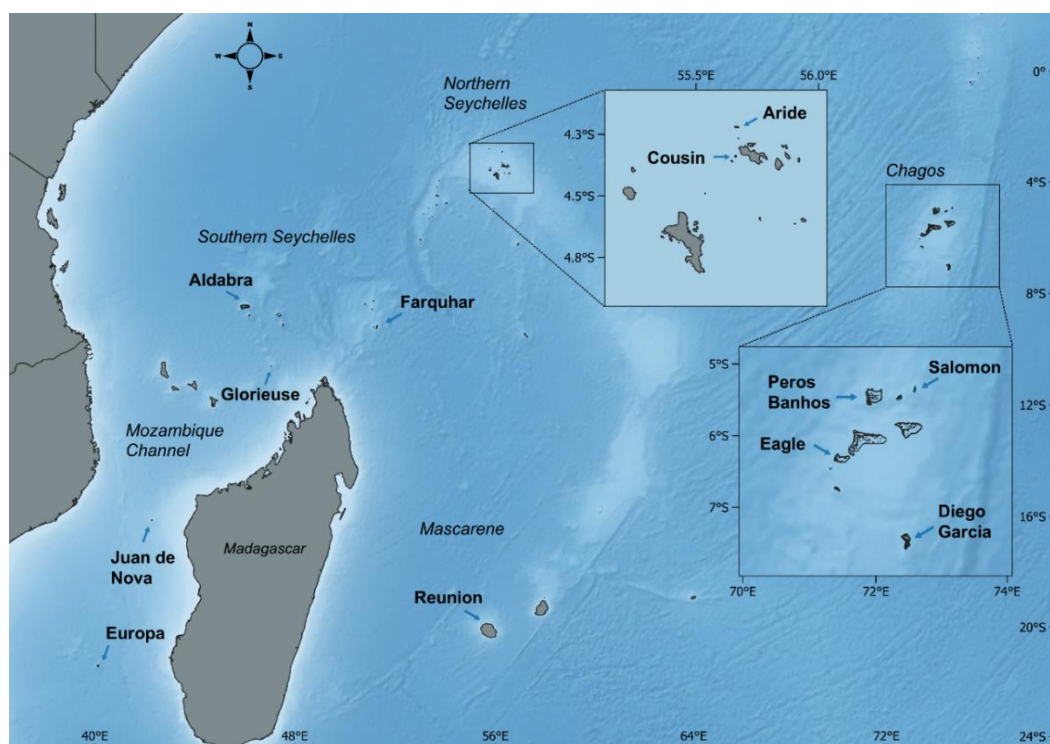


Figure 1. Location of seabird populations in the tropical Western Indian Ocean included in this study (see Table 1).

2.2. Seabird isotopic compositions

Multiple collaborative research programs involving seabird stable isotopes have been conducted in the tropical WIO. Published studies have documented stable isotopic compositions for colonies in the northern Seychelles (2003–2006, Monticelli et al., 2008; Catry et al., 2009), Mozambique Channel (2003–2004; Cherel et al., 2008; Jaquemet et al., 2008) and Mascarene region (2001–2004, Kojadinovic et al., 2008; 2010–2019, Danckwerts, 2014; Chandelier et al., 2023). These studies document isotopic compositions of blood and breast feathers of adult birds. Blood is a metabolically active tissue and the isotopic ratios of seabird whole blood reflect the diet over the previous 12–15 days (Bearhop et al., 2002). Blood isotopic ratios of birds sampled on nests therefore correspond to their breeding period. Seabird feather isotopic ratios exhibit similar assimilation rates, but because keratin is metabolically inert after synthesis, isotopic ratios of feathers represent the diet during time of growth of the feathers (Hobson & Clark, 1992). Since most adult seabirds start moulting after reproduction (Bridge, 2006), feathers therefore reflect isotopic signatures of diet during the non-breeding period (Cherel et al., 2000).

To increase coverage of the study region, we sampled blood and breast feathers from seabird colonies in the Chagos archipelago (2022) and southern Seychelles (2022–2023). We sampled five

species of seabird in colonies in the Chagos archipelago and on Aldabra and Farquhar atolls (Figure 1). In the Chagos, we sampled red-footed boobies *Sula sula* and lesser noddies *Anous tenuirostris*, on Aldabra we sampled red-footed boobies and lesser frigatebirds *Fregata ariel*, and on Farquhar we sampled red-footed boobies, brown noddies *Anous stolidus* and sooty terns *Onychoprion fuscatus*. Adult birds were randomly caught on nests, either incubating or chick rearing, except for lesser noddies, which were captured by mist-net since nests were inaccessible. From each individual, we collected up to 1 ml of blood with a syringe by venipuncture in the wing or leg and five breast feathers.

Whole blood was dried at 50 °C for up to 48 h and then powdered using a ball-mill. The low lipid content of avian blood negates the need for lipid extraction (Bearhop et al., 2000), which we confirmed with the low C:N mass ratios (C:N < 3.5, Post et al., 2007). Feathers were cleaned of surface contaminants for two minutes using a 2:1 chloroform:methanol solution in a ultrasonic bath, then washed in two successive methanol rinses (Jaeger et al., 2009). Feathers were dried at 50 °C for 48 h, then cut into very small fragments. For each sample, around 1 mg of homogenized material were packed in tin cups for stable isotope analyses. Samples were combusted using an Elementar Vario Micro Cube Elemental Analyser and $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ were measured using an Isoprime 100 Isotope Ratio Mass Spectrometer with international standards IAEA 600 and USGS 41, at the stable isotope facility at Lancaster University (Lancaster, UK). Accuracy based on internal standards was within 0.2 ‰ standard deviation and selected samples were run in triplicate to further ensure accuracy of readings.

2.3. Final dataset

To examine the isotopic structure of the seabird assemblage, we combined blood and feather isotopic compositions from the published studies and field sampling in the tropical WIO. This consists of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values for 34 seabird populations from 2003 to 2023, comprising 13 species, including six terns, two shearwaters, two frigatebirds, one booby, one tropicbird and one petrel (Table 1). Because we were interested in breeding individuals, we excluded data from three studies reporting isotopic ratios from samples collected on dead birds, comprising lesser noddies and roseate terns *Sterna dougalli* from Aride Island (Monticelli et al., 2008), and Barau's petrel *Pterodroma baraui*, tropical shearwater *Puffinus bailloni* and white-tailed tropicbirds *Phaethon lepturus* from Reunion Island (Kojadinovic et al., 2008; Chandelier et al., 2023). Our final dataset comprised of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values for 29 seabird populations.

Table 1. Stable isotope values ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) of blood and feathers sampled from adult seabirds at colonies in the tropical Western Indian Ocean.

Species	Location	Sampling period	Abbreviation	n	Blood (Mean \pm SD, ‰)		n	Feather (Mean \pm SD, ‰)		Reference
					$\delta^{15}\text{N}$	$\delta^{13}\text{C}$		$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	
Chagos										
Red-footed booby <i>Sula sula</i>	Diego Garcia	February 2022	DGA-RFB	8	11.9 \pm 0.2	-18.2 \pm 0.2	14	13.3 \pm 0.4	-15.9 \pm 0.2	This study
	Eagle Island	February 2022	EI-RFB	-	-	-	6	13.1 \pm 0.3	-15.9 \pm 0.1	
Lesser noddy <i>Anous tenuirostris</i>	Peros Banhos	February 2022	PBA-LN	11	11.0 \pm 0.2	-18.5 \pm 0.2	16	13.1 \pm 0.3	-17.0 \pm 0.2	
	Salomon	February 2022	SAL-LN	24	11.1 \pm 0.3	-18.6 \pm 0.2	27	13.2 \pm 0.3	-17.1 \pm 0.3	
Northern Seychelles										
Tropical shearwater <i>Puffinus bailloni</i>	Cousin	August 2005	COU5-TS	10	12.7 \pm 0.3	-17.8 \pm 0.2	10	13.3 \pm 0.5	-15.8 \pm 0.2	Catry et al., 2008
	Cousin	March 2006	COU6-TS	-	-	-	10	13.3 \pm 0.6	-16.0 \pm 0.3	
	Aride	August 2005	ARI-TS	-	-	-	10	13.5 \pm 0.7	-15.8 \pm 0.3	
Wedge-tailed shearwater <i>Ardenna pacifica</i>	Cousin	August 2005	COU5-WTS	10	12.6 \pm 0.2	-17.8 \pm 0.2	10	13.5 \pm 0.8	-15.8 \pm 0.3	
White-tailed tropicbird <i>Phaethon lepturus</i>	Cousin	August 2005	COU5-WTB	10	12.6 \pm 0.2	-17.5 \pm 0.2	10	13.7 \pm 0.5	-14.9 \pm 0.3	
	Cousin	March 2006	COU6-WTB	-	-	-	10	13.5 \pm 0.5	-15.4 \pm 0.3	
	Aride	August 2005	ARI-WTB	-	-	-	10	13.7 \pm 0.6	-15.1 \pm 0.2	
White tern <i>Gygis alba</i>	Cousin	August 2005	COU5-WT	8	12.5 \pm 0.4	-17.8 \pm 0.2	8	14.7 \pm 0.7	-15.3 \pm 0.3	
	Cousin	March 2006	COU6-WT	-	-	-	10	14.9 \pm 0.8	-15.6 \pm 0.5	
	Aride	August 2005	ARI-WT	-	-	-	4	14.8 \pm 0.4	-15.4 \pm 0.1	
Sooty tern <i>Onychoprion fuscatus</i>	Aride	August 2005	ARI-ST	-	-	-	10	13.8 \pm 0.9	-15.4 \pm 0.2	
Bridled tern <i>Onychoprion anaethetus</i>	Cousin	August 2005	COU5-BT	6	12.8 \pm 0.1	-17.8 \pm 0.2	6	14.3 \pm 0.3	-15.8 \pm 0.1	
Brown noddy <i>Anous stolidus</i>	Cousin	August 2005	COU5-BN	10	13.1 \pm 0.3	-17.4 \pm 0.2	10	13.8 \pm 0.7	-15.9 \pm 0.4	
	Cousin	March 2006	COU6-BN	-	-	-	10	13.6 \pm 0.5	-16.0 \pm 0.6	
	Aride	August 2005	ARI-BN	-	-	-	10	13.7 \pm 1.3	-15.6 \pm 0.2	
Lesser noddy <i>Anous tenuirostris</i>	Cousin	August 2005	COU5-LN	10	13.2 \pm 0.1	-17.9 \pm 0.2	10	14.1 \pm 0.7	-16.2 \pm 0.3	
	Cousin	March 2006	COU6-LN	-	-	-	7	14.1 \pm 0.5	-16.4 \pm 0.3	
	Aride	August 2005	ARI5-LN	-	-	-	10	12.9 \pm 1.4	-16.0 \pm 0.4	
	Aride	August 2004	ARI4-LN	-	-	-	7	13.6 \pm 0.7	-16.6 \pm 0.2	
	Aride	August 2003	ARI3-LN	-	-	-	5	13.6 \pm 0.6	-16.9 \pm 0.2	
Roseate tern <i>Sterna dougalli</i>	Aride	August 2004	ARI-RT	-	-	-	19	11.4 \pm 0.8	-16.4 \pm 0.3	Monticelli et al., 2008
Southern Seychelles										

Lesser frigatebird <i>Fregata ariel</i>	Aldabra	February 2023	ALD-LF	24	13.3 ± 0.2	-18.1 ± 0.1	24	14.1 ± 0.3	-16.4 ± 0.3	This study
Red-footed booby <i>Sula sula</i>	Aldabra	February 2023	ALD-RFB	25	12.4 ± 0.2	-18.1 ± 0.1	26	13.4 ± 0.2	-15.9 ± 0.2	
	Farquhar	April 2022	FAR-RFB	25	12.3 ± 0.2	-18.0 ± 0.1	28	13.6 ± 0.3	-15.9 ± 0.2	
Brown noddy <i>Anous stolidus</i>	Farquhar	April 2022	FAR-BN	25	12.1 ± 0.2	-18.4 ± 0.2	25	13.9 ± 0.3	-16.2 ± 0.2	
Sooty tern <i>Onychoprion fuscatus</i>	Farquhar	August 2022	FAR-ST	24	13.0 ± 0.2	-18.4 ± 0.2	25	14.2 ± 0.9	-16.1 ± 0.2	
Mozambique Channel										
Great frigatebird <i>Fregata minor</i>	Europa	August 2003	EUR-GF	12	12.2 ± 0.3	-17.8 ± 0.3	12	14.0 ± 0.9	-16.1 ± 0.4	Cherel et al., 2008
Lesser frigatebird <i>Fregata ariel</i>	Europa	August 2003	EUR-LF	5	12.2 ± 0.2	-18.0 ± 0.1	5	11.7 ± 0.7	-16.2 ± 0.3	
Red-footed booby <i>Sula sula</i>	Europa	August 2003	EUR-RFB	21	11.6 ± 0.2	-18.0 ± 0.1	21	11.2 ± 0.7	-15.7 ± 0.4	
White-tailed tropicbird <i>Phaethon lepturus</i>	Europa	August 2003	EUR-WTB	7	12.3 ± 0.1	-18.3 ± 0.1	7	11.1 ± 0.4	-15.2 ± 0.2	
Sooty tern <i>Onychoprion fuscatus</i>	Europa	August 2003	EUR-ST	18	11.7 ± 0.2	-18.4 ± 0.1	18	12.4 ± 0.4	-16.4 ± 0.4	
	Juan de Nova	January 2003	JDN-ST	13	10.7 ± 0.2	-17.7 ± 0.2	13	11.7 ± 0.4	-16.9 ± 0.3	Jaquemet et al., 2008
	Glorieuse	May 2004	GLO-ST	-	-	-	15	13.5 ± 1.0	-16.3 ± 0.4	
Mascarene										
Barau's petrel <i>Pterodroma baraui</i>	Reunion	2013–2014	REU-BP	62	12.7 ± 0.6	-18.5 ± 0.3	62	12.9 ± 0.9	-15.1 ± 0.3	Danckwerts, 2014
	Reunion	2001–2004	REU-BP	-	-	-	14	13.9 ± 1.2	-15.8 ± 0.3	Kojadinovic et al., 2008
Tropical shearwater <i>Puffinus bailloni</i>	Reunion	2001–2004	REU-TS	-	-	-	21	11.7 ± 1.4	-16.6 ± 0.5	
White-tailed tropicbird <i>Phaethon lepturus</i>	Reunion	2001–2004	REU-WTB	-	-	-	31	13.7 ± 1.0	-15.2 ± 0.3	
	Reunion	2010–2019	REU-WTB	11	11.4 ± 1.1	-18.2 ± 0.7	-	-	-	Chandelier et al., 2023

2.4. Data analysis

2.4.1. Structure of seabird isotopic ratios

We plotted the isotopic niche of seabird populations with ellipses containing 40% of the data during the breeding and non-breeding periods using the isotopic ratios of blood and feathers, respectively. We assessed the structure of seabird isotopic ratios based on biological, ecological, spatial, and temporal features separately during breeding and non-breeding periods. We used non-parametric one-way ANOVAs (Kruskal-Wallis or Wilcoxon rank sum tests) to compare $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values separately, between seabird taxonomic group, foraging range (i.e., nearshore and offshore; Table S1) and monsoon season corresponding to their breeding and non-breeding periods, i.e., austral summer and winter monsoons. Where differences were significant ($P < 0.05$), we used Dunn's post-hoc test with Bonferroni correction to identify the differing groups. Size is a dominant trait influencing feeding ecology and therefore isotopic ratios of communities (Cohen et al., 1993). Seabird body mass information was not available for all populations; therefore, we assessed the linear correlation between body mass and $\delta^{15}\text{N}$ values of blood and feathers for available data using Spearman's rank correlation. To ensure correct interpretations, relationships were assessed for seabirds grouped according to taxonomy (Spear et al., 2007).

To determine whether there were spatial patterns in isotopic ratios, we assessed the linear correlation between colony latitude and longitude and blood $\delta^{15}\text{N}$ values and $\delta^{13}\text{C}$ values for all combined species using Spearman's rank correlation. We verified spatial patterns by running separate tests for species where we had data for three or more colonies, i.e., sooty terns and red-footed boobies. We used blood values only corresponding to the period when seabirds were engaged in central-place foraging at their colony.

We measured the isotopic niche space of seabird populations during the breeding and non-breeding periods. Isotopic niche sizes were calculated using standard ellipse areas corrected for small sample size (SEAc). To account for uncertainty in the data, we also determined Bayesian estimates of the standard ellipse areas (SEAB) with 95% credibility intervals using Monte Carlo simulation with 10^4 iterations. Isotopic niche metrics were obtained with the R package *SIBER* (Jackson et al., 2011). We used parametric one-way ANOVAs to compare breeding and non-breeding SEAc estimates separately,

between seabird taxonomic group, foraging range and the monsoon season corresponding to their breeding and non-breeding periods.

2.4.2. Drivers of seabird isotopic ratios

We constructed generalized additive mixed models (GAMMs) with the Gaussian family and identity link function to identify the drivers of seabird isotopic ratios using the *gamm4* package (Wood & Scheipl, 2020). We used blood values as response variables and not feather values to avoid variability in isotopic signatures linked to migration (Hobson et al., 2010). Predictor variables were first modelled on their own to determine which predictors explained the most variation in seabird blood $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ ratios; biological (species), spatial (longitude and latitude), environmental (sea surface temperature, chlorophyll-*a* concentration) and temporal (year, monsoon season) variables. A tensor product smooth was used to model colony location (longitude and latitude) and season was modelled as month number (nmonth). Environmental parameters for each seabird population was extracted from the MODIS Aqua mapped-products (NASA Ocean Biology Processing Group) using Google Earth Engine (Gorelick et al., 2017). Mean monthly averages of sea surface temperature and chlorophyll-*a* concentration (a proxy for marine productivity), for each population were obtained in a 300 x 300 km square around the colony, based on the mean maximum foraging distances for most species during breeding period (cf., references in Table S1). Oceanographic data was obtained at the time of sampling with a 0.04° (ca. 4.6 km) spatial resolution.

Different combinations of these predictor variables were then tested, with 'atoll' included as a random effect to account for spatial dependencies. Before constructing GAMMs, we assessed collinearity among the predictor variables using matrix scatterplots and Spearman rank correlations. Monsoon season was excluded from the models since it correlated with sea surface temperature ($r_s = -0.71$, $P < 0.0001$) and chlorophyll-*a* ($r_s = 0.81$, $P < 0.0001$), and sea surface temperature and chlorophyll-*a* were correlated ($r_s = -0.56$, $P < 0.0001$), so they were included in separate models. Initial GAMMs revealed that year had no significant effect on seabird blood $\delta^{15}\text{N}$ which was therefore excluded from subsequent $\delta^{15}\text{N}$ models (Table S3). The best model was identified based on the minimal Akaike Information Criterion using the *AICcmodavg* package (Mazerolle, 2023). Model assumptions of independence and homogeneity were verified using diagnostic plots on model residuals.

3. RESULTS

3.1. Structure of seabird isotopic ratios

Across the study region, seabird blood $\delta^{15}\text{N}$ values ranged from 10.4 to 13.7‰ (12.2 ± 0.8 ‰, Mean \pm SD, $n = 306$) and blood $\delta^{13}\text{C}$ values ranged from -19.3 to -17.2 ‰ (-18.1 ± 0.4 ‰; Figure S1). Feather $\delta^{15}\text{N}$ values ranged from 9.9 to 16.4 ‰ (13.4 ± 1.0 ‰, $n = 447$) and feather $\delta^{13}\text{C}$ values ranged from -17.5 to -14.4 ‰ (-16.0 ± 0.6 ‰; Figure S2). Seabird blood $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values differed between taxonomic groups ($\delta^{15}\text{N}$: $\chi^2 = 18.2$, $P = 0.0001$, $\delta^{13}\text{C}$: $\chi^2 = 46.7$, $P < 0.0001$), foraging ranges ($\delta^{15}\text{N}$: $W = 7716.5$, $P = 0.0017$, $\delta^{13}\text{C}$: $W = 7069$, $P < 0.0001$) and monsoon seasons ($\delta^{15}\text{N}$: $W = 8048.5$, $P < 0.0001$, $\delta^{13}\text{C}$: $W = 7664.5$, $P < 0.0001$), with depleted $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values for Charadriiformes, for nearshore-feeding birds, as well as for birds breeding during the summer monsoon (Figure 2).

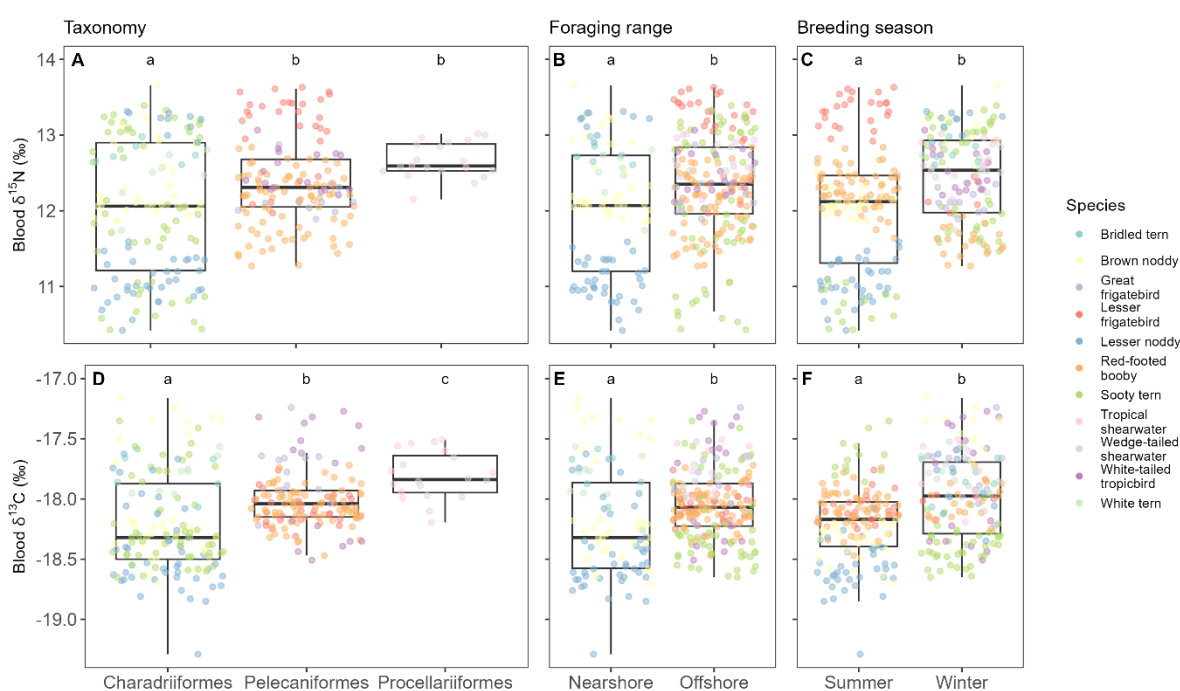


Figure 2. Comparisons of $\delta^{15}\text{N}$ (top panels) and $\delta^{13}\text{C}$ (bottom panels) values of seabird blood, corresponding to the breeding period, by (A, D) taxonomy, (B, E) foraging range and (C, F) monsoon season. Different letters denote significant ($P < 0.05$) differences between means.

Feather $\delta^{15}\text{N}$ values differed between taxonomic groups ($\chi^2 = 8.7$, $P = 0.013$) and foraging ranges ($W = 28800$, $P < 0.0001$) but not between monsoon seasons ($W = 24126$, $P = 0.54$). Feather

$\delta^{15}\text{N}$ values were more enriched for Charadriiformes than Pelecaniformes and nearshore-feeding birds (Figure 3A, 3B). Feather $\delta^{13}\text{C}$ values differed between taxonomic groups ($\chi^2 = 54.2$, $P < 0.0001$), foraging ranges ($W = 17064$, $P < 0.0001$) and monsoon seasons ($W = 34961$, $P < 0.0001$), with depleted $\delta^{13}\text{C}$ values for Charadriiformes, for nearshore-feeding birds and during the winter monsoon (Figure 3D–3F).

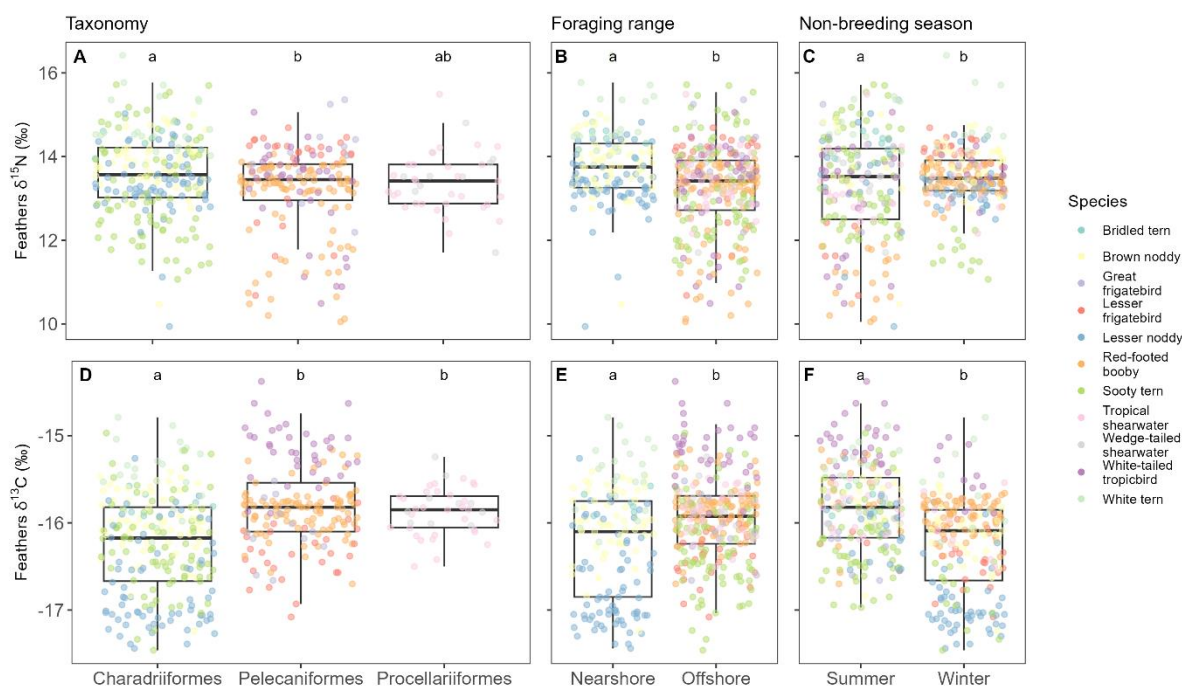


Figure 3. Comparisons of $\delta^{15}\text{N}$ (top panels) and $\delta^{13}\text{C}$ (bottom panels) values of seabird feathers, corresponding to the non-breeding period, by (A, D) taxonomy, (B, E) foraging range and (C, F) monsoon season. Different letters denote significant ($P < 0.05$) differences between means.

Body mass of Charadriiformes were positively correlated with blood and feather $\delta^{15}\text{N}$ values (blood: $r_s = 0.8$, $P < 0.0001$, $n = 84$, feathers: $r_s = 0.7$, $P < 0.0001$, $n = 93$; Figure 4A). For Pelecaniformes, body mass and blood and feather $\delta^{15}\text{N}$ values were negatively correlated ($r_s = -0.5$, $P < 0.0001$, $n = 82$, feathers: $r_s = -0.4$, $P = 0.0003$, $n = 98$; Figure 4B).

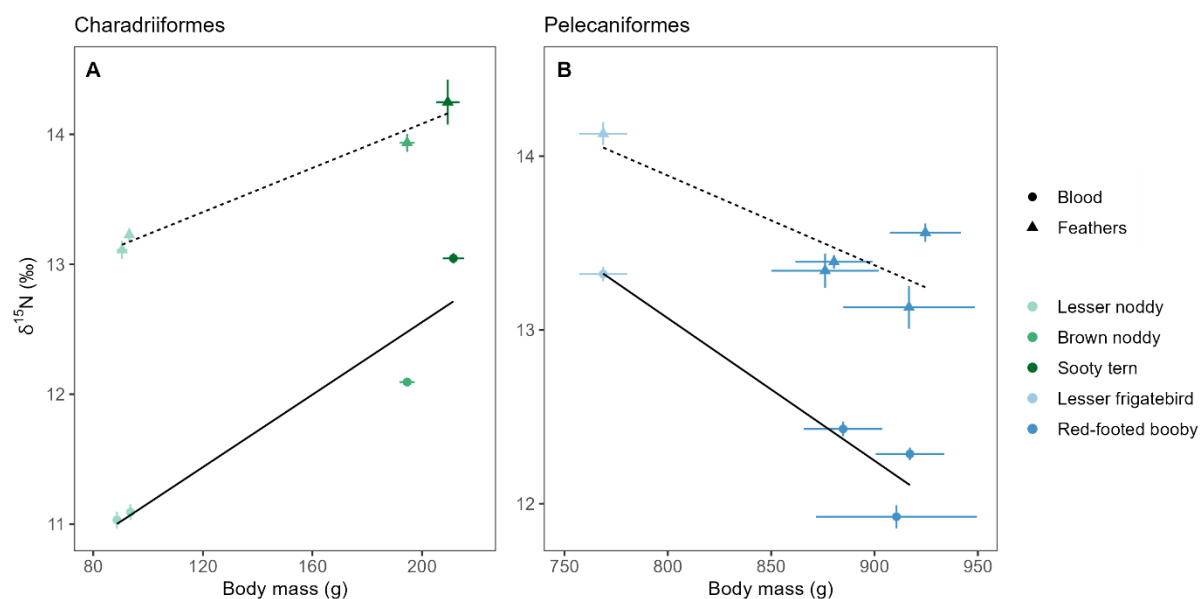


Figure 4. Linear correlations between seabird body mass and $\delta^{15}\text{N}$ values of blood (solid line) and feathers (dashed line). Seabird species are grouped into (A) Charadriiformes and (B) Pelecaniformes. Points represent means \pm SE. Error bars not visible in some cases due to scaling.

Blood $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values for all species combined were linearly correlated with latitude, and decreased southwards ($\delta^{15}\text{N}$: $r_s = 0.4$, $P < 0.0001$, $\delta^{13}\text{C}$: $r_s = 0.2$, $P = 0.0006$; Figure 5A, 5C). When tested separately, blood $\delta^{15}\text{N}$ for sooty terns and red-footed boobies also decreased at higher latitudes (sooty tern: $r_s = 0.7$, $P < 0.0001$, red-footed booby: $r_s = 0.5$, $P < 0.0001$), however for blood $\delta^{13}\text{C}$, we detected no patterns for sooty terns ($r_s = -0.1$, $P = 0.404$) and a negative correlation for red-footed boobies ($r_s = -0.4$, $P = 0.0002$). For longitude, we detected no linear correlations with blood $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values for all species combined ($\delta^{15}\text{N}$: $r_s = 0.1$, $P = 0.299$, $\delta^{13}\text{C}$: $r_s = -0.1$, $P = 0.107$, Figure 5B, 5D). For separate tests, only blood $\delta^{15}\text{N}$ were positively correlated with longitude for sooty terns ($r_s = 0.4$, $P = 0.0006$) and red-footed boobies ($r_s = 0.7$, $P < 0.0001$).

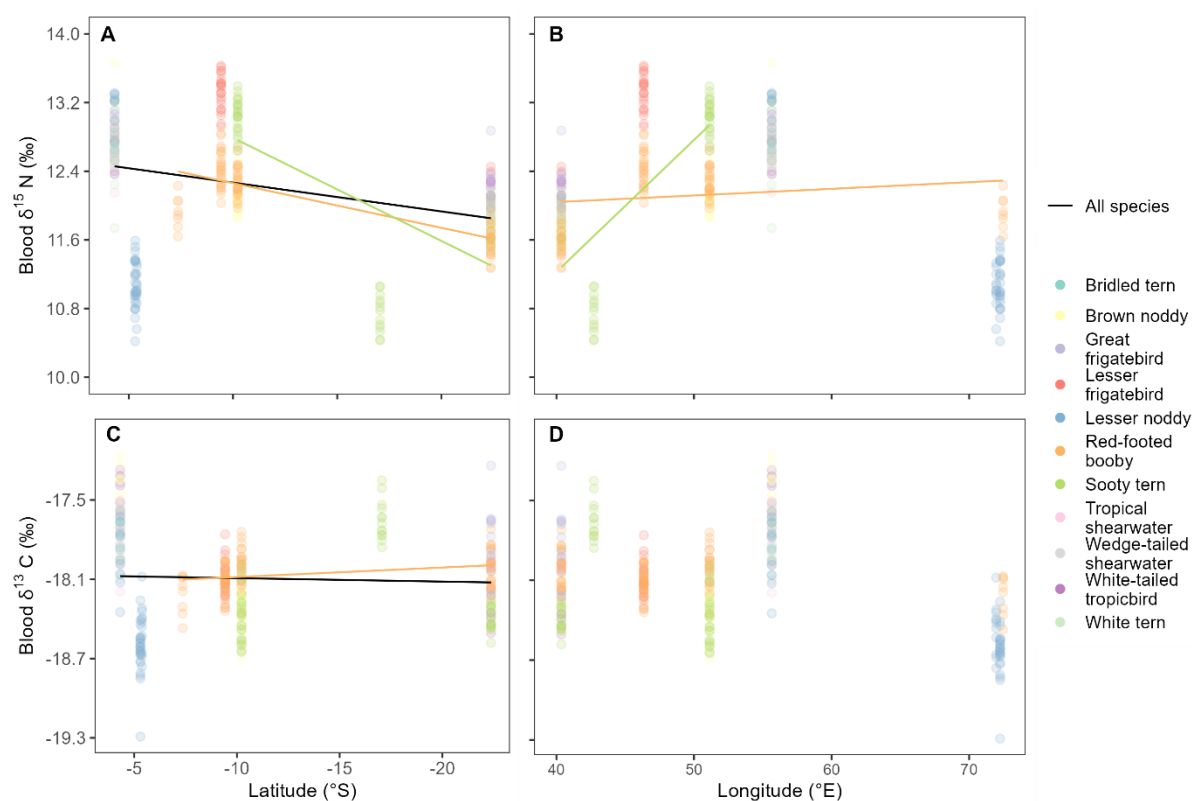


Figure 5. Linear relationships between seabird blood $\delta^{15}\text{N}$ (top panels) and $\delta^{13}\text{C}$ (bottom panels) values with (A, C) colony latitude, and (B, D) colony longitude. Only significant ($P < 0.05$) linear correlations shown for all species combined (black line), red-footed booby (orange line) and sooty tern (green line).

During the breeding period, seabird isotopic niche sizes, indicated by SEA_c of blood isotopic ratios, ranged 0.02–0.22 ‰² (0.1 ± 0.1 ‰², $n = 21$), while isotopic niche sizes during non-breeding period, indicated by SEA_c of feather isotopic ratios, ranged 0.06–1.5 ‰² (0.6 ± 0.4 ‰², $n = 34$, Figure S3). We found no differences in seabird isotopic niche sizes during the breeding period between taxonomic groups, foraging ranges, and monsoon seasons (taxonomy: $F_{2,18} = 3.0$, $P = 0.07$, foraging range: $F_{1,19} = 1.4$, $P = 0.25$; monsoon season: $F_{1,19} = 0.2$, $P = 0.69$, Table S2). Similarly, seabird isotopic niche sizes during the non-breeding period did not differ between taxonomic groups ($F_{2,31} = 0.9$, $P = 0.43$), foraging ranges ($F_{1,32} = 0.09$, $P = 0.76$) and monsoon seasons ($F_{1,32} = 4.1$, $P = 0.05$, Table S2).

3.2. Drivers of seabird isotopic ratios

Species was the best stand-alone predictor variable for seabird blood $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, with 53.0% and 51.1 % of the variance explained, respectively (Table S3). This was followed by environmental

parameters, sea surface temperature and chlorophyll-*a*, both explaining around 27.3% of the variance for blood $\delta^{15}\text{N}$ and 4.1% for blood $\delta^{13}\text{C}$. The best combined model based on AIC_c for seabird blood $\delta^{15}\text{N}$ included species, colony location and sea surface temperature, with 60.5% of the variance explained (Table S3). The second-best combined model included species and chlorophyll-*a* (60.8% deviance explained). Sea surface temperature and chlorophyll-*a* concentrations in these two models had a significant effect (both $P < 0.0001$), with $\delta^{15}\text{N}$ values decreasing at higher sea surface temperatures but increasing with chlorophyll-*a* concentrations (Figure 6A, 6B). In contrast, the best combined model based on AIC_c for seabird blood $\delta^{13}\text{C}$ included species, year, and colony location (50.8% deviance explained, species: $P < 0.0001$, year: $P < 0.0001$, location: $P = 0.0004$), and describing a decrease in $\delta^{13}\text{C}$ over the sampling period (Figure 6C).

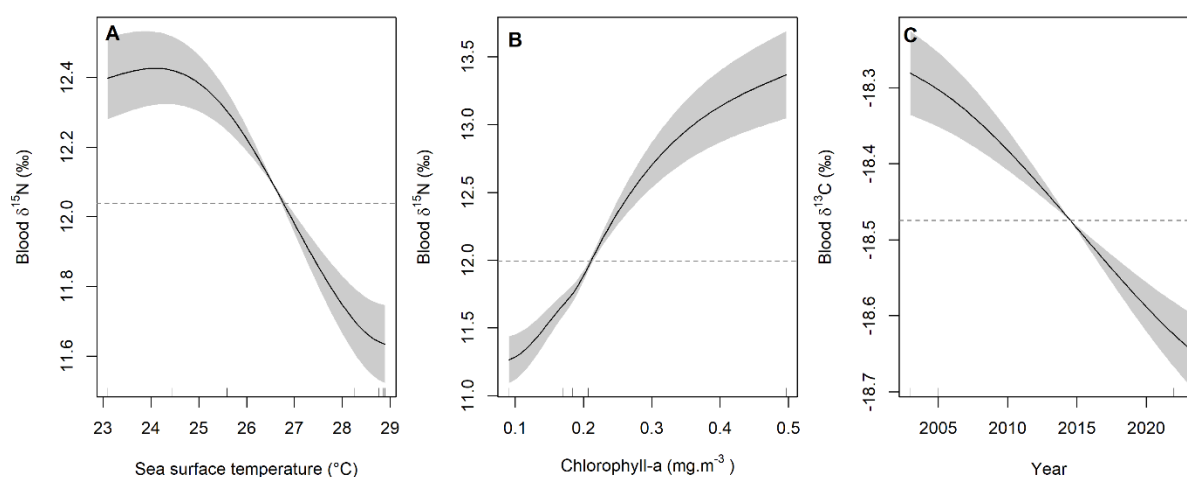


Figure 6. Smoother plots from the best combined generalized additive mixed models showing the relationships between (A) $\delta^{15}\text{N}$ and sea surface temperatures, (B) $\delta^{15}\text{N}$ and chlorophyll-*a* concentrations and (C) $\delta^{13}\text{C}$ and year. The horizontal dashed line represents the model intercept. The shaded areas around the response curves show the confidence limits of the model and are twice the standard error.

4. DISCUSSION

In this study, we combined isotopic ratios of seabird blood and feathers from populations in the tropical WIO sampled over the last two decades. We observed that seabirds in this area exhibit narrow ranges in isotopic ratios and niche space, during both breeding and non-breeding periods, indicating low diversity in foraging resources and habitats. We found that seabird isotopic ratios are structured by

biological characteristics such as taxonomic group and body mass, ecological traits such as foraging range, and temporal variables such as monsoon season. Seabird blood $\delta^{15}\text{N}$ values are linearly correlated with latitude and decrease southwards. For seabird blood, $\delta^{13}\text{C}$ values are best predicted by biological, spatial and temporal variables, whereas $\delta^{15}\text{N}$ values are best predicted by the combined influence of biological, spatial and environmental variables, increasing with lower sea surface temperatures and higher chlorophyll-*a* concentrations. This suggests that blood $\delta^{15}\text{N}$ values of tropical seabirds in this region could serve as an indicator of marine environmental conditions.

4.1. Isotopic ratios and niche sizes

The average isotopic values of seabirds across the tropical WIO were consistent among the different populations, with narrow ranges, during both breeding and non-breeding periods. Accordingly, isotopic niche sizes were small ($\text{SEAc} < 2 \text{‰}^2$), indicating low diversity in resource and habitat use for seabirds across the region. This consistency in isotopic values is also observed in other tropical seabird populations in the Atlantic (Mancini et al., 2014) and Pacific Oceans (Young et al., 2010). It sharply contrasts with temperate and polar seabirds, whereby populations in the same region can exhibit larger ranges in isotopic values (Jaeger et al., 2013) and greater variation in isotopic niche sizes (Bodey et al., 2014; Cherel & Carrouée, 2022).

The restricted range and low variability in isotopic niche of tropical seabirds is linked to their foraging habits and the large-scale uniform oceanographic conditions of tropical regions (Cherel et al., 2008). Tropical seabirds are mainly piscivorous surface foragers (Ballance & Pitman, 1999; Spear et al., 2007), while temperate or polar seabird communities forage at multiple trophic levels (i.e., $\delta^{15}\text{N}$) and employ various foraging methods to access different parts of the water column (e.g., benthic or pelagic; Shealer, 2001). Moreover, tropical marine regions are characterized by smaller gradients in sea surface temperatures and lower marine productivity than higher latitudes, leading to lower heterogeneity in $\delta^{13}\text{C}$ baselines (Magozzi et al., 2017). In contrast, various water masses and fronts in temperate and polar regions generates strong gradients in $\delta^{13}\text{C}$ baselines and consequently, higher variability in $\delta^{13}\text{C}$ values between seabird populations (Jaeger et al., 2013; Mills et al., 2024).

4.2. Structuring mechanisms

Seabird isotopic ratios in the tropical WIO were structured by taxonomic group and ecological traits, with nearshore-foraging terns mainly occupying lower trophic levels (depleted $\delta^{15}\text{N}$) and tropicbirds, boobies, frigatebirds and shearwaters feeding offshore and at higher trophic levels (enriched $\delta^{15}\text{N}$). This trophic structure was less apparent during the non-breeding period when birds were not restricted to their colonies. Most seabird species in our study exhibit a widespread at-sea dispersal during their non-breeding period (Trevail et al., 2023). In polar seabird communities, the isotopic structure is mainly shaped by ecological traits rather than taxonomic group, owing to the large diversity in feeding guilds and diet (Cherel & Carrouée, 2022). Surprisingly, our foraging categories reflected the opposite of expected $\delta^{13}\text{C}$ nearshore-offshore gradients, i.e. depleted $\delta^{13}\text{C}$ values for pelagic waters and enriched $\delta^{13}\text{C}$ values for coastal waters (Hobson et al., 1994). Instead, we observed depleted $\delta^{13}\text{C}$ values for nearshore-feeding birds and enriched $\delta^{13}\text{C}$ values for birds foraging offshore, in both breeding and non-breeding periods. Inter-specific $\delta^{13}\text{C}$ comparisons on Aride Island in Seychelles show similar contrasting results (Catry et al., 2008), suggesting that in the absence of *in situ* isotopic baseline measurements, $\delta^{13}\text{C}$ values of tropical seabirds in this region may not be an appropriate indicator of seabird habitat use.

Seabird body mass was positively correlated with $\delta^{15}\text{N}$ values for the smaller-sized Charadriiformes, whereas the larger-sized Pelecaniformes displayed the opposite trend. Generally, predators are larger than their prey, and therefore trophic positions increase with body size in food webs (Romanuk et al., 2011). The negative correlation in Pelecaniformes was due to lesser frigatebirds feeding at higher trophic levels than red-footed boobies. The higher $\delta^{15}\text{N}$ values observed in frigatebirds may be attributed to species-specific physiological factors such as fractionation and metabolic rate (Young et al., 2010). Similar patterns are observed in seabird communities in Brazil (Mancini et al., 2014) and on Palmyra Atoll (Young et al., 2010), indicating that other confounding factors may obscure the relationship between body mass and seabird $\delta^{15}\text{N}$. This suggests that while body mass may reliably indicate trophic position in temperate or polar seabird communities (Cherel & Carrouée, 2022), it may not be a suitable parameter for investigating size-based trophic structure in tropical seabird assemblages. Moreover, considering the seasonal variability of body mass, alternative ecomorphological parameters that reflect foraging capabilities such as aspect ratio or wing loading may

be more appropriate for assessing body size relationships with trophic level in tropical species (Gagne et al., 2018).

Our study revealed strong seasonal differences in seabird isotopic ratios during both breeding and non-breeding periods. Seasonal shifts in oceanographic conditions such as marine productivity are accompanied by changes in prey assemblages and distribution, subsequently influencing seabird diet (Grémillet et al., 2008). However, investigations into the dietary habits of tropical seabirds in the Indian and Eastern Pacific Oceans indicate minimal seasonal changes (Spear et al., 2007; Catry et al., 2009). Seasonal shifts in oceanographic conditions could also influence isotopic baselines linked to alterations in the structure and functioning of marine food webs (Ramírez et al., 2021). In the tropical WIO, oceanographic conditions during the austral winter monsoon are characterized by cooler waters and higher marine productivity. Our seasonal comparisons show enriched seabird $\delta^{15}\text{N}$ values in the austral winter monsoon during both breeding and non-breeding periods. The GAMMs confirmed sea surface temperatures and chlorophyll-*a* concentrations as strong predictors of seabird blood $\delta^{15}\text{N}$, with modelled relationships showing higher $\delta^{15}\text{N}$ values at lower sea surface temperatures and higher chlorophyll-*a* concentrations. Similarly, Catry et al., (2008) found that seabird chicks raised during the more productive austral winter monsoon on Aride Island in Seychelles were enriched in $\delta^{15}\text{N}$ compared to those raised during the less productive austral summer monsoon. Seasonal variations in muscle $\delta^{15}\text{N}$ values of predatory fishes in the region have also been observed, showing contrasting patterns due to their migratory behaviours. Yellowfin tuna *Thunnus albacares* and swordfish *Xiphias gladius* exhibited higher $\delta^{15}\text{N}$ values in the less productive austral summer monsoon (Ménard et al., 2007), while albacore tuna *Thunnus alalunga* showed the opposite trend (Dhurmeea et al., 2020). Furthermore, our results contrast with studies on temperate Atlantic seabirds, where lower seabird blood $\delta^{15}\text{N}$ values were observed during periods of higher marine productivity (Ramírez et al., 2021). This underscores the need for additional data such as *in situ* isotopic baseline measurements or dietary information to confirm the mechanistic processes underlying seabird isotopic responses. Nevertheless, collectively, our findings show that seabird blood $\delta^{15}\text{N}$ values are highly responsive to environmental conditions in the tropical WIO, suggesting that they could serve as biomarkers for monitoring marine environmental conditions in this region.

Our seasonal comparisons showed higher seabird $\delta^{13}\text{C}$ values during the austral winter monsoon breeding period. Likewise, temperate Atlantic seabirds had enriched $\delta^{13}\text{C}$ values during

periods of high marine productivity (Ceia et al., 2018; Ramírez et al., 2021). However, the GAMMs indicated environmental variables were not strong predictors of seabird blood $\delta^{13}\text{C}$. No seasonal differences in $\delta^{13}\text{C}$ values were observed in seabird chicks on Aride Island (Catry et al., 2008), nor in yellowfin tuna and swordfish muscles from the region (Ménard et al., 2007). Moreover, during the non-breeding period, we observed lower seabird $\delta^{13}\text{C}$ values in the austral winter monsoon. Further sampling is needed to clarify relationships between seabird $\delta^{13}\text{C}$ and marine environmental conditions in our study region. Year was a strong predictor for seabird blood $\delta^{13}\text{C}$ values, showing a decrease of ca. 0.3 ‰ between 2003 and 2023. Similar long-term decline in tissue $\delta^{13}\text{C}$ has been observed in tropical tunas (Lorrain et al., 2020) and temperate Atlantic seabirds (Ramos et al., 2020). This decline is linked to the absorption of isotopically lighter carbon in marine environments, caused by the increased burning of fossil fuels since the Industrial Revolution, known as the Suess effect (Eide et al., 2017).

Our best combined GAMMs revealed geographical location as a predictor of seabird blood isotopic values. We observed a decreasing southward pattern in seabird blood $\delta^{15}\text{N}$ values. This latitudinal gradient in isotopic ratios in the tropical Indian Ocean has been previously described in particulate organic matter, filter-feeding barnacles and predatory fishes (Ménard et al., 2007; Lorrain et al., 2015; Zudaire et al., 2015; Dhurmeea et al., 2020), but never before in seabirds. The latitudinal gradient in seabird $\delta^{15}\text{N}$, ca. 0.9 ‰ decrease over 18° for all species combined, is mainly related to nitrogen biogeochemical cycling processes affecting baseline $\delta^{15}\text{N}$. In the Arabian Sea in the north of the Indian Ocean, anoxic conditions prevail due to denitrification processes (Gruber & Sarmiento, 1997). This leads to the accumulation of isotopically enriched nitrate in sub-surface waters and consequently higher phytoplankton $\delta^{15}\text{N}$ values (Gaye-Haake et al., 2005; Naqvi et al., 2006). Denitrification decreases southwards, while nitrogen fixation increases in the waters of the Mozambique region, influenced by the subtropical gyre. This introduces isotopically light atmospheric nitrogen into the ocean and results in lower phytoplankton $\delta^{15}\text{N}$ (Somes et al., 2010).

We also observed latitudinal variations in seabird blood $\delta^{13}\text{C}$. Generally, phytoplankton $\delta^{13}\text{C}$ are higher in warmer waters and lower in colder regions, and therefore, are expected to decrease from low to high latitudes, in the absence of temperate and polar fronts (Jaeger et al., 2013). This is associated with the slower turnover of heavier carbon isotopes in photosynthetic processes at colder temperatures (Atkins et al., 2023). While we observed a decrease in seabird $\delta^{13}\text{C}$ from north to south for all species combined, we did not detect the same pattern in the relationships between latitude and

blood $\delta^{13}\text{C}$ for sooty tern and red-footed booby populations separately. Latitudinal variations in baseline $\delta^{13}\text{C}$ are weak in tropical regions because of the homogenous sea surface temperatures (Ménard et al., 2007). Instead, other factors influencing phytoplankton communities exert greater influence on spatial variations of phytoplankton $\delta^{13}\text{C}$, such as physiology and community composition (Magozzi et al., 2017). Phytoplankton dynamics can vary within ocean basins based on broad biogeochemical conditions, delimiting isotopic bioregions (Lorrain et al., 2015). Our study area encompasses three main biogeochemical provinces, known as Longhurst provinces, comprising of the *West Indian Monsoon Gyre* in the Chagos and Seychelles region, the *East African Coastal* in the Mozambique Channel and *Indian South Subtropical Gyre* in the Mascarene region (Longhurst, 1998). Additionally, oceanographic features which locally enhance marine productivity, such as eddies and seamounts, are numerous in our study area, and contribute to spatial variation in phytoplankton biomass and isotopic baselines (Kolasinski et al., 2012). This may also explain the longitudinal increase detected in sooty tern and red-footed booby blood $\delta^{15}\text{N}$ from East to West. Overall, our results suggest the use of seabird $\delta^{15}\text{N}$ to inform spatial isotopic patterns across the region.

4.3. Limitations of the study

Our dataset is limited in biological, spatial and temporal resolution, generating uncertainty in our GAMMs results. Numerous factors affecting seabird isotopic composition are unaccounted for, which may explain why species emerged as the primary driver of variation in the GAMMs. Seabird isotopic variability could arise from species-specific individual traits associated with foraging, such as sex, breeding stage, and individual strategies (Ceia et al., 2014; Bourgeois et al., 2022; Almeida et al., 2021), as well as physiological factors such as metabolic rate and body condition (Bond & Jones, 2009). Consequently, combining multiple species hinders the ability to disentangle the biological mechanisms driving seabird isotopic responses. Furthermore, colony location does not precisely capture species-specific foraging conditions and the localized variation in marine environmental conditions that can be accurately identified by geo-referenced seabird isotopes obtained through bird-borne GPS tracking (Ceia et al., 2018; Ramos et al., 2020; Cerveira et al., 2020; Clark et al., 2021). In addition to seasonality, large-scale climatic oscillations, such as the Indian Ocean Dipole, also induce fluctuations in oceanographic conditions (Perez-Correa et al., 2020), resulting in annual isotopic variations in marine consumers (Will & Kitaysky, 2018; Harris et al., 2023). In essence, our model findings should be viewed

as a preliminary assessment of the main drivers of seabird isotopic variability in this region and should be validated with consistent isotopic sampling efforts.

5. CONCLUSION

Our study identified the relationships between seabird isotopic compositions and biological, ecological, spatial and temporal variables in the tropical Indian Ocean. We found that seabird isotopic compositions are shaped by biological attributes such as taxonomic group and body mass, ecological characteristics such as foraging range, and temporal variables such as monsoon season and year. Moreover, we observed a spatial trend, with $\delta^{15}\text{N}$ values decreasing towards higher latitudes. Seabird blood $\delta^{15}\text{N}$ values were sensitive to variations in sea surface temperatures and chlorophyll-*a* concentrations, indicating their potential as indicators of marine environmental conditions in this region. Approaches that integrate telemetry with tissue isotopes are needed to validate our findings and provide further insights into isotopic variation within tropical marine ecosystems, and to monitor the impacts of climatic and anthropogenic changes on tropical marine food webs. Seabird isotopic ratios also serve as a tool for monitoring ecosystem changes in communities receiving seabird nutrient subsidies. Our study therefore also provides references and baseline data for understanding variations between seabird-subsidized ecosystems across the region.

ACKNOWLEDGEMENTS

We thank Seychelles Islands Foundation, Island Conservation Society of Seychelles, Island Development Company and the crew of the BPV Grampian Frontier (BIOT Reef1 2022 expedition) for providing island access and logistical support during the fieldwork in 2022 and 2023. Thanks to the following individuals who assisted with field sampling in 2022 and 2023: Nia Stephens, Jake Letori, Aurélie Hector, Christopher W. Jones. Funding was provided by the Bertarelli Foundation through a Marine Science grant to Nicholas A.J. Graham. JA was supported by a doctoral fellowship from the Reunion Island Regional Council. Fieldwork and ethical approval in 2022 and 2023 were provided by the British Indian Ocean Territory (Chagos) and Seychelles Bureau of Standards (permit number A0157).

AUTHOR CONTRIBUTIONS

Conceptualization: J.A, N.B and S.J. Data curation and methodology: J.A and S.J. Formal analysis, writing - original draft: J.A. Writing - review and editing: N.B and S.J.

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SUPPLEMENTAL INFORMATION

Table S1. Seabird species breeding foraging range classification.

Species	Approx. mean max foraging distance (km)	References
Nearshore (coastal shelf waters)		
Bridled tern	70	Dunlop, 1997; Schreiber & Burger, 2001
Lesser noddy	80	Jaquemet et al., 2004; Surman et al., 2017
Brown noddy	100	Bailey, 1968; Surman & Wooller, 2003
White tern	60	Bailey, 1968; Carlile & O'Dwyer, 2022
Offshore (pelagic waters)		
Sooty tern	580	Jaquemet et al., 2004; Neumann et al., 2017
Tropical shearwater	590	Schreiber & Burger, 2001; Calabrese, 2015
Wedge-tailed shearwater	500	Catry et al., 2009; Keys, 2018
White-tailed tropicbird	170	Schreiber & Burger, 2001; Ensanyar-Volle et al., 2023
Red-footed booby	113	Schreiber & Burger, 2001; Trevail et al., 2023
Great frigatebird	944	Schreiber & Burger, 2001; Weimerskirch et al., 2010
Lesser frigatebird	104	Bailey, 1968; Mott et al., 2016

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Table S2: Standard ellipse areas corrected for small sample size (SEAc) of blood and feather isotopic ratios, representing seabird isotopic niche sizes during the breeding and non-breeding periods, respectively. SEAc estimates were compared between taxonomic groups, foraging ranges and seasons.

	SEAc (Mean ± SD, ‰ ²)	
	Breeding	Non-breeding
Taxonomy		
Charadriiformes	0.12 ± 0.04	0.61 ± 0.40
Pelecaniformes	0.08 ± 0.04	0.44 ± 0.31
Procellariiformes	0.17 ± 0.08	0.61 ± 0.28
Foraging range		
Nearshore	0.13 ± 0.05	0.57 ± 0.43
Offshore	0.10 ± 0.05	0.53 ± 0.32
Season		
Summer	0.10 ± 0.04	0.64 ± 0.37
Winter	0.11 ± 0.06	0.40 ± 0.30

Table S3. Comparable performance of generalized additive mixed models tested for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of seabird blood sampled from colonies in the Western Indian Ocean from 2003 to 2023. The best combined model fit is highlighted in bold. AIC_c : Akaike information criteria for small sample sizes, ΔAIC_c : difference in model AIC_c value relative to model with lowest AIC_c , %DE: percent deviance explained. For the models, s: smoother for parameter, t: tensor product smooth for colony location, sst: average monthly sea surface temperature ($^{\circ}\text{C}$), chl-a: average monthly chlorophyll-a ($\text{mg}\cdot\text{m}^{-3}$).

	Model	Model type	AIC_c	ΔAIC_c	%DE	F	P
$\delta^{15}\text{N}$	1	species	121.13	0	53.01	33.41	< 2e-16
	2	s(year)	324.67	203.53	0	0.074	0.786
	3	s(nmonth)	22.26	108.13	27.36	114.3	< 2e-16
	4	t(lon, lat)	313.64	192.51	0.30	109.1	< 2e-16
	5	s(sst)	235.47	114.34	27.36	109.1	< 2e-16
	6	s(chl-a)	235.36	114.23	27.33	109.1	< 2e-16
Best combined models:							
	1	species + t(lon, lat) + s(sst)	63.69	0	60.46		
	4	species + s(chl-a)	71.67	7.98	60.82		
	3	species + s(sst)	75.78	12.09	60.83		
$\delta^{13}\text{C}$	1	species	-193.45	0	51.10	30.87	< 2e-16
	2	s(year)	-9.15	184.30	0.04	10.45	0.0014
	3	s(nmonth)	-10.44	183.01	4.15	10.72	0.0012
	4	t(lon, lat)	-9.41	184.04	1.31	49.88	< 2e-16
	5	s(sst)	-9.13	184.32	4.11	9.776	0.0019
	6	s(chl-a)	-10.37	183.07	4.14	8.608	0.0053
Best combined models:							
	5	species + s(year) + t(lon, lat)	-193.06	0	50.82		
	6	species + s(year)	-192.96	0.10	51.06		
	4	species + s(year) + s(chl-a)	-189.43	3.62	50.97		

Figure S1. Isotope biplots of seabird populations in (A) Chagos, (B) Northern Seychelles: Cousin, (C) Southern Seychelles and (D) Mozambique Channel. Points represent raw data from seabird blood, corresponding to the breeding period, and solid lines represent standard ellipse areas containing 40% of the data. Note differences in x and y axes scales.

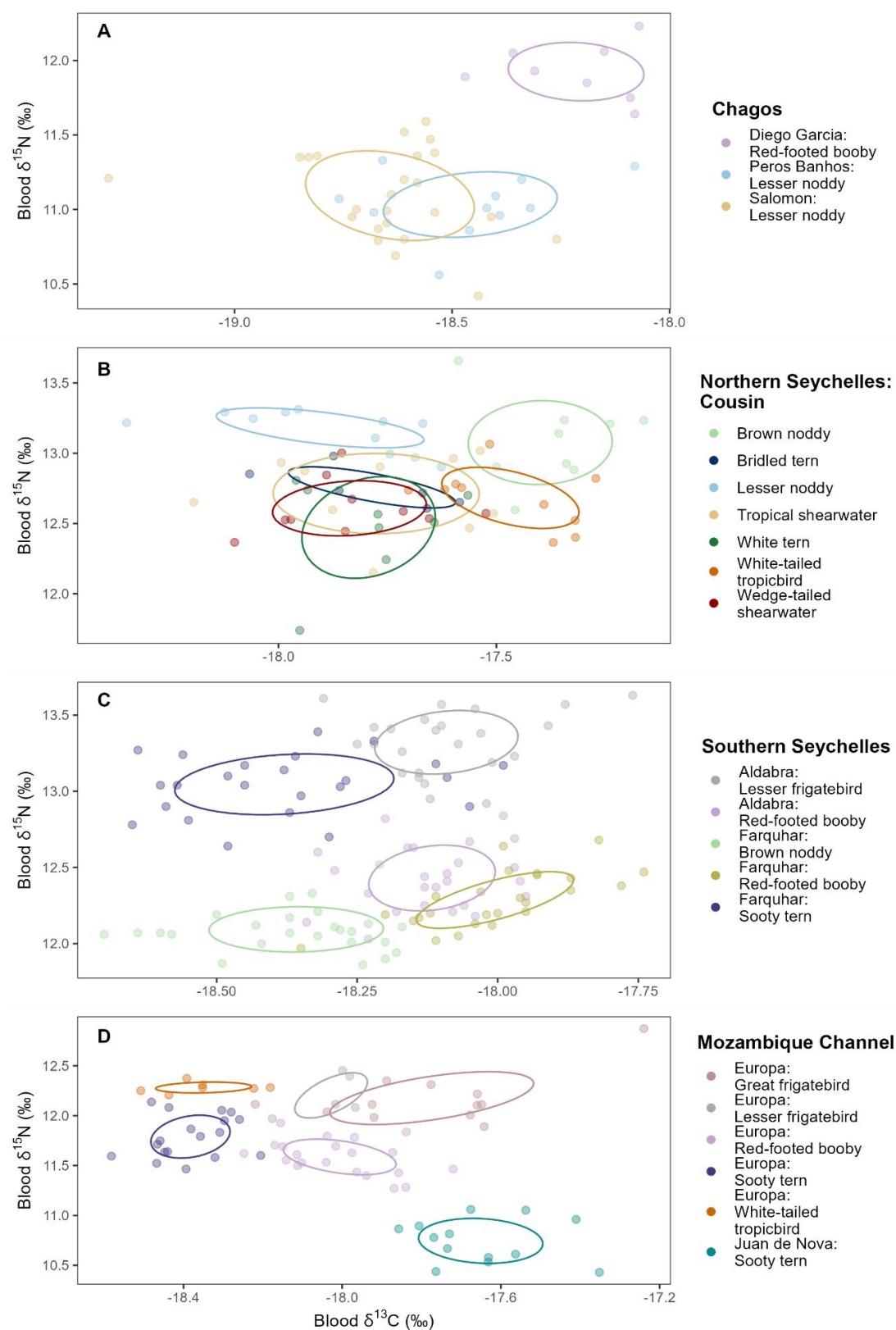


Figure S2. Isotope biplots of seabird populations in (A) Chagos, (B) Northern Seychelles: Cousin, (C) Northern Seychelles: Aride, (D) Southern Seychelles and (E) Mozambique Channel. Points represent raw data from seabird feathers, corresponding to the non-breeding period, and solid lines represent standard ellipse areas containing 40% of the data. Note differences in x and y axes scales.

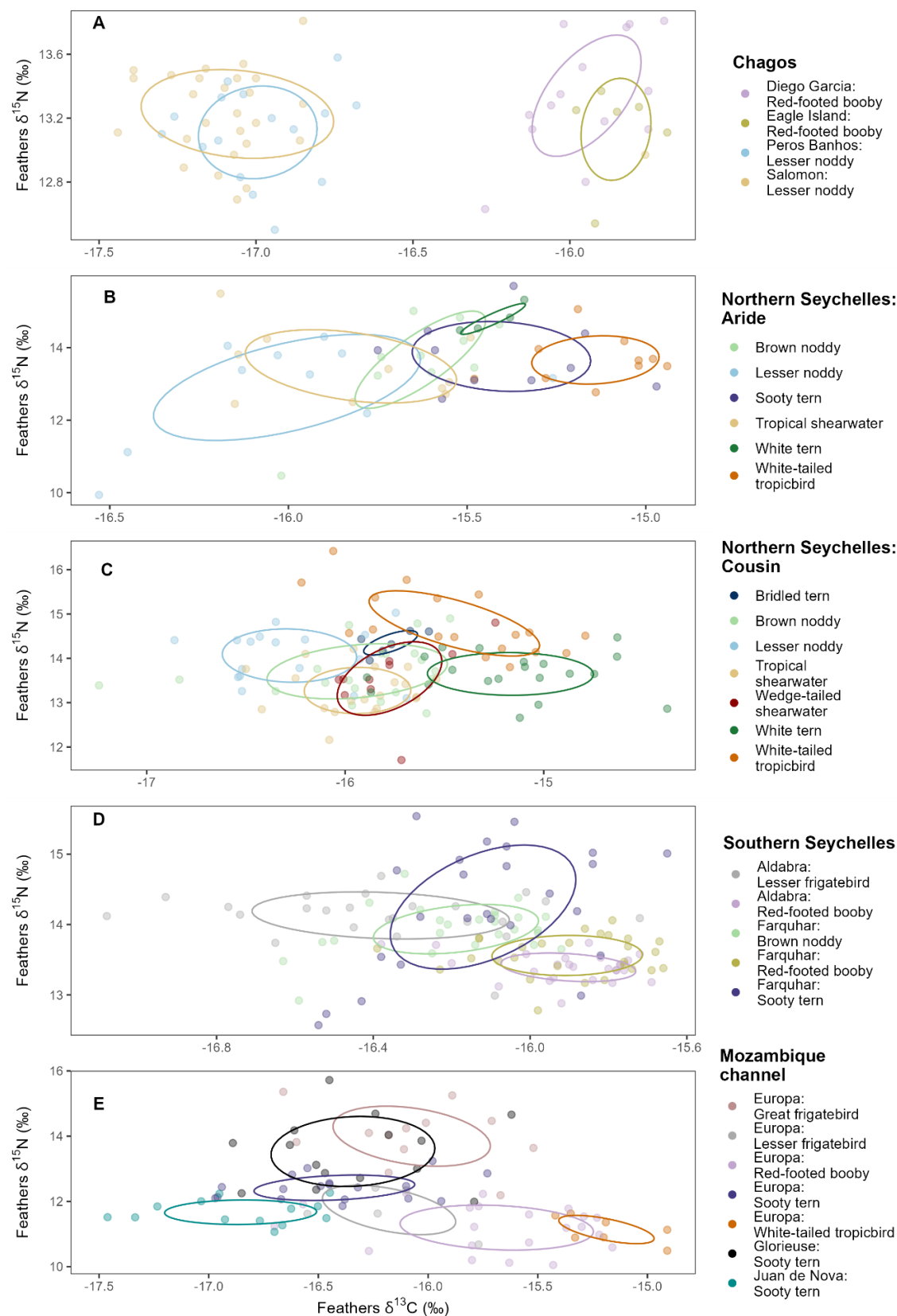
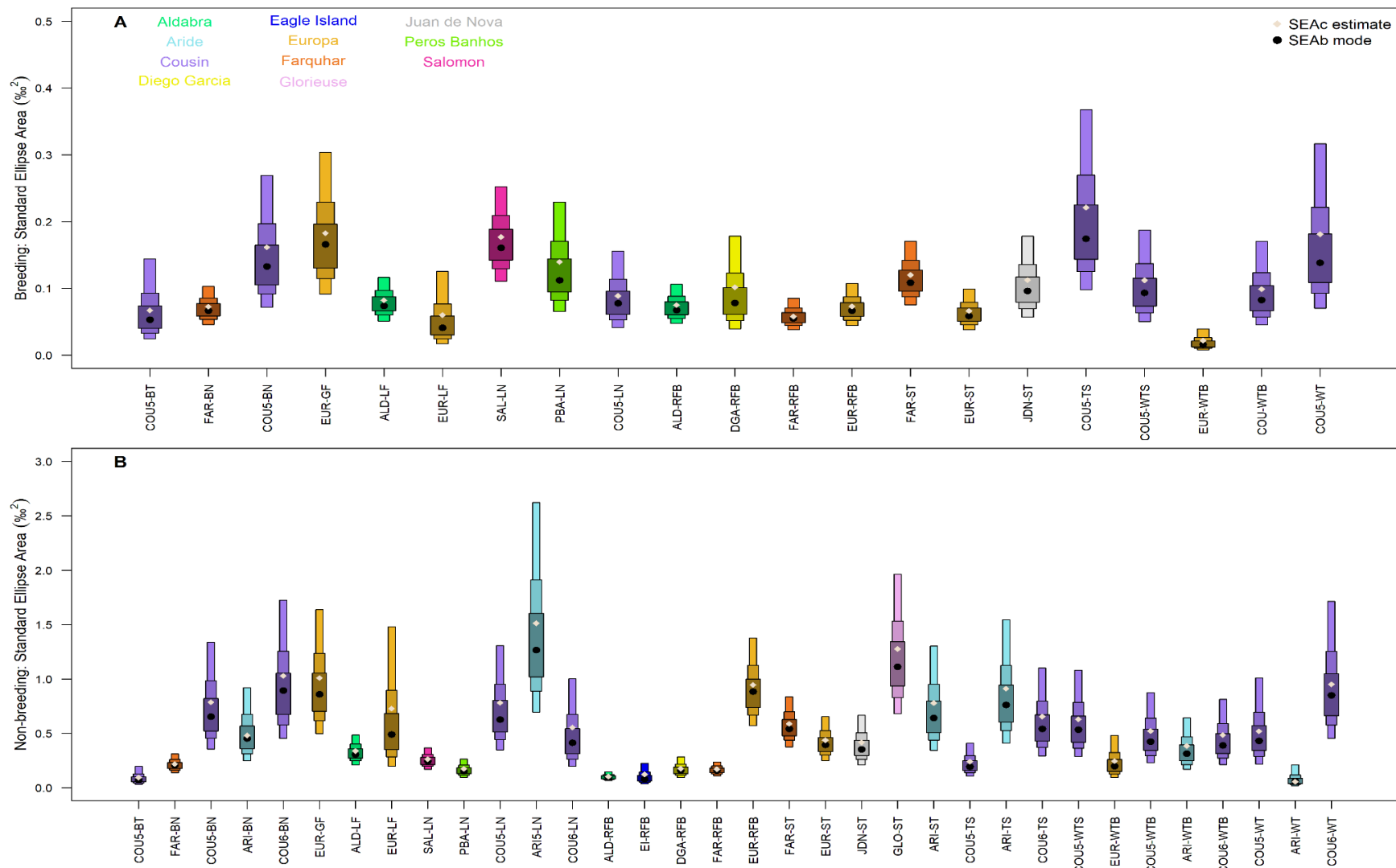


Figure S3. Bayesian standard ellipse areas (SEA_B) of seabird populations during (A) breeding and (B) non-breeding period, calculated from blood and feathers, respectively. Shaded boxes represent the 50, 75 and 95% credibility intervals, with SEA_B mode indicated by black dot and SEA_C estimate by white diamond. See Table 1 for abbreviations.



CHAPTER 3

Seabird presence and seasonality influence nutrient dynamics of atoll habitats

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Manuscript published

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 dynamics of atoll habitats. *Biotropica*, 00, e13354. <https://doi.org/10.1111/btp.13354>

Seabird presence and seasonality influence nutrient dynamics of atoll habitats

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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 71.2N 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

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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 near-shore 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 km²), 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 stolidus* 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

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-NH₄⁺), nitrate (N-NO₃⁻) 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).

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

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.

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-NH₄⁺ and N-NO₃⁻, bioavailable phosphorus (P-a) and exchangeable cations (Ca²⁺, Mg²⁺, 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 ($\delta^{15}\text{N}$) (Mizutani & Wada, 1988). Because they feed at high trophic levels in the marine environment, seabirds acquire a high $\delta^{15}\text{N}$ signature, making $\delta^{15}\text{N}$ a reliable tracer of seabird-derived nutrients (Pascoe et al., 2021). We determined $\delta^{15}\text{N}$ on subsamples of seabird guano, soil and plant material. Additionally, we determined carbon isotopic ratios ($\delta^{13}\text{C}$) on samples of coastal plants and seagrass. In plants, $\delta^{13}\text{C}$ 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 1M HCl to remove carbonates for $\delta^{13}\text{C}$ analyses and once without this treatment for $\delta^{15}\text{N}$. Accuracy based on internal standards was within 0.2 ‰ SD for $\delta^{15}\text{N}$ and 0.1 ‰ SD for $\delta^{13}\text{C}$.

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 $\delta^{15}\text{N}$ 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 $\delta^{15}\text{N}$ 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 $\delta^{13}\text{C}$ 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 $\delta^{15}\text{N}$ against %N to verify whether seabird subsidies (enrichment in $\delta^{15}\text{N}$) 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/

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 $\mu\text{g/g}$ and 29.2 $\mu\text{g/g}$ dry weight, respectively), while red-footed booby droppings had the highest Zn and Mg (319 $\mu\text{g/g}$ and 16.8 $\mu\text{g/g}$ dry weight, respectively; Table 1).

3.2 | Seabird-derived nutrient transfer across taxa and seasons

Sooty tern guano $\delta^{15}\text{N}$ was higher than for brown noddy (adjusted $p = .04$; Table 2). Soil $\delta^{15}\text{N}$ 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 $\delta^{15}\text{N}$ 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, $\delta^{15}\text{N}$ 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 $\delta^{15}\text{N}$ was higher than the control during the wet season only (adjusted $p = .02$; Figure 1b). Coastal vegetation $\delta^{15}\text{N}$ 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 \pm SD, $n = 36$) and CEC (12.1 ± 10.4 , mean \pm SD,

TABLE 1 Nutrient concentrations (total nitrogen [%N], total phosphorus [%P], ammonium [N-NH_4^+], nitrate [N-NO_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-NH ₄ ⁺ mg/g	N-NO ₃ ⁻ $\mu\text{g/g}$	Fe	Cu	Zn	Mn
Red-footed booby <i>Sula sula</i>	10.7	10.6	16.7	18.0	212	25.1	319	16.8
Brown noddy <i>Anous stolidus</i>	10.4	9.8	16.8	29.2	330	29.2	280	15.8
Sooty tern <i>Onychoprion fuscata</i>	11.1	8.2	32.2	17.7	295	21.6	171	11.3

$n = 36$). 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 $\delta^{15}\text{N}$ 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

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

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

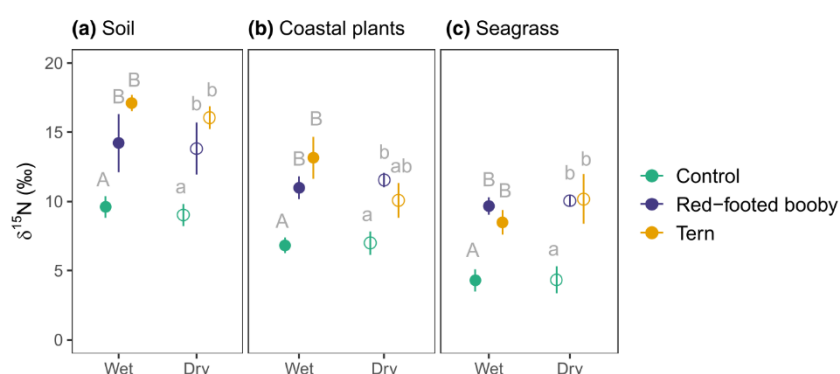


FIGURE 1 $\delta^{15}\text{N}$ ‰ (Mean ± SE) of each treatment (control, red-footed booby, tern) in wet and dry seasons, for (a) soil, (b) coastal plants and (c) seagrass. Closed and open circles represent the wet and dry season, respectively. Different uppercase and lowercase letters denote significant ($p \leq .05$) 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 $\delta^{13}\text{C}$ 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, $\delta^{13}\text{C}$ 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, $\delta^{13}\text{C}$ 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

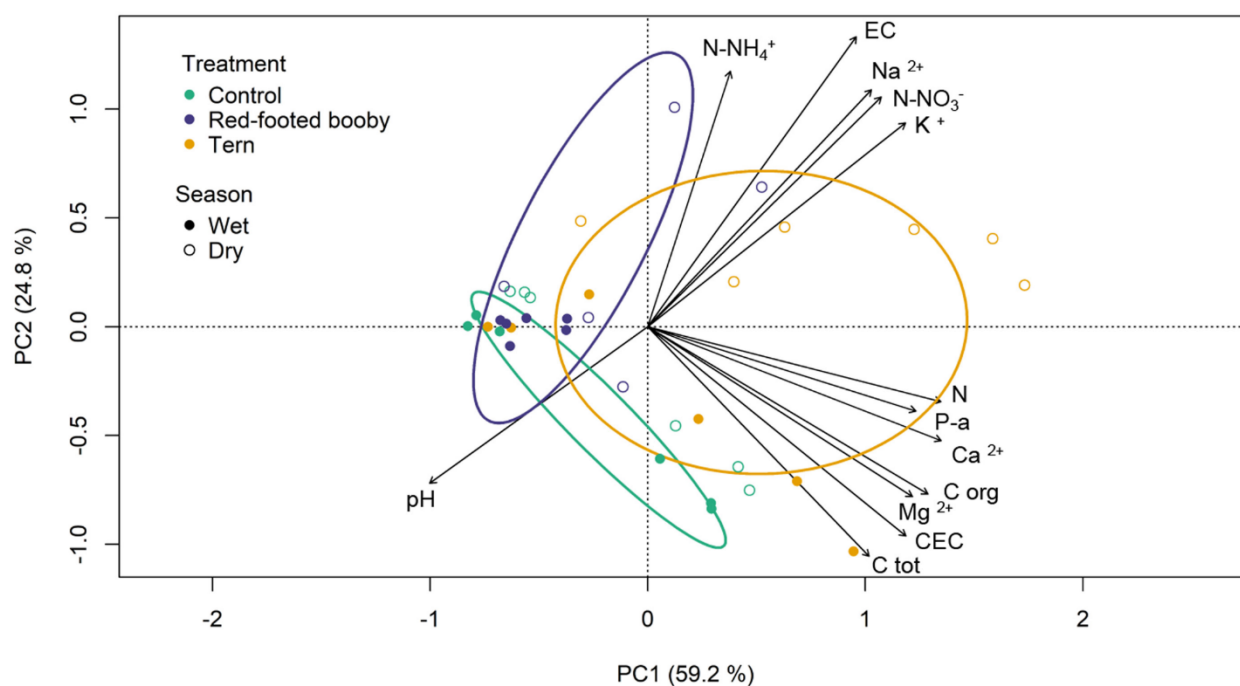


FIGURE 2 Results from principal component analysis (PCA) on the relationships between soil physical and chemical parameters across treatment and season. Points represent transect observations, with color depicting the treatment group and shape depicting the season. Black arrows represent the strength (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; Chereil 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 $\delta^{15}\text{N}$ 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 $\delta^{15}\text{N}$ 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 $\delta^{15}\text{N}$ 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 $\delta^{15}\text{N}$ 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 $\delta^{15}\text{N}$ 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

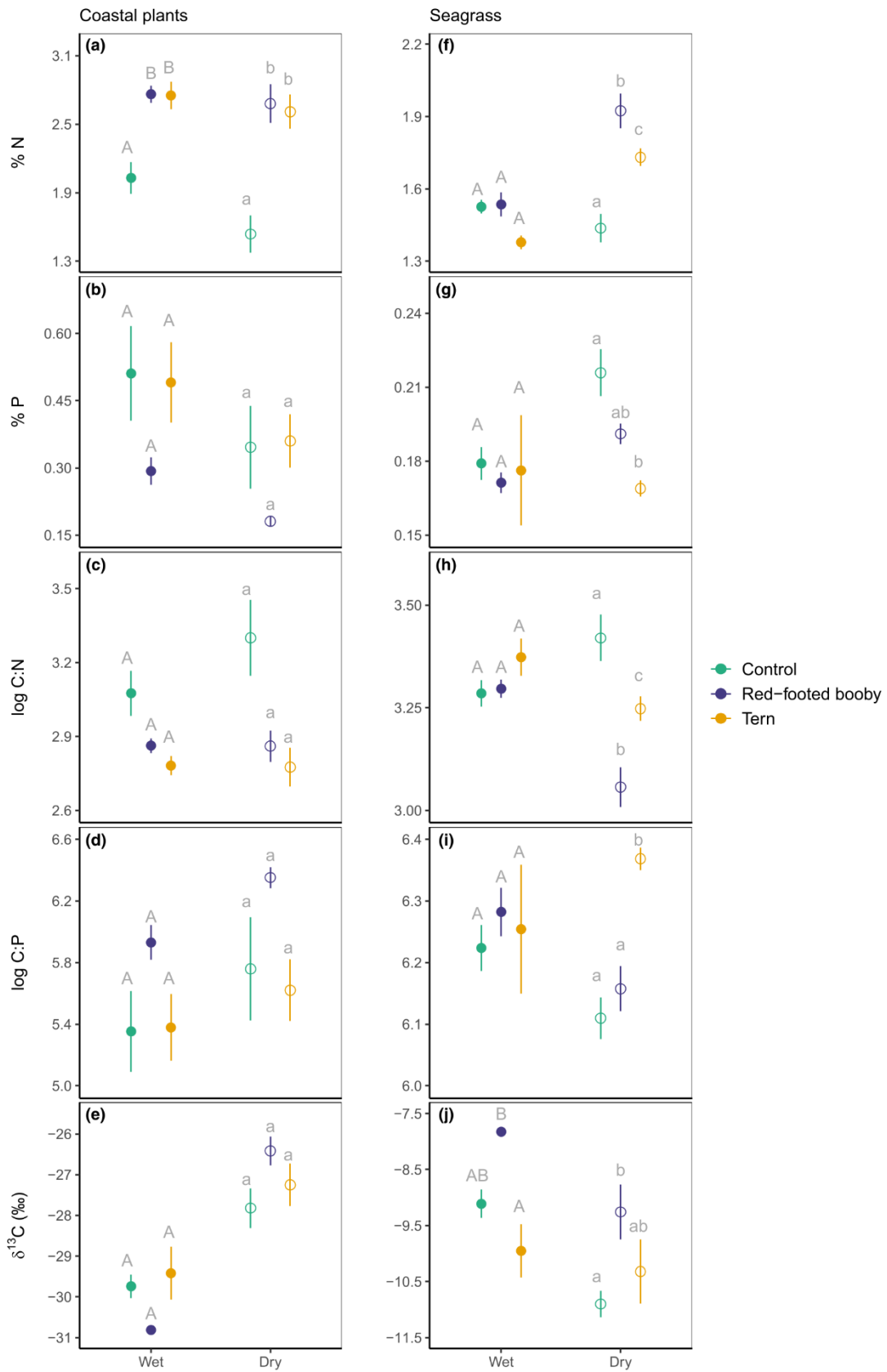
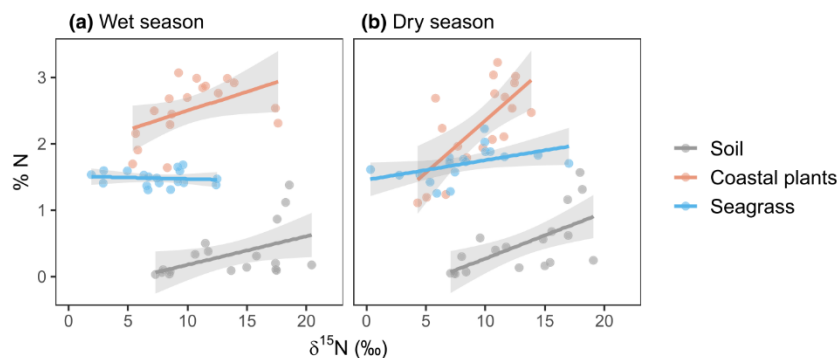


FIGURE 3 Mean (\pm SE) of nutrient levels (expressed in % dry weight), log nutrient ratios and $\delta^{13}\text{C}$ ‰ of each group (control, red-footed booby, tern) in wet and dry seasons, for (a–e) coastal plants and (f–j) seagrass. Closed and open circles represent the wet and dry season, respectively. 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 $\delta^{15}\text{N}$ 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 $\delta^{15}\text{N}$ 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; Mutillo 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, $\delta^{15}\text{N}$ 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.

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 $\delta^{13}\text{C}$. In temperate locations, positive correlations between higher foliar seabird-derived nutrient levels and $\delta^{13}\text{C}$ 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 $\delta^{13}\text{C}$ 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 $\delta^{13}\text{C}$ 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>

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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*, 00, e13354. <https://doi.org/10.1111/btp.13354>

SUPPLEMENTAL INFORMATION

Methods

1. Study area

Farquhar Atoll (10°11' S, 51°06' E) is the most southerly atoll of the Seychelles archipelago in the Western Indian Ocean. Farquhar lies ca. 770 km from Mahé, the main island of Seychelles, and 285 km northeast of Madagascar (Figure S1). It is a low-lying, triangular-shaped atoll (total area 178 km²), consisting of 11 islands (total landmass 8 km²) surrounding a shallow lagoon (Duvat et al., 2017). The majority of Farquhar's landmass consists of North Island (3.32 km²), South Island (3.69 km²) and Goëlettes (0.32 km²). Anthropogenic activity on Farquhar is limited to a small settlement on North Island managed by Islands Development Company. The settlement supports an ecotourism establishment based on a seasonal catch and release fly fishing activity operated by Blue Safaris Seychelles. The environmental NGO Island Conservation Society is also present on the island.

On North and South Islands, the vegetation cover along the beach margin of the ocean and lagoon shores consists of native coastal shrubs including *Scaevola taccada*, *Heliotropium arboreum* and *Suriana maritima*. Moving inland, the vegetation transitions into a mix of indigenous and introduced grasses, sedges and trees. The interior of the islands has been heavily altered by historical exploitation of copra and timber, and is covered in introduced *Cocos nucifera* and *Casuarina equisetifolia* (Stoddart & Poore, 1970). Distinctively, three tidal swamps enclosed by sand bars can be found on South Island's lagoon shore, which are dominated by *Pemphis acidula*. In contrast, Goëlettes is treeless and almost entirely covered in a low herb plant community comprised of *Boerhavia repens*, *Achyranthes aspera*, grasses and sedges, and with some coastal shrubs along its lagoon shore (Stoddart & Poore, 1970). Adjacent to island shores in the lagoon and on the reef flats, there are large expanses of seagrass, dominated by *Thalassodendron ciliatum* (Stokes et al., 2019).

Farquhar is home to large breeding colonies of red-footed boobies *Sula sula*, brown noddies *Anous stolidus* and sooty terns *Onychoprion fuscatus*, on separate islands (Duhec et al., 2017). Sooty terns and brown noddies nests on Goëlettes, with estimated population sizes of 208,625 and 19,139 breeding pairs, respectively (Table S1; ICS unpubl. data). Sooty terns and brown noddies are similar in

size (140–240 g and 160–205 g, respectively; Schreiber & Burger, 2001) and form simple nests, consisting of a shallow depression on the ground. Brown noddies breed mainly between May and October and in much lower numbers throughout the year, whereas sooty terns only breed between May and October. Two large red-footed booby colonies are located in the tidal swamps and along the lagoon coastline of South Island, estimated at a total of 11,069 breeding pairs annually (Figure S1, Table S1; ICS unpubl. data). Red-footed boobies are heavier (800–1500 g; Schreiber & Burger, 2001) and breed year-round with peaks in March-April and November-December. They build nests around 1–2 m from the ground in *P. acidula* and along the lagoon shore in *H. arboreum*. All three species are surface pelagic feeders, preying mainly on fish and cephalopods (Weimerskirch et al., 2005; Catry et al., 2009). Other seabirds breed on Farquhar's islets but in smaller 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). Due to these attributes, Farquhar's islets are designated as Important Bird Area by BirdLife International (Rocamora & Skerrett, 2001). North Island, in contrast, has very few breeding seabirds, attributed to the islands' historical use the main center for human settlement and coconut exploitation (Duhec et al., 2017). Most rain on Farquhar fall between November and April (average total 969.8 mm; ICS, unpubl. 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, unpubl. data; Piggot, 1961).

2. Sampling design

We investigated the influence of seabird traits 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 they make a relatively small 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 season (August 2022).

3. Sampling of seabird droppings

We collected fresh seabird droppings of the three breeding species within their colonies to determine nutrient concentrations. For red-footed boobies, 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 August. 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. All samples were kept cool in the field and stored frozen until further processing.

We determined macro- and micro-nutrient content of fresh seabird droppings for each species. Nitrogen (N) was determined according to the Kjeldahl method (Kjeldahl, 1883) (Büchi KjelMaster K-375, Switzerland). Ammonium (N-NH₄⁺) was assayed by distillation and titration with sulphuric acid, while nitrate (N-NO₃⁻) was extracted in water with volume ratio of 1:4 and assayed by continuous flow colorimetry (Proxima, Alliance Instrument, USA). Phosphorus (P) and micro-nutrients were determined by preliminary dry combustion (600 °C), then dissolving the residual material in 6 M HCl. P concentration was obtained by extraction using ammonium molybdate and ascorbic acid and measured with a continuous flow colorimeter, while concentration of iron (Fe), manganese (Mn), zinc (Zn) and copper (Cu) were determined by atomic absorption spectrophotometry (AAAnalyst 400 spectrometer, PerkinElmer, USA).

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

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

Annual input per nutrient type and species ($Nutrient_{gi}$, t/yr) 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⁻¹.day⁻¹), the number of breeding adults of 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.

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 sub-sample 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 *H. arboreum* in the coastal shrub habitat and *A. 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 sub-sampled one leaf from each plant individual for isotope analysis and the remaining leaves were homogenized for nutrient analyses.

For the 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 sub-sample 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.

5. Nutrient analyses

Upon collection, plant material was rinsed with freshwater, dried to a constant mass in a drying-oven and powdered using a ball mill. Soil was equally dried in an oven and soil pH were measured in a soil:water ratio of 1:5 (PHM220 pH meter, Radiometer analytical, France) and electrical conductivity (EC) was measured in a 1:5 soil:water suspension (CDM 210 conductivity meter, Radiometer analytical, France). Total carbon (C) for soil and terrestrial plant samples was determined using an element analyzer (Vario Max Cube, Germany). Organic carbon (C_{org}) for soil and seagrass, and total N for soil and plant samples were determined using the Dumas method (Black et al., 1965) with an element analyzer. Soil N-NH₄⁺ and N-NO₃⁻ were determined in a 1:5 soil extract with 1 M KCl solution by continuous flux colorimetry. Bioavailable phosphorus (P-a) in soil was determined by the Olsen-Dabin method (Dabin, 1967) using 0.5 M sodium hydrogen carbonate solution and a continuous flow colorimeter. Soil cationic exchange capacity (CEC) and exchangeable cations (Ca²⁺, Mg²⁺, Na⁺ and K⁺) were determined by hexamine cobalt chloride extraction (Ciesielski et al., 1997) and assayed by atomic absorption spectrophotometry. Total P in plant samples was analyzed similarly to seabird droppings. Sample blanks and reference materials were analyzed within each analytical run. Nutrient analyses were conducted at the CIRAD-Reunion in the laboratory of agronomic analyses.

6. Isotopic analyses

Sub-samples of seabird guano, soil and plant material were dried in a drying oven at 50°C for minimum of 48 h and powdered using a ball mill. All samples were combusted using an Elementar Vario Micro Cube Elemental Analyser and $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ were measured using an Isoprime 100 Isotope Ratio Mass Spectrometer with international standards IAEA 600, USGS 41 and CH6, at the stable isotope facility at Lancaster University (Lancaster, UK). Soil and seagrass samples were run twice, once after repeated acidifications with 1 M HCl to remove carbonates for $\delta^{13}\text{C}$ analyses and once without this treatment for $\delta^{15}\text{N}$. Accuracy based on internal standards was within 0.2 ‰ standard deviation for $\delta^{15}\text{N}$ and 0.1 ‰ standard deviation for $\delta^{13}\text{C}$. Selected samples were run in triplicate to further ensure accuracy of readings.

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Figure S1. (a) Farquhar Atoll (in red), Seychelles territorial waters (dashed line), in the Western Indian Ocean; (b) Study islands and locations of sampling sites. Locations of (c) red-footed booby colony on South Island and (d) tern (comprising brown noddies and sooty terns) colony on Goëlettes, delimited in black lines. Satellite images © ICS, 2022

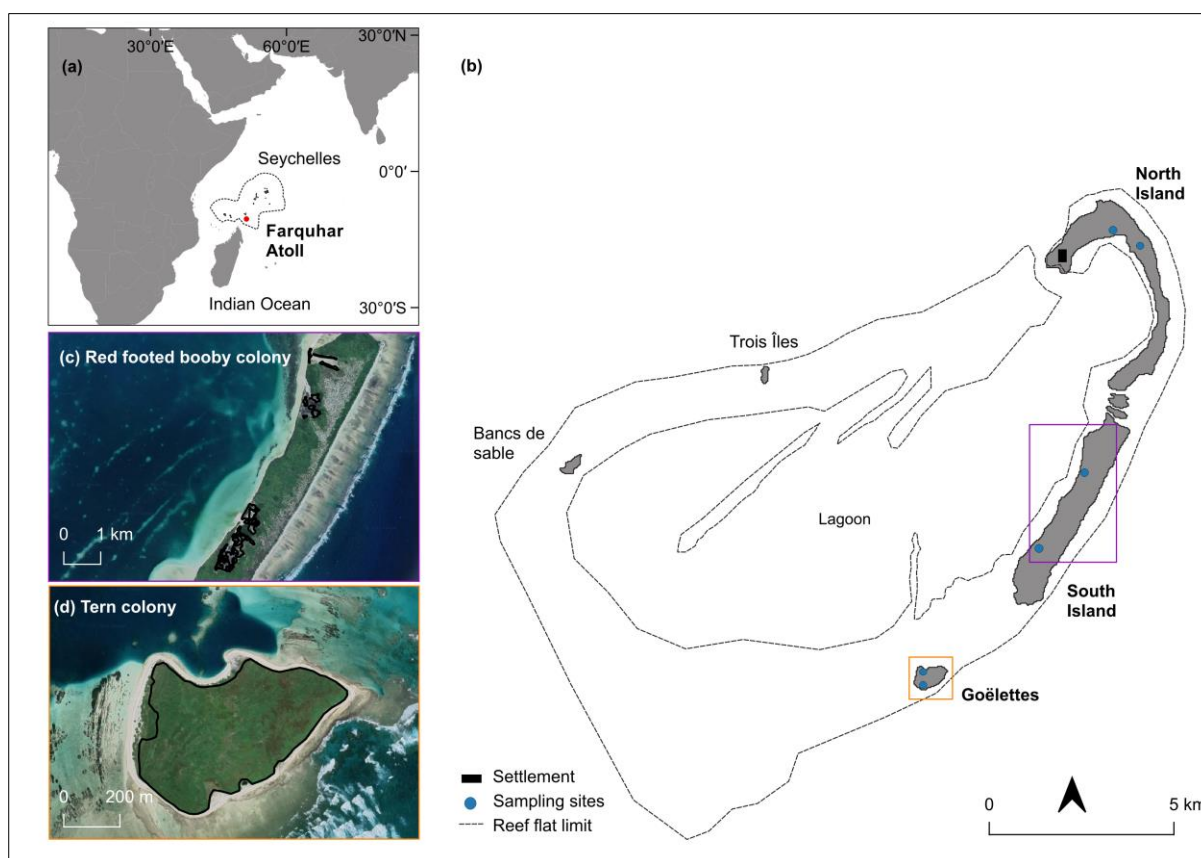


Table S1. Island size and seabird characteristics (ICS, unpublished data) of the three study islands of Farquhar Atoll, with the amount of total nitrogen and total phosphorus deposited annually by large breeding seabird colonies. *na* = not applicable.

Island	Total area (ha)	Main breeding species (number of breeding pairs; year of census)	Colony area (ha)	Nest density (nests/m)	Seabird biomass (kg/ha)	N input (min–max, t/yr)	P input (min–max, t/yr)
North Island	379	<i>na</i>		<i>na</i>	<i>na</i>	<i>na</i>	<i>na</i>
South Island	394	Red-footed booby <i>Sula sula</i> (11 069 ± 1678; 2021)	15.3	0.07	22.4	9.12 (7.74–10.5)	9.07 (7.70–10.4)
Goëlettes	32	Brown noddy <i>Anous stolidus</i> (19 139 ± 2649; 2017)	2.0	0.95	48.0	6.30 (5.42–7.17)	5.90 (5.09–6.72)
		Sooty tern <i>Onychoprion fuscata</i> (208 625 ± 16 113; 2021)	6.72	3.10	496.8	71.2 (65.7–76.7)	52.2 (48.2–56.2)

Table S2. Results of linear mixed models fitted to test changes in $\delta^{15}\text{N}$ for soil, coastal plants and seagrass under different seabird influence (control, red footed booby, tern) and seasons (wet, dry), with sample location as a random effect. Statistically significant results ($p \leq 0.05$) are indicated in bold. *df*: Degree of freedom.

Variable	Fixed effects	Mean square	df	F value	P value	Conditional R2	Marginal R2
Soil							
$\delta^{15}\text{N}$	Treatment	178.570	2	20.570	0.046	0.56	0.56
	Season	4.189	1	0.483	0.493		
	Habitat	54.692	1	6.300	0.129		
	Treatment x Season	0.329	2	0.038	0.963		
Terrestrial coastal plant							
$\delta^{15}\text{N}$	Treatment	45.666	2	18.764	0.050	0.79	0.73
	Season	5.554	1	2.282	0.142		
	Habitat	39.412	1	16.194	0.057		
	Treatment x Season	24.106	2	4.953	0.015		
Seagrass							
$\delta^{15}\text{N}$	Treatment	69.356	2	14.489	0.0003	0.63	0.52
	Season	4.438	1	0.927	0.351		
	Treatment x Season	2.291	2	0.479	0.629		

Table S3. Soil physical and chemical characteristics for each treatment group (control, red-footed booby and tern; $n = 12$ each group) over the study period. EC = Electrical conductivity, P-a = bioavailable phosphorus, CEC = Cationic Exchange Capacity.

	Control		Red-footed booby		Tern	
	range	Mean \pm SD	range	Mean \pm SD	range	Mean \pm SD
pH	8.05 – 9.49	8.48 \pm 0.42	7.30 – 9.09	8.06 \pm 0.49	7.20 – 9.18	7.83 \pm 0.61
EC (mS/cm)	0.05 – 0.28	0.16 \pm 0.07	0.05 – 2.90	0.67 \pm 0.97	0.07 – 2.10	0.88 \pm 0.79
Total C (mg/g)	115 – 145	126 \pm 10.3	111 – 138	121 \pm 6.86	111 – 143	128 \pm 9.57
C organic (mg/g)	4.71 – 66.2	31.7 \pm 26.2	8.03 – 24.5	14.4 \pm 5.12	7.78 – 100	51.6 \pm 33.0
Total N (mg/g)	0.30 – 5.81	2.45 \pm 2.12	0.61 – 6.18	1.92 \pm 1.54	0.92 – 15.7	7.76 \pm 5.31
N-NO ₃ ⁻ (mg/g)	0.002 – 0.04	0.02 \pm 0.02	0.006 – 1.15	0.27 \pm 0.42	0.01 – 1.34	0.44 \pm 0.45
N-NH ₄ ⁺ (mg/g)	0.0008 – 0.003	0.002 \pm 0.001	0.0008 – 0.22	0.02 \pm 0.06	0.0009 – 0.03	0.01 \pm 0.008
P-a (mg/g)	0.05 – 3.49	1.53 \pm 1.56	0.06 – 3.69	0.90 \pm 1.06	0.39 – 11.9	6.56 \pm 4.93
CEC (cmol ₍₊₎ /kg)	0.58 – 31.1	14.5 \pm 13.0	2.02 – 15.7	6.58 \pm 4.39	2.18 – 31.2	16.1 \pm 10.5
Ca ²⁺ (cmol ₍₊₎ /kg)	0.34 – 24.3	11.3 \pm 10.2	1.54 – 17.4	7.12 \pm 4.98	1.76 – 28.1	15.1 \pm 9.61
Mg ²⁺ (cmol ₍₊₎ /kg)	0.14 – 9.71	4.00 \pm 3.52	0.62 – 3.18	1.57 \pm 0.92	0.63 – 9.58	4.42 \pm 3.21
Na ⁺ (cmol ₍₊₎ /kg)	0.03 – 0.95	0.36 \pm 0.34	0.05 – 3.21	0.77 \pm 1.02	0.05 – 4.85	1.67 \pm 1.62
K ⁺ (cmol ₍₊₎ /kg)	0.007 – 0.29	0.10 \pm 0.09	0.01 – 1.14	0.25 \pm 0.36	0.02 – 1.46	0.43 \pm 0.48

Table S4. Results of linear mixed models fitted to test changes in foliar nutrient parameters of coastal vegetation under different seabird influence (control, red footed booby, tern) and season (wet, dry), with habitat type (coastal shrub, low herb) as a covariate and sample location as a random effect. Statistically significant results ($p \leq 0.05$) are indicated in bold. df: Degree of freedom.

Fixed effects	Mean square	df	F value	P value	Conditional R2	Marginal R2
% N						
Treatment	2.341	2	23.276	0.041	0.70	0.68
Season	0.514	1	5.113	0.032		
Habitat	0.320	1	3.180	0.217		
Treatment x Season	0.147	2	1.457	0.251		
% P						
Treatment	0.0006	2	0.012	0.988	0.88	0.86
Season	0.166	1	33.420	< 0.0001		
Habitat	0.364	1	73.296	0.014		
Treatment x Season	0.002	2	0.431	0.654		
log C:N						
Treatment	0.163	2	8.468	0.106	0.77	0.64
Season	0.047	1	2.430	0.131		
Habitat	0.141	1	7.307	0.114		
Treatment x Season	0.052	2	2.713	0.084		
log C:P						
Treatment	0.005	2	0.137	0.880	0.91	0.86
Season	1.145	1	33.037	< 0.0001		
Habitat	1.682	1	48.517	0.020		
Treatment x Season	0.030	2	0.862	0.434		
$\delta^{13}\text{C}$						
Treatment	1.008	2	2.346	0.299	0.88	0.84
Season	72.024	1	167.595	< 0.0001		
Habitat	7.255	1	16.883	0.054		
Treatment x Season	5.566	2	12.952	< 0.0001		

Table S5. Results of linear mixed models fitted to test changes foliar nutrient parameters of seagrass under different seabird influence (control, red footed booby, tern) and season (wet, dry), with sample location as a random effect. Statistically significant results ($p \leq 0.05$) are indicated in bold. df: Degree of freedom.

Fixed effects	Mean square	df	F value	P value	Conditional R2	Marginal R2
% N						
Treatment	0.092	2	10.155	0.002	0.82	0.71
Season	0.426	1	47.028	< 0.0001		
Treatment x Season	0.212	2	23.385	< 0.0001		
% P						
Treatment	0.002	2	2.836	0.090	0.28	0.28
Season	0.002	1	3.573	0.078		
Treatment x Season	0.001	2	2.189	0.146		
log C:N						
Treatment	0.052	2	7.750	0.005	0.71	0.58
Season	0.053	1	7.827	0.014		
Treatment x Season	0.110	2	16.302	0.0002		
log C:P						
Treatment	0.064	2	3.843	0.045	0.30	0.30
Season	0.015	1	0.925	0.351		
Treatment x Season	0.055	2	3.273	0.066		
$\delta^{13}\text{C}$						
Treatment	3.586	2	7.100	0.007	0.74	0.52
Season	12.876	1	25.492	0.0001		
Treatment x Season	1.637	2	3.241	0.068		

CHAPTER 4

Seabird nutrient subsidies enrich mangrove ecosystems and are exported to nearby coastal habitats

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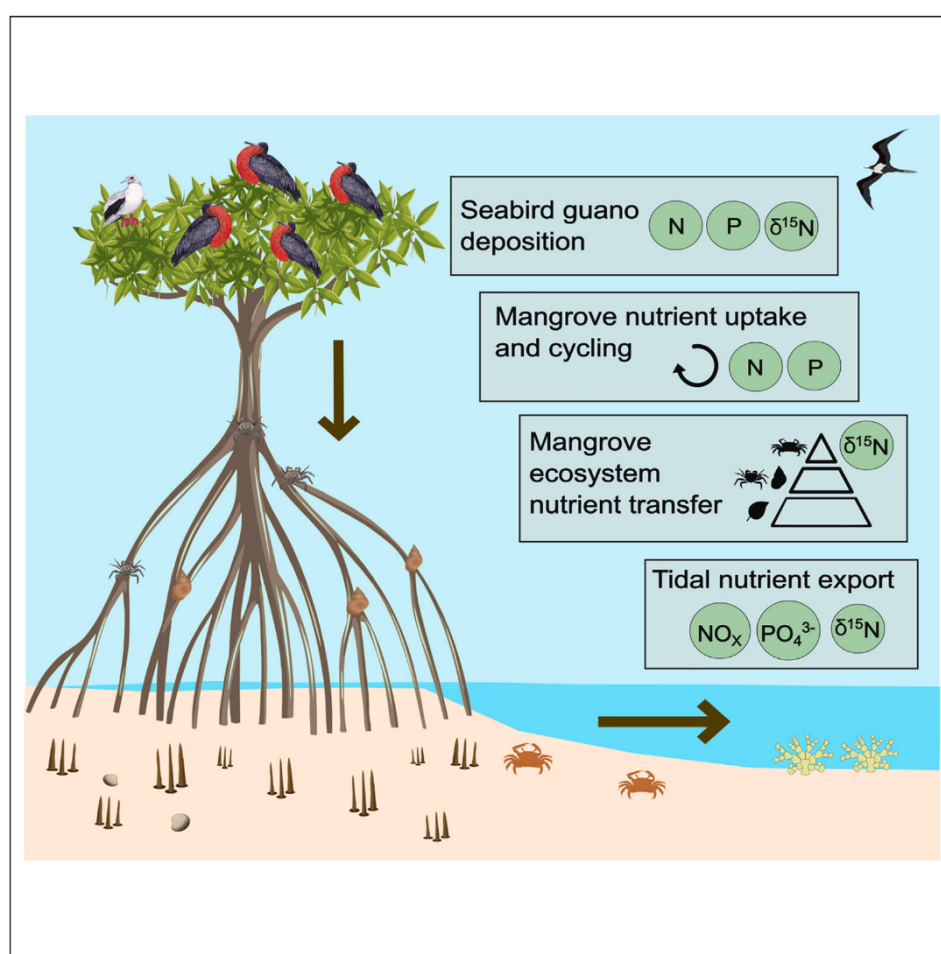
Manuscript published

Appoo, J., Bunbury, N., Jaquemet, S., & Graham, N. A. J. (2024). Seabird nutrient subsidies enrich mangrove ecosystems and are exported to nearby coastal habitats. *iScience*, 27(4), 109404.

<https://doi.org/10.1016/j.isci.2024.109404>

Article

Seabird nutrient subsidies enrich mangrove ecosystems and are exported to nearby coastal habitats



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Highlights

Mangroves are enriched by oceanic nutrients delivered by nesting seabirds

Uptake of seabird-derived nutrients reverses mangrove nutrient limitations

Trophic transfer of seabird-derived nutrients enriches mangrove-associated fauna

Tidal flow exports seabird-derived nutrients from mangroves to adjacent habitats

Appoo et al., iScience 27,
109404
April 19, 2024 © 2024 The
Authors.
[https://doi.org/10.1016/
j.isci.2024.109404](https://doi.org/10.1016/j.isci.2024.109404)



Article

Seabird nutrient subsidies enrich mangrove ecosystems and are exported to nearby coastal habitats

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SUMMARY

Eutrophication by human-derived nutrient enrichment is a major threat to mangroves, impacting productivity, ecological functions, resilience, and ecosystem services. Natural mangrove nutrient enrichment processes, however, remain largely uninvestigated. Mobile consumers such as seabirds are important vectors of cross-ecosystem nutrient subsidies to islands but how they influence mangrove ecosystems is poorly known. We assessed the contribution, uptake, cycling, and transfer of nutrients from seabird colonies in remote mangrove systems free of human stressors. We found that nutrients from seabird guano enrich mangrove plants, reduce nutrient limitations, enhance mangrove invertebrate food webs, and are exported to nearby coastal habitats through tidal flow. We show that seabird nutrient subsidies in mangroves can be substantial, improving the nutrient status and health of mangroves and adjacent coastal habitats. Conserving mobile consumers, such as seabirds, is therefore vital to preserve and enhance their role in mangrove productivity, resilience, and provision of diverse functions and services.

INTRODUCTION

Mangrove forests occupy the interface between land and sea, where they play critical roles in sustaining biodiversity and maintaining ecological functions and services.^{1,2} For example, mangrove habitat provides protection against coastal erosion and tidal surges,³ provides essential food, protection, and habitat to numerous taxa during part or all of their life cycles,⁴ and sequesters large amounts of carbon, contributing substantially to climate change adaptation and mitigation.⁵ The provisioning of these functions and services are dependent on the status and health of mangrove forests,⁶ which are increasingly threatened by human activities. Eutrophication, caused by excessive human-derived nutrient inputs, is a major threat for coastal ecosystems, including mangroves.⁷ Nutrient inputs from anthropogenic activities tend to be rich in nitrogen (N) but poor in phosphorus (P), and can reduce mangrove growth, cause death of pneumatophores and soil anoxia,⁸ and increase mortality of mangrove forests.⁹ Although strong links have been documented between human-derived nutrient enrichment and mangrove ecosystem functioning, there has been far less attention on the impacts of mangrove nutrient enrichment by natural sources.

Mobile consumers play a key role in the movement of nutrients across ecosystem boundaries.¹⁰ Seabirds comprise an important group of mobile consumers involved in the transport of nutrients from sea to land, by feeding in oceanic areas and depositing large amounts of guano in their colonies.¹¹ Enriched in both N and P compounds, seabird-derived nutrients enhance primary productivity around their colonies, and in coastal habitats such as coral reefs, resulting in increased growth rate of reef fish^{12,13} and coral,¹⁴ as well as increased fish biomass.¹² Despite the widespread occurrence of seabirds nesting in mangroves,⁷ much less is known about the influence of seabird-derived nutrients in mangrove ecosystems. Previous studies documented positive relationships between seabird nutrient subsidies and mangrove productivity¹⁵ and nutrient status,^{16–18} but these studies only focused on mangroves in northern and central America in proximity to urban centers. How seabird-derived nutrients influence mangrove forests in regions such as the extensive and mangrove-rich Indo-Pacific, and in the absence of human influence, is unknown. Additionally, no studies have explored the vertical transfer of seabird-derived nutrients within mangrove food webs. Tides strongly mediate connectivity of mangroves with adjacent coastal habitats through the exchange of detritus, fauna, and nutrients.¹⁹ Seabird influence may extend beyond mangroves in the coastal seascape; however, the horizontal transfer of seabird-derived nutrients across mangrove boundaries has not been studied. Documenting these relationships and linkages is increasingly important given the accelerated declines in both mangrove habitats²⁰ and seabird populations^{21,22} due to numerous anthropogenic threats.

Here, we examined the contribution, uptake, and transfer of seabird-derived nutrients in mangrove habitats on Aldabra Atoll, in the Southern Seychelles, one of the largest mangrove-nesting seabird colonies in the Indian Ocean. Aldabra hosts the largest area of mangroves in the

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<https://doi.org/10.1016/j.isci.2024.109404>



Seychelles archipelago, which supports the largest breeding populations of frigatebirds, *Fregata minor* and *F. ariel*, in the Indian Ocean,²³ as well as one of the largest breeding populations of red-footed boobies *Sula sula* in the region. Frigatebirds and red-footed boobies nest exclusively in mangrove forests around Aldabra's lagoon shores.²⁴ With only a small research station, human impact on Aldabra is minimal, presenting ideal conditions to assess the effects of seabird subsidies in a relatively undisturbed mangrove system. We aimed to answer the following questions: (1) What quantities of marine-derived nutrients are contributed by mangrove-nesting seabirds? (2) Are seabird-derived nutrients transferred to and assimilated by mangroves? (3) Do seabird-derived nutrients alleviate nutrient limitation and reduce nutrient resorption efficiency of mangroves? (4) Are seabird-derived nutrients trophically transferred to mangrove fauna? and (5) Are seabird-derived nutrients in mangroves exported to adjacent coastal habitats?

We achieved this using biogeochemical assays of multiple ecosystem components, including seabird guano, mangrove sediment, leaves, gastropods, crabs, adjacent macroalgae, and seawater, sampled at 10 sites with ($n = 5$) and without ($n = 5$) nesting seabirds. Using seabird demography metrics, we find that seabird nutrient subsidies in mangroves can be substantial. Nutrient assays reveal seabird-derived nutrients enrich mangroves and reduce their nutrient limitations, but do not influence their resorption efficiency. Seabird-derived nutrients enrich mangrove invertebrates through trophic transfer and are exported to nearby coastal habitats through tidal flow. By showing that seabird-derived nutrients promote nutrient status and health of mangroves, our results increase understanding about the implications of declines of seabird populations, and suggest that efforts to maintain or restore their populations and breeding grounds should be prioritized.

RESULTS

Seabird nutrient contributions to mangroves are substantial

Red-footed booby guano contained $10.1\% \pm 2.92\%$ N and $10.2\% \pm 0.87\%$ P (mean \pm SD, $n = 4$) and frigatebird guano had $10.9\% \pm 2.06\%$ N and $10.3\% \pm 1.14\%$ P (mean \pm SD, $n = 4$). Guano nitrogen isotopic values ($\delta^{15}\text{N}$) for red-footed booby were $10.8\text{‰} \pm 2.71\text{‰}$ (mean \pm SD, $n = 20$) and for frigatebirds $12.9\text{‰} \pm 3.63\text{‰}$ (mean \pm SD, $n = 20$). Based on seabird population size and breeding metrics, and guano nutrient concentrations (see experimental procedures), estimated total annual nutrient contributions were higher for red-footed boobies (28.6 N tonne \cdot year $^{-1}$; 28.9 P tonne \cdot year $^{-1}$) than for frigatebirds (12.8 N tonne \cdot year $^{-1}$; 12.0 P tonne \cdot year $^{-1}$).

Seabird-derived nutrients are transferred and assimilated by mangroves

We recorded mangrove forest metrics at all sites, resulting in a total of 923 surveyed trees, with *R. mucronata* making up 79% of individuals and being the dominant species at all surveyed sites (Table S1). $\delta^{15}\text{N}$ in *R. mucronata* leaves and mangrove sediment was higher at seabird sites compared to non-seabird sites (mean \pm SD, leaves: seabird = $6.43\text{‰} \pm 2.63\text{‰}$, non-seabird = $2.74\text{‰} \pm 3.57\text{‰}$, $p = 0.05$; sediment: seabird = $6.34\text{‰} \pm 0.94\text{‰}$, non-seabird = $3.34\text{‰} \pm 1.13\text{‰}$, $p = 0.002$; Figures 1D and 1E; Table S2). Nutrient levels in *R. mucronata* leaves were higher in the presence of nesting seabirds (Table S2), for both N (mean \pm SD: seabird = $1.02\% \pm 0.21\%$, non-seabird = $0.73\% \pm 0.09\%$, $p < 0.0001$) and P (seabird = $0.09\% \pm 0.02\%$, non-seabird = $0.07\% \pm 0.01\%$, $p = 0.01$; Figures 2A and 2B).

Seabird-derived nutrients reduce mangrove nutrient limitations but not resorption efficiency

Nutrient ratios, an indicator for nutrient limitation, were lower at seabird sites (C:N: seabird = 43.3 ± 8.64 , non-seabird = 58.0 ± 6.95 , $p < 0.0001$; and C:P: seabird = 524.4 ± 122.6 , non-seabird = 643.2 ± 115.0 , $p = 0.031$; Figures 2C and 2D). The overall average N:P ratio of mangroves was 11.7 ± 2.45 . Nutrient resorption efficiency was similar between sites with and without seabirds (N resorption efficiency [RE-N]: seabird = $53.5\% \pm 13.1\%$, non-seabird = $59.5\% \pm 7.39\%$, $p = 0.15$; and P resorption efficiency [RE-P]: seabird = $50.1\% \pm 25.2\%$, non-seabird = $59.2\% \pm 10.9\%$, $p = 0.24$; Figures 2E and 2F; Table S2).

Seabird-derived nutrients are transferred to mangrove invertebrate food web

$\delta^{15}\text{N}$ values were higher at seabird sites compared to non-seabird sites at all trophic levels, including for herbivorous gastropods (seabird = $13.5\text{‰} \pm 4.64\text{‰}$, non-seabird = $4.45\text{‰} \pm 3.42\text{‰}$, $p < 0.0001$; Figure 1C), herbivorous sesarmid crabs (seabird = $12.03\text{‰} \pm 2.16\text{‰}$, non-seabird = $6.79\text{‰} \pm 1.47\text{‰}$, $p < 0.001$; Figure 1B), and omnivorous portunid crabs (seabird = $11.78\text{‰} \pm 1.09\text{‰}$, non-seabird = $8.32\text{‰} \pm 1.62\text{‰}$, $p < 0.005$; Figure 1A).

Seabird-derived nutrients are exported to nearby coastal habitats

Surface seawater in the lagoon had higher NO_x (nitrate + nitrite) at seabird sites than non-seabird sites only during outgoing tides (post-hoc tests: $p = 0.033$; Figure 3A; Table S3), whereas phosphate concentrations were higher at seabird than non-seabird sites during both incoming and outgoing tides (post hoc tests: incoming: $p < 0.0001$, outgoing: $p = 0.0051$; Figure 3B; Table S3). Macroalgae *Halimeda* spp. sampled on substrates adjacent to mangroves had higher $\delta^{15}\text{N}$ at seabird than non-seabird sites (seabird = $9.63\text{‰} \pm 1.62\text{‰}$, non-seabird = $5.98\text{‰} \pm 0.91\text{‰}$, $p = 0.021$; Figure 3C).

DISCUSSION

The ecological functions and ecosystem services provided by mangroves are reliant on the status and health of mangrove forests.⁶ It is therefore important to understand mangrove responses to natural processes that influence their status and health. Our study presents insights into

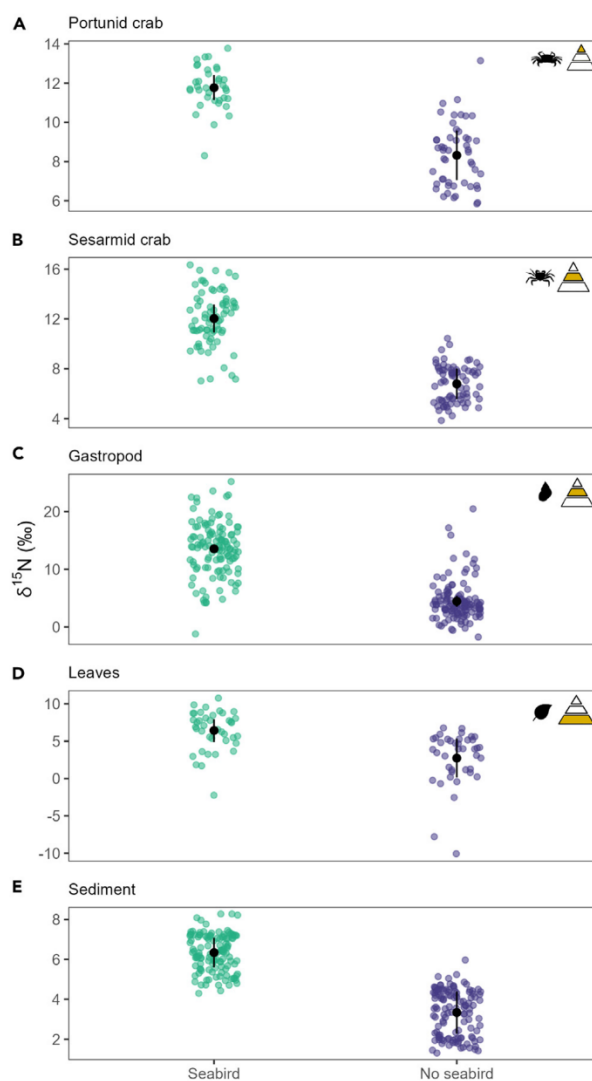


Figure 1. Nitrogen isotopic values in mangrove abiotic and biotic (trophic) components at seabird and non-seabird sites

$\delta^{15}\text{N}$ values of portunid crabs *Thalamita crenata* (A), sesarmid crabs *Sesarma leptosoma* (B), gastropods *Littoraria* spp. (C), mangrove leaves *Rhizophora mucronata* (D), and mangrove sediment (E) at seabird and non-seabird breeding sites on Aldabra Atoll. Black points and error bars display predicted means \pm SD of linear mixed models and green and purple points display raw data. Error bars not visible in some cases because of scaling. Trophic level of each biotic component is indicated by the triangular icon in the top right of each plot.

the scale and extent of influence of cross-ecosystem nutrient subsidies on the ecology and function of Indo-Pacific mangroves and in the absence of human influence. Seabirds feed in open ocean and excrete substantial quantities of nutrients in mangrove forests where they nest, similar to other seabird nesting habitats.^{12,25} Mangroves with nesting seabirds were enriched in N and P and relieved of their nutrient limitations, although seabirds did not influence their nutrient resorption efficiencies. Through trophic pathways, seabird-derived nutrients were transferred to mangrove-associated invertebrate food webs. Furthermore, we documented the export of seabird-derived nutrients from mangroves to nearby coastal habitats through tidal flow, showing that the influence of nutrient contributions by mangrove-nesting seabirds extends beyond mangrove boundaries. Our study highlights the important roles of mobile consumers such as seabirds in maintaining functional connectivity between oceanic systems and coastal seascapes,²⁶ and in improving the nutrient status of coastal habitats (Figure 4) and isolated island ecosystems. Our study adds more weight and nuance to the growing body of research on the influence of seabirds on highly productive coastal ecosystems.^{27–29}

Oceanic atolls are particularly nutrient deficient as they are isolated from mainland anthropogenic nutrient sources and surrounded by oligotrophic waters. On atolls with seabird colonies, seabirds represent one of the main sources of marine-derived nutrient subsidies.³⁰

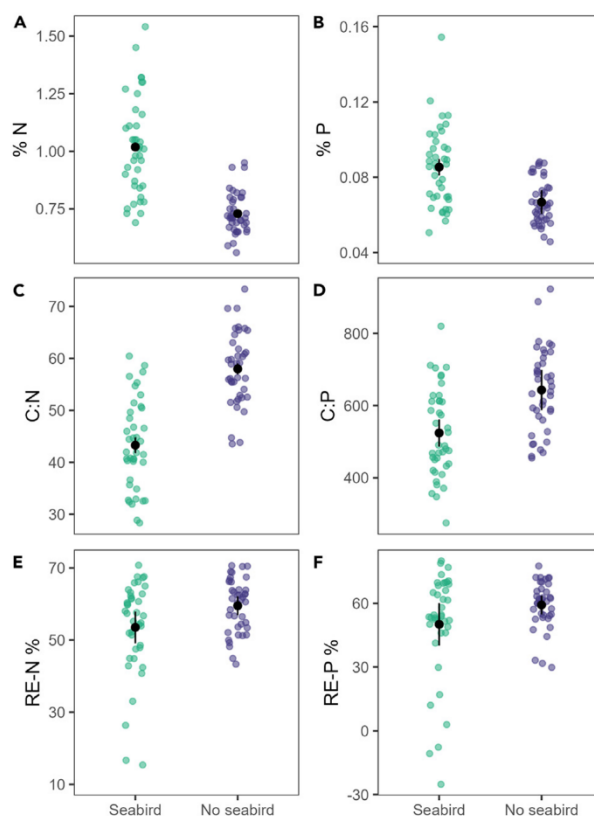


Figure 2. Nutrient parameters in mangrove leaves at seabird and non-seabird sites

Nutrient concentrations, %N (A) and %P (B), nutrient ratios C:N (C) and C:P (D), and nutrient resorption efficiencies RE-N (E) and RE-P (F) of mangrove leaves *Rhizophora mucronata* at seabird and non-seabird breeding sites on Aldabra Atoll. Black points and error bars display predicted means \pm SD of linear mixed models and green and purple points display raw data. Error bars not visible in some cases because of scaling. RE-N: nitrogen resorption efficiency, RE-P: phosphorus resorption efficiency.

Breeding red-footed boobies and frigatebirds delivered a combined total of 41.4 N tonne \cdot year $^{-1}$ and 40.9 P tonne \cdot year $^{-1}$ to Aldabra's mangroves. This represents a minimum estimate since we did not account for non-breeding individuals. Furthermore, due to the bi-annual breeding of red-footed boobies and protracted breeding of frigatebirds,³¹ seabird-derived nutrient subsidies are delivered year-round. Our estimated nutrient inputs are higher than in seabird colonies on Heron Island (16 ha, 9.4 tonne \cdot year $^{-1}$ N and 1.9 tonne \cdot year $^{-1}$ P),³² but lower than the inputs from penguin colonies on Macquarie Island (12,785 ha, 239 tonne \cdot year $^{-1}$ N),³³ and fall within the range estimated for seabird colonies in the tropical Indian Ocean (10–200 tonne \cdot year $^{-1}$ N and 5–100 tonne \cdot year $^{-1}$ P).²⁵ The majority of seabirds on Aldabra nest in tall mangrove trees along the northern and eastern lagoon shores.²⁴ Accordingly, seabird nutrient contributions are disproportionately distributed, with Aldabra's southern lagoon shores and terrestrial habitats deprived of seabird-derived nutrient subsidies. Additional sources of marine subsidies on Aldabra include algal wrack from seagrass beds,³⁴ nesting sea turtles,³⁵ and shorebirds,³⁶ all of which contribute mainly to the sandy beach habitat around the atoll. Local upwellings associated to the atoll may also provide nutrient input to Aldabra's coasts.³⁷ Quantifying these additional sources and assessing their influence on the land- and seascape would provide a more holistic overview of marine nutrient budgets and functioning of marine-subsidized ecosystems on the atoll.

The mangrove forests in our study were dominated by *R. mucronata*, a species widespread in the Indo-Pacific region, and the only *Rhizophora* species occurring in the Western Indian Ocean.^{38,39} The higher $\delta^{15}\text{N}$ concentration found in sediment and leaves at seabird sites confirms that seabird-derived nutrients are transferred to mangroves. Foliar N and P concentrations of *R. mucronata* were 39% and 28% higher, respectively, at seabird sites, providing evidence of seabird-derived nutrient uptake by mangroves. Our results corroborate documented increases in nutrients at seabird sites relative to control sites for coastal *Rhizophora* species in Central and North America, for example *R. mangle* (Belize: +37% N⁴⁰, Honduras: +41% N and +20% P¹⁸; Mexico: +25% N and +17% P¹⁶; Florida: +33% N¹⁵). Mangroves on Aldabra grow in a lagoonal low-lying carbonate environment and do not receive large volumes of terrigenous sediment supply and nutrients compared to mangroves growing in deltas or estuaries.^{41,42} In this nutrient-limiting environment, our results show that seabirds contribute essential macronutrients and improve the nutrient status of mangroves (Figure 4).

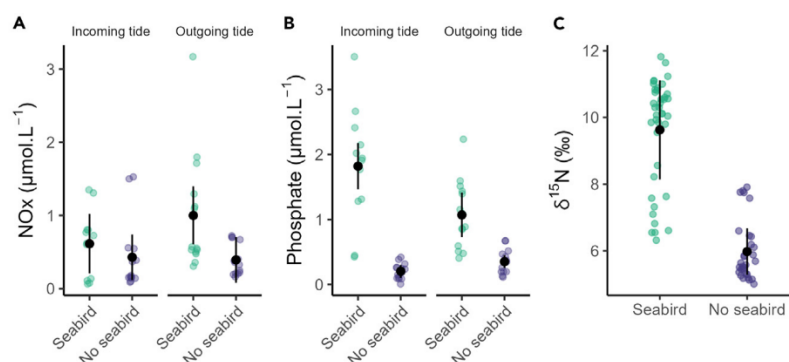


Figure 3. Nutrient levels in abiotic and biotic components adjacent to mangroves at seabird and non-seabird sites

Nutrient concentrations in surface seawater, NO_x (A) and phosphate (B) during incoming and outgoing tides, and δ¹⁵N values of macroalgae *Halimeda* spp. (C) adjacent to mangroves, at seabird and non-seabird breeding sites on Aldabra Atoll. Black points and error bars display predicted means ± SD of linear mixed models and green and purple points display raw data. NO_x = nitrate + nitrite.

Responses of mangroves to nutrient enrichment are site- and species specific, with the main limiting nutrient of the site governing species nutrient requirement and tolerances.⁴³ Nutrient limitation in mangroves is usually attributed to N or P limitation.⁴⁴ Foliar N:P ratios can be used to infer nutrient limitation,⁴⁵ with N:P ratios >32 indicating P limitation in mangroves.^{7,46} Foliar N:P ratio in our study was 11.7 ± 2.45 (mean ± SD), suggesting mangroves in our study are N limited, which is typical for fringe mangroves influenced by frequent tidal flushing.^{7,47} N limitation at our study site is further indicated by the equally low N:P ratios documented in previous analyses on mangrove soil⁴⁸ and lagoonal sediment porewater on Aldabra.⁴⁹ At our seabird sites, uptake of seabird-derived nutrients alleviated mangrove nutrient limitations of both N and P, observed by reductions in foliar C:N and C:P ratios of *R. mucronata*. Nutrient enrichment in N-limited mangroves can generate multiple higher order effects. For example, in Florida, seabird-derived nutrients increased primary production, leaf nutritional value, and herbivory.¹⁵ Similarly, experimental nutrient enrichment in N-limited mangroves has demonstrated increases in shoot biomass and tree growth.⁴³

Resorption of nutrients prior to leaf fall, a process in which nutrients are resorbed from senescent leaves and are directly available for continued plant growth, is a vital nutrient recycling and conservation mechanism in mangroves.^{7,50} When nutrients become available, mangroves reduce their nutrient resorption efficiency.^{51,52} Based on this, we expected reductions in resorption efficiency at our seabird sites compared to non-seabird sites; however, no differences in RE-N or RE-P were detected. Furthermore, given that our study site is N limited, we would expect greater resorption of N compared to P⁵⁰; however, average RE-N values were similar to average RE-P values at both seabird and non-seabird sites. Seabird-derived nutrient enrichment has been documented to reduce mangrove resorption efficiency in Mexico¹⁶ but not in Belize.⁴⁰ Similar contrasting patterns are shown in experimental nutrient enrichment studies,^{53,54} suggesting internal nutrient cycling by mangroves is complex, regulated by the interacting effects between species-specific physiological capacity to conserve nutrients,⁵² nutrient demand (through increased growth rate), and supply.^{7,54}

A consequence of nutrient enrichment is that it can reduce stability and resilience of mangrove forests.^{9,55,56} Nutrient enrichment causes plants to invest more in aboveground growth and less in belowground biomass.^{57,58} Furthermore, nutrient availability increases rates of microbial decomposition of organic matter.^{51,59} A forest with lower root biomass and higher decomposition rates is likely to have reduced accretion of sediment organic matter,⁶⁰ resulting in reduced shoreline stability⁵⁵ and increased probability of mangrove death when faced with environmental stressors or events.^{9,56} On this basis, seabird-derived nutrient enrichment has been linked to declines of mangrove cays in Belize.⁴⁰ However, in contrast to Belize, some of the greatest increases in mangrove extent on Aldabra over the past two decades coincided with seabird nesting locations.⁶¹ Furthermore, mangroves on Aldabra are far from urban or agricultural centers compared to Belize, and are therefore not influenced by additional anthropogenic nutrient sources. Natural nutrient sources provide N and P in optimal ratios,^{62,63} generating contrasting responses in coastal habitat structure and functions compared to anthropogenic sources.⁶⁴ In addition, seabirds on Aldabra nest primarily in tall trees in the mangrove fringes, which receive constant tidal flushing, limiting over-enrichment of nutrients.⁹ Altogether, this suggests that seabird-derived nutrient enrichment is unlikely to be causing declines in mangroves on Aldabra. Soil nutrient content is a main driver of mangrove aboveground biomass on Aldabra.⁴⁸ Therefore, by fertilizing mangroves where they nest, seabirds likely enhance mangrove productivity in their breeding areas, further promoting suitable nesting habitat, likely creating a positive-feedback loop for seabird populations.¹⁰ Indeed, both mangroves and mangrove-nesting seabird populations on Aldabra have increased over the last few decades.^{23,61}

Multiple pathways of energy and nutrient flow exist in mangrove food webs due to the wide range of available food sources, such as plankton, benthic microalgae, mangroves, macroalgae, and macrophytes.^{4,65} By assessing the trophic transfer of seabird-derived nutrients, we found that seabirds also enriched the mangrove invertebrate food web. We detected higher δ¹⁵N at seabird sites at all trophic levels, including baseline (sediments), primary producers (mangrove leaves), primary consumers (gastropods and sesarmid crabs), and a secondary consumer (portunid crab; Figure 4). Invertebrate food web enrichment by seabird guano has been documented in other coastal ecosystems such as littoral habitats,⁶⁶ fjords,⁶⁷ and coastal ponds,⁶⁸ but not previously in mangrove forests. Invertebrates are key components of mangrove-associated macrofauna, playing substantial roles in nutrient cycling of detritus.⁷ Further research should explore additional

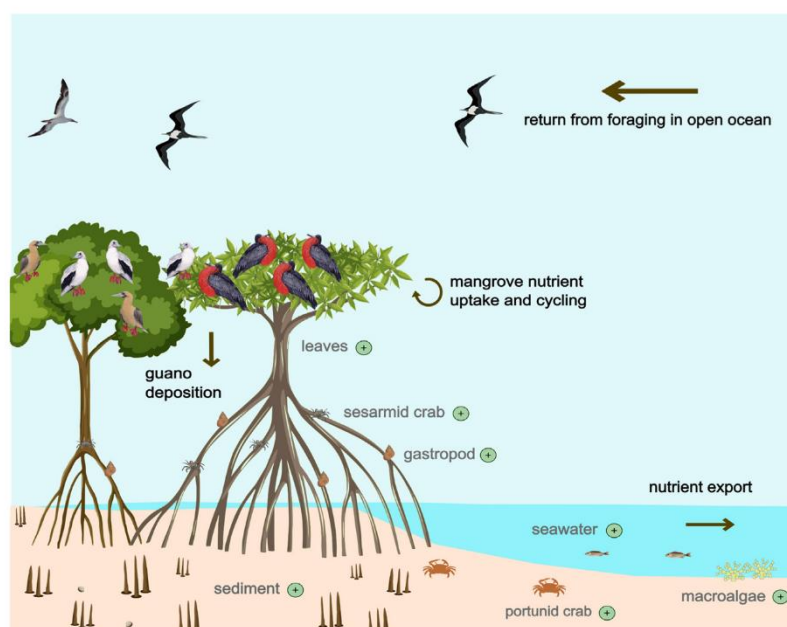


Figure 4. Summary figure illustrating the transfer of seabird-derived nutrients in mangrove forests

Seabirds forage at sea and deposit nutrient-rich guano in their mangrove breeding colonies. Seabird-derived nutrients enrich mangroves and associated invertebrate fauna, and are exported to adjacent habitats by tidal flow. Nutrient enrichment is indicated by plus (+) signs.

pathways of seabird-derived nutrient flow in mangroves, as well as how seabird nutrient enrichment affects invertebrate trophic structure, interactions, and ecological functions.

Given the absence of anthropogenic influence in Aldabra's lagoon, the higher levels of NO_x and phosphate in seawater adjacent to mangroves with seabird colonies can be attributed to seabird guano inputs. Increased levels of seawater nutrients around seabird colonies in remote oligotrophic locations confirm seabird-derived nutrients as an important source of marine productivity.⁶⁹ Indeed, $\delta^{15}\text{N}$ levels of macroalgae *Halimeda* spp. growing adjacent to mangroves were also higher compared to non-seabird sites (Figure 3C), similar to other studies examining macroalgae $\delta^{15}\text{N}$ enrichment near seabird colonies.^{70,71} These results indicate horizontal transfer of seabird-derived nutrients, from mangroves through tidally mediated nutrient exchange (Figure 4). Nutrients can also be transferred to adjacent coastal habitats (such as coral reefs or seagrass areas) via mangrove leaf litter, which plays a key role in sustaining adjacent marine food webs.⁶⁵ Leaves with higher nutrient content or nutritive value are more rapidly broken down than less nutrient-rich leaves.¹⁵ Seabird-derived nutrients from mangroves may therefore extend to adjacent marine communities through trophic pathways, for example via fish communities from nearby reefs or seagrass beds that utilize mangroves as nursery or feeding habitat.

Mangroves on Aldabra support a wide range of biodiversity and ecosystem service benefits. In addition to supporting large breeding populations of seabirds, Aldabra's mangroves sustain threatened and regionally important populations of numerous marine species. Aldabra's mangroves provide nursery habitat for one of the largest green turtle populations in the region,³⁵ and play a critical role as feeding, breeding, and nursery habitats for numerous bony fish and shark species.⁷² Aldabra's mangroves support the highest biomass of herbivorous fish and the highest abundance of sharks in Seychelles.^{73,74} Furthermore, Aldabra's mangroves comprise one of Seychelles' largest blue carbon ecosystems.⁴⁸ By improving mangrove nutrient status and health, we show that seabirds nesting on Aldabra boost biodiversity and ecosystem services.

Our study provides important insights to nutrient contribution, cycling, and transfer in a system with strong land-sea connectivity and without human stressors. We present critical data to start unraveling the mechanisms and extent of nutrient connectivity in mangroves, linked to the cross-ecosystem ocean-derived subsidies provided by seabirds to islands. Given the critical roles of mobile consumers such as seabirds in maintaining ecosystem health and functions, conservation and management actions should focus on restoring seabird populations and their breeding grounds. Such efforts will present maximum benefits for people and biodiversity at multiple scales.⁷⁵

Limitations of the study

Additional data on mangrove hydro-edaphic characteristics such as salinity, pH, or hydroperiod would help to interpret and strengthen our conclusions. Specifically, salinity strongly influences mangrove growth and development, even under nutrient enrichment.⁷⁶ Hydroperiod, which is the frequency, duration, and depth of water in mangroves, plays an important role in nutrient availability. Nevertheless, we provide seawater nutrient concentrations as evidence for nutrient availability, and previous studies on Aldabra indicate hydroperiod, not salinity, is an important driver for mangrove growth.⁴⁸ Although our study focuses on the impacts of guano contributions, nesting seabirds may also have

physical impacts by defoliating trees.⁷⁷ Incorporating data on physical disturbance, such as the number of defoliated trees, would provide additional insights on seabird impacts in mangroves.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

- KEY RESOURCES TABLE
- RESOURCE AVAILABILITY
 - Lead contact
 - Materials availability
 - Data and code availability
- METHOD DETAILS
 - Study site
 - Experimental design
 - Seabird nutrient contributions
 - Mangrove forest structure
 - Mangrove foliar nutrient analyses
 - Isotope sampling and analyses
 - Surface seawater nutrient concentrations
- QUANTIFICATION AND STATISTICAL ANALYSIS

SUPPLEMENTAL INFORMATION

Supplemental information can be found online at <https://doi.org/10.1016/j.isci.2024.109404>.

ACKNOWLEDGMENTS

We thank Seychelles Islands Foundation staff at head office and on Aldabra Atoll for providing administrative and logistical support during the fieldwork, especially Ervin Ally, Elma Balette, Sebastian Cowin, Nikita Pothin, Michelle Jones, Christopher Jones, Annabelle Cupidon, Guilly Mellie, and Francis Solomon. Funding was provided by the African World Heritage Fund through a Moses Mapesa Research grant to J.A., the PADI Foundation marine research grant to J.A., and the Bertarelli Foundation under the Bertarelli Marine Science Program to N.A.J.G. J.A. was supported by a doctoral fellowship from the Reunion Island Regional Council. Fieldwork was conducted with approval of the Seychelles Bureau of Standards under permit number A0157 and the Seychelles Islands Foundation. Icons for Figure 4 were obtained from University of Maryland Center for Environmental Science, Integration and Application Network (<https://ian.umces.edu/media-library/>), Freepik (<https://www.freepik.com/>), and Birds Caribbean (<https://www.birdscaribbean.org/>).

AUTHOR CONTRIBUTIONS

Conceptualization: J.A., N.B., N.A.J.G., and S.J.; methodology: J.A. and N.B.; data collection: J.A.; formal analysis: J.A.; writing – original draft: J.A.; writing – review and editing: N.A.J.G., N.B., and S.J.

DECLARATION OF INTERESTS

The authors declare no competing interests.

Received: November 24, 2023

Revised: January 19, 2024

Accepted: February 29, 2024

Published: March 4, 2024

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Biological samples		
Mangrove leaves (<i>Rhizophora mucronata</i>)	This study	Table S2
Sediment	This study	Table S2
Gastropod (<i>Littoraria</i> spp.)	This study	Table S2
Sesarmid crab (<i>Sesarma leptosoma</i>)	This study	Table S2
Portunid crab (<i>Thalamita crenata</i>)	This study	Table S2
Macroalgae (<i>Halimeda</i> spp.)	This study	Table S2
Guano (<i>Sula sula</i>)	This study	N/A
Guano (<i>Fregata</i> spp.)	This study	N/A
Deposited data		
Nitrogen, phosphorus and $\delta^{15}\text{N}$ values of seabird guano	This study	Dryad Digital Repository https://doi.org/10.5061/dryad.0rxwdb579
$\delta^{15}\text{N}$ of mangrove leaves, sediment, gastropod, sesarmid crab, portunid crab and halimeda	This study	Dryad Digital Repository https://doi.org/10.5061/dryad.0rxwdb579
Nitrogen and phosphorus concentrations in mangrove green and brown leaves	This study	Dryad Digital Repository https://doi.org/10.5061/dryad.0rxwdb579
Seawater nutrient concentrations	This study	Dryad Digital Repository https://doi.org/10.5061/dryad.0rxwdb579
Software and algorithms		
R software (version 4.3.0)	R Core Team ⁷⁸	https://www.r-project.org/
R package <i>nlme</i> (version 3.1-162)	Pinheiro et al. ⁷⁹	https://cran.r-project.org/web/packages/nlme/nlme.pdf
R package <i>emmeans</i> (version 1.8.6)	Lenth ⁸⁰	https://cran.r-project.org/web/packages/emmeans/index.html
Custom code to complete all analyses	This study	Zenodo https://doi.org/10.5281/zenodo.10521660

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources should be directed to and will be fulfilled by the lead contact, Jennifer Appoo jennifer.appoo@univ-reunion.fr.

Materials availability

This study did not generate new unique reagents.

Data and code availability

- All the raw data has been deposited at Dryad Digital Repository and are publicly available as of the date of publication. DOIs are listed in the [key resources table](#).
- All original code has been deposited on Zenodo and is publicly available as of the date of publication. DOIs are listed in the [key resources table](#).
- Any additional information required for reanalyzing the data reported in this paper is available from the [lead contact](#) upon request.

METHOD DETAILS

Study site

Aldabra Atoll (9°24' S, 46°20' E) is part of the Seychelles archipelago (Figure S1). The atoll comprises four main islands (land area 15,500 ha, mean elevation 8 m asl), encircling a large shallow lagoon (20,500 ha) and separated by deep (10–30 m depth) narrow channels.^{81,82} Aldabra's mangroves occur primarily along the lagoon shores, covering 1,720 ha.⁸³ Mangrove habitat on the northern and south-eastern lagoon shores consists of tall trees forming closed canopies, while mangrove areas on Aldabra's southern shores are smaller and scattered (see Table S1).

Seven mangrove species occur, with *Rhizophora mucronata*, *Bruguiera gymnorhiza*, *Ceriops tagal* and *Avicennia marina* being the most common.⁸⁴ Mangrove sediments are mainly sand (53%) and loamy sand (26%) and with an average salinity of 8.3 ± 3.1 (practical salinity scale).⁶¹ Aldabra is influenced by a semi-diurnal meso-tidal regime (range: 2–3 m), resulting in strong tidal currents that drain approximately 75% of the lagoon at low tide through the main channels.^{82,85} Rainfall patterns on Aldabra show marked seasonal variations influenced by monsoon winds.³¹ The majority of rain is concentrated between November and April with a mean of $975 \text{ mm}\cdot\text{year}^{-1}$, however rainfall does not influence primary productivity of the mangroves.⁸⁶

On Aldabra, great and lesser frigatebirds, *Fregata minor* and *F. ariel* respectively, nest together in four separate colonies, with a combined breeding population estimated at 16,534 pairs (SIF, *unpubl. data*). The red-footed booby *Sula sula* nests together with or outside the frigatebird colonies, totaling 36,720 pairs (SIF, *unpubl. data*). Great frigatebird breeding peaks in October, while lesser frigatebirds and red-footed boobies have two breeding peaks, in June and October, and February and August, respectively (SIF, *unpubl. data*). The distribution of mangrove-nesting seabirds is not uniform, with seabirds found only in mangroves on the northern, eastern and south-eastern lagoon shores.³¹ Mangroves and seabirds on Aldabra are recognized globally, as a Ramsar Wetland Site of International Importance and an Important Bird Area (BirdLife International), respectively. Furthermore, Aldabra's mangroves and seabirds have been strictly protected since designation of the atoll as a Strict Nature Reserve in 1981 and UNESCO World Heritage Site in 1982.

Experimental design

We investigated the effects of breeding seabirds on Aldabra's mangroves during the rainy season and the nesting period of all three species (November 2022 to March 2023). Sampling was conducted at 10 sites comprising five sites with no or low numbers of nesting seabirds (< 20 nests) and five sites with high numbers of nesting seabirds (250–700 nests; [Figure S1](#)). Sites were distributed along the lagoon shore around the atoll and situated at least 1 km apart. All sampling sites were located on the seaward fringe of mangroves, which is where the majority of seabirds roost and nests on Aldabra. Within each site, we conducted mangrove measurements within eight quadrats of $5 \times 5 \text{ m}$, separated by a minimum of 50 m. Mangrove sampling was conducted at spring low tide when mangroves and intertidal areas were exposed.

Seabird nutrient contributions

To determine the amount of nutrients deposited by mangrove-nesting seabirds, we collected droppings around nests of red-footed boobies and frigatebirds. For the latter, droppings were sampled around nests with big chicks. Given the difficulty of correctly identifying frigatebird species with chicks, the samples were generalized to represent both great and lesser frigatebirds. Droppings were kept cool in the field and then stored frozen in the laboratory until further processing. Total nitrogen (N) content in seabird droppings was obtained by mineralization according to the Kjeldahl method⁸⁷ (Büchi KjelMaster K-375, Switzerland). Total phosphorus (P) was determined by preliminary dry combustion (600°C), then dissolving the residual material in 6 M HCl. P concentration was obtained by extraction using ammonium molybdate and ascorbic acid and measured with a continuous flow colorimeter (Proxima, Alliance Instrument, USA). Nutrient analyses were conducted at the CIRAD laboratory of agronomy in Reunion Island (France). Additional seabird droppings were collected for isotope analysis (see below).

We used N and P concentrations in seabird droppings to estimate the total annual N and P input from breeding seabirds using previously used methods:^{12,88}

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

where Nutrient_{gi} , $\text{t}\cdot\text{yr}^{-1}$ is the annual input per nutrient type and species, Q_{gi} , $\text{mg}\cdot\text{g}^{-1}$ is the concentration of N or P measured in seabird droppings for each species, Bd_i is number of breeding adults for that species, T_i is the length of the breeding period (number of days from courtship to chick-rearing), f_i is the proportion of time spent at the colony during breeding to account for absence due to feeding forays and P_i is the productivity of the species (fledged chicks per breeding pair). Defecation rate for red-footed boobies was obtained from Young et al.,⁸⁹ For frigatebirds, we estimated defecation rates based on red-footed booby measurements, scaled allometrically to body size following Staunton-Smith and Johnson,³² and using a median value of the adult body sizes of lesser and great frigatebirds. Values for the length of the breeding period, proportion of time at the colony, productivity and adult body sizes for each species were obtained from Riddick et al.,⁸⁸ Our estimates do not account for nutrient contributions by non-breeding individuals since we lacked data on numbers and diurnal movement patterns.

Mangrove forest structure

We assessed forest characteristics in each quadrat following methods previously employed on Aldabra.⁴⁸ We recorded the species of all trees >2 m in height and measured their diameter at breast height (DBH, 1.3 m height) using a measuring tape, following guidelines for trees with anomalies such as prop roots.⁹⁰ We counted the number of seedlings and used an inclinometer (Suunto PM-5/66 PC, Vantaa, Finland) to measure tree height to the nearest $\pm 0.5 \text{ m}$. We applied the allometric equation by Chave et al.,⁹¹ to determine aboveground biomass (ABG) following Constance et al.,⁴⁸ Aboveground biomass (ABG, kg) per tree was obtained from the wood density (ρ , $\text{g}\cdot\text{cm}^{-3}$), the DBH (D, cm), and height (H, m).

$$\text{ABG} = 0.0509 \times \rho \times D^2 \times H$$

Mangrove foliar nutrient analyses

To test the effects of seabird subsidies on mangrove nutrients, we measured leaf nutrient concentrations of the dominant species *R. mucronata*. In each sampling quadrat, we collected six young fully expanded green leaves exposed to the sun and six yellow (senescent) leaves from at least three individual trees. The leaves were pooled per quadrat to form one composite green and yellow leaf sample. Leaves were rinsed with fresh water, oven-dried at 60°C for a minimum of 48 hrs and powdered using a ball mill. Total carbon (C) and N were determined using an elemental-analyser (Elementar Vario Micro Cube, Lancaster University, UK). Total P content was determined by the Olsen-Dabin method using 0.5 M sodium hydrogen carbonate solution with a continuous flow colorimeter (Proxima, Alliance Instrument, USA) at the CIRAD laboratory of agronomy in Reunion Island (France). Sub-samples were obtained for isotope analysis.

We derived foliar nutrient ratios (C:N, C:P mass basis) to explore nutrient limitations to mangrove growth.^{7,16} As an indicator of nutrient cycling, we calculated the nutrient resorption efficiency of N (RE-N) and P (RE-P), which corresponds to the percentage of N or P recovered from senescing leaves prior to leaf fall,^{43,50} based on the equation by Chapin and Cleve:⁹²

$$RE \% = \frac{N \text{ or } P \text{ green leaves} - N \text{ or } P \text{ senescent leaves}}{N \text{ or } P \text{ green leaves}} \times 100$$

Isotope sampling and analyses

To assess the transfer of seabird-derived nutrients in mangroves we conducted isotopic analyses on seabird droppings, mangrove sediment and green *R. mucronata* leaves. Surface sediments were sampled by inserting a PVC corer ($\phi = 22$ mm) in the top 2 cm sediment layer at three random positions in each quadrat. To assess the trophic transfer of seabird-derived nutrients to mangrove fauna we conducted isotopic analyses on mangrove invertebrates comprising of gastropods and crabs occupying different trophic levels. As primary consumers, we collected herbivorous gastropods of the genus *Littoraria* from mangrove roots and trunk within each quadrat, and leaf-eating sesarmid crab *Sesarma leptosoma* on mangrove trees at each site. As secondary consumers, we collected omnivorous portunid crab *Thalmita crenata* on the intertidal mudflat adjacent to mangrove forests. We sampled foot muscle from gastropods, body muscle from sesarmid crabs and limb muscle from portunid crabs. We collected macroalgae on rocky outcrops of the intertidal mudflat and within 50 m of the mangrove fringe for isotopic analyses to assess nutrient uptake in the adjacent habitat. We selected macroalgae since they incorporate nutrients over a relatively long period (weeks to months), constituting an ideal proxy for ambient nutrient conditions.⁹³ At each site, we randomly collected thalli of the macroalgae *Halimeda* spp. The latter has proven a good proxy for seabird nutrients since it responds positively to seabird subsidies.⁶³

Isotopic values of seabird-derived nutrients are enriched in nitrogen ($\delta^{15}\text{N}$) due to the high trophic position of seabirds in the marine food chain and enrichment of $\delta^{15}\text{N}$ in seabird guano after deposition.⁹⁴ $\delta^{15}\text{N}$ is therefore used to trace seabird-derived nutrients in recipient communities.²⁸ All samples for isotopic analyses were dried at 60°C and ground into a homogeneous powder using a ball mill. Isotopic ratios were measured using an Isoprime 100 Isotope Ratio Mass Spectrometer with international standards IAEA 600, USGS 41 and CH6, at the stable isotope facility at Lancaster University (Lancaster, UK). Accuracy based on internal standards was within 0.1 ‰ SD and selected samples were run in triplicate to further ensure accuracy of readings.

Surface seawater nutrient concentrations

The semi-diurnal tidal fluctuations at Aldabra generate large and rapid changes in water levels, causing strong tidal currents.⁸² Most of the guano inputs by mangrove-nesting seabirds on Aldabra are deposited directly in the water or are washed away during the subsequent high tide when deposited at low tide.⁹⁵ To assess nutrient export from the seabird colonies, we sampled surface seawater in 30-ml containers at each site on two occasions; on the incoming tide while the lagoon fills and on the outgoing tide while the lagoon drains. Samples were collected in duplicate at each location and occasion and treated at 80°C in a drying oven for a minimum of 2.5 hrs. Samples were stored at room temperature in the dark until laboratory analysis. NO_x (nitrate NO_3^- + nitrite NO_2^-) and phosphate (PO_4^{3-}) concentrations were determined using an AA3 auto-analyser (Seal Analytical) following the method of Aminot and K erouel.⁹⁶ Samples were processed at IRD laboratory in Plouzan  (France) and had an accuracy of $0.5 \mu\text{mol.L}^{-1}$ and $0.7 \mu\text{mol.L}^{-1}$, for NO_x and PO_4^{3-} , respectively.

QUANTIFICATION AND STATISTICAL ANALYSIS

We assessed the influence of seabirds on nutrient parameters using univariate tests of differences between seabird and non-seabird sites. We formulated linear mixed models (LMMs) for each nutrient parameter (%N, %P, C:N, C:P, RE-N, RE-P) of mangrove leaves and $\delta^{15}\text{N}$ for mangrove leaves, sediment, gastropod, crabs and macroalgae with seabird status (seabird/no seabird) as fixed effect and site as random effect. For some parameters, variances were heterogeneous between the predictor levels (i.e., higher within seabird than non-seabird sites), therefore we included the 'VarIdent' error structure on seabird status, which allows different variance of predictor levels. We assessed residual spatial autocorrelation of each model by plotting residuals against location and found no spatial autocorrelation in any of these models. This was confirmed by comparing models with and without spatial weights matrix using Akaike's Information Criterion (AIC), and models without had the lowest AIC values. Model diagnostics were performed by plotting residuals against fitted values and explanatory variables to verify assumptions of homogeneity of variance and independence following Zuur and Ieno.⁹⁷



We assessed differences in surface seawater nutrient concentrations separately for NO_x and phosphate. We used LMMs with seabird status, including an interaction with tidal regime (incoming/ outgoing) as fixed effects and site as random effect. These models included the 'VarIdent' error structure on seabird status. Where significant differences were detected, we performed post-hoc tests using the *emmeans* package.⁸⁰ Model residuals were assessed to verify model assumptions and to confirm there were no spatial dependencies.⁹⁷ All models were formulated using the function 'lme' from package *nlme*⁷⁹ and analyses were conducted on R version 4.3.0.⁷⁸

iScience, Volume 27

Supplemental information

**Seabird nutrient subsidies enrich mangrove
ecosystems and are exported
to nearby coastal habitats**

Jennifer Appoo, Nancy Bunbury, Sébastien Jaquemet, and Nicholas A.J. Graham

SUPPLEMENTAL INFORMATION

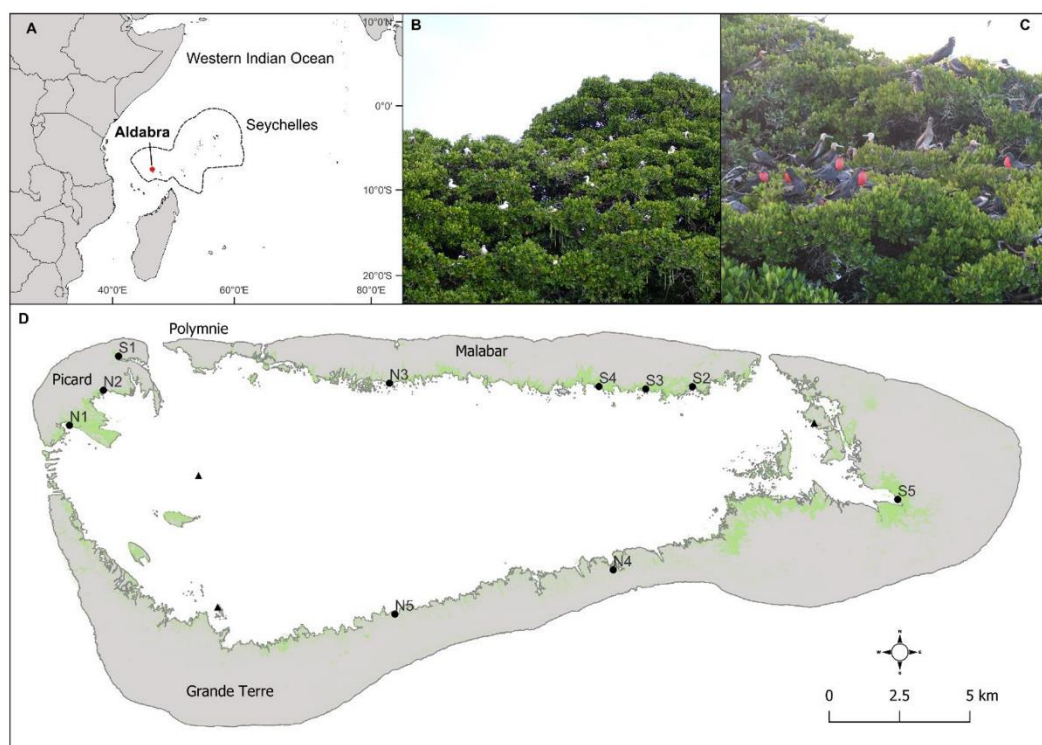


Figure S1. Study site and sampling locations, Related to STAR Methods.

(A) Location of Aldabra Atoll (Seychelles) in the Western Indian Ocean.

(B) Red-footed boobies nesting in mangroves at Aldabra.

(C) Frigatebird breeding colony in mangroves at Aldabra.

(D) Sampling locations (circles) on Aldabra at sites with seabirds (S1–S5) and sites with no/few seabirds (N1–N5), with mangrove distribution shown in green. Triangles show locations of additional seawater sampling sites in the lagoon.

Table S1. Mangrove forest structure at each site on Aldabra Atoll, Related to STAR Methods.

Sites with nesting seabirds (S1–S5) and no nesting seabirds (N1–N5). Community composition of main mangrove species shown; Rm: *Rhizophora mucronata*, Bg: *Brugueira gymnorrhiza*, Ct: *Ceriops tagal*. DBH: diameter at breast height.

Site	Species composition			Tree density (trees. ha ⁻¹)	Tree DBH (cm)	Tree height (m)	Above-ground biomass (Mg. ha ⁻¹)
	% Rm	% Bg	% Ct				
Seabird							
S1	100	0	0	2700 ± 1885	12.6 ± 6.6	7.4 ± 2.5	219.5 ± 246.6
S2	88	9	3	4650 ± 1788	13.3 ± 5.5	7.2 ± 2.1	335.8 ± 114.7
S3	84	10	6	4100 ± 1957	10.1 ± 5.1	6.9 ± 2.4	195.4 ± 84.6
S4	65	26	9	4600 ± 1750	10.9 ± 5.8	7.5 ± 2.9	254.4 ± 126.2
S5	98	0	0	4350 ± 4957	8.1 ± 5.8	6.9 ± 3.2	178.1 ± 105.6
No seabird							
N1	78	13	9	9450 ± 4017	6.3 ± 4.2	4.4 ± 2.1	160.3 ± 90.2
N2	99	0	1	5150 ± 2708	9.3 ± 4.4	6.5 ± 2.3	194.8 ± 83.8
N3	52	8	40	9350 ± 6552	8.3 ± 5.3	4.8 ± 2.3	252.5 ± 134.5
N4	96	0	4	1350 ± 1299	5.6 ± 2.9	2.2 ± 0.2	7.1 ± 6.48
N5	78	22	0	450 ± 334	5.7 ± 4.6	2.3 ± 0.2	3.1 ± 3.3

Table S2. Results of linear mixed models to test differences of nutrient parameters between seabird and non-seabird sites, Related to Figure 1, 2 and 3.

Significant differences ($P \leq 0.05$) are marked in bold. RE-N: nitrogen resorption efficiency, RE-P: phosphorus resorption efficiency.

Nutrient parameter	F-value	P-value	Conditional R2	Marginal R2
Mangrove leaves <i>Rhizophora mucronata</i> (N _{obs} = 80, N _{site} = 10)				
% N	50.7	< 0.0001	0.75	0.71
% P	10.2	0.013	0.61	0.38
C:N	44.1	< 0.0001	0.51	0.47
C:P	6.86	0.031	0.40	0.19
RE-N %	2.61	0.15	0.40	0.11
RE-P %	1.59	0.24	0.53	0.09
$\delta^{15}\text{N} \text{‰}$	5.09	0.05	0.66	0.24
Sediment (N _{obs} = 240, N _{site} = 10)				
$\delta^{15}\text{N} \text{‰}$	21.4	0.0017	0.95	0.65
Gastropod (N _{obs} = 240, N _{site} = 10)				
<i>Littoraria</i> spp. $\delta^{15}\text{N} \text{‰}$	113.8	< 0.0001	0.68	0.64
Sesarmid crab (N _{obs} = 150, N _{site} = 10)				
<i>Sesarma leptosoma</i> $\delta^{15}\text{N} \text{‰}$	35.2	< 0.001	0.93	0.73
Portunid crab (N _{obs} = 86, N _{site} = 9)				
<i>Thalamita crenata</i> $\delta^{15}\text{N} \text{‰}$	16.8	0.005	0.83	0.55
Macroalgae (N _{obs} = 70, N _{site} = 7)				
<i>Halimeda</i> spp. $\delta^{15}\text{N} \text{‰}$	11.0	0.021	0.94	0.58

Table S3. Results of linear mixed models to test differences in surface seawater nutrients, Related to Figure 3.

Significant differences ($P \leq 0.05$) are marked in bold.

	Fixed effects	F-value	P-value	Conditional R2	Marginal R2
Lagoon surface seawater nutrients					
NOx (N _{obs} = 54, N _{site} = 14)	Seabird	2.80	0.12	0.85	0.23
	Tide	0.22	0.64		
	Seabird: Tide	5.76	0.021		
Phosphate (N _{obs} = 54, N _{site} = 14)	Seabird	34.1	0.0001	0.97	0.78
	Tide	4.02	0.052		
	Seabird: Tide	17.8	0.0001		

CHAPTER 5

Seabird nutrient subsidy alters size and resource use of functionally important mangrove macroinvertebrates

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Manuscript submitted

Appoo, J., Graham, N. A. J., Jones, C. W., Jaquemet, S., & Bunbury, N. Seabird nutrient subsidy alters size and resource use of functionally important mangrove macroinvertebrates. *Ecosphere*. *In review*.

ABSTRACT

Invertebrates have a central role in food webs and ecosystem functioning. By boosting productivity, allochthonous nutrient inputs influence the food webs of recipient communities. Understanding how allochthonous nutrient subsidies affect invertebrates is crucial, particularly in highly productive coastal areas. Here, we examine how mangrove macroinvertebrates are impacted by nutrient-rich guano delivered by nesting seabird populations at Aldabra Atoll in the Indian Ocean. We compare nitrogen and carbon stable isotope ratios and nitrogen composition of basal resources and macroinvertebrate consumers in mangroves with and without nesting seabirds. Seabird-derived nutrient enrichment increased the nitrogen content of basal food sources and herbivorous littorinid gastropods and sesarmid crabs. In mangroves with breeding seabirds, mean carapace widths of sesarmid and omnivorous portunid crabs were 6% and 11% larger, respectively. Isotopic niches of littorinid gastropods and sesarmid crabs were larger and had higher overlap at seabird compared to non-seabird sites. Epiphytic macroalgae and guano comprised >50% of resource contributions to littorinid gastropods and sesarmid crabs at seabird sites. This differed markedly from non-seabird sites where the main resource contributions were 77% mangrove leaves for littorinid gastropods, 36% sediment organic matter and 41% mangrove leaves for sesarmid crabs. The increased sizes of mangrove crabs suggest that seabird nutrient enrichment can promote mangrove crab fisheries productivity and benefit the provisioning of mangrove ecosystem services. By shifting resource use of functionally important macroinvertebrates, we discuss how seabirds modify trophic interactions, with potential consequences for mangrove ecosystem processes and resilience.

Keywords: allochthonous nutrients, crabs, gastropods, isotopic niche, mangrove trophodynamics, resource contribution, Seychelles, stable isotopes

1. INTRODUCTION

The movement of nutrient resources across ecosystem boundaries considerably impacts on the functioning and dynamics of recipient communities (Anderson & Polis, 2004). Natural allochthonous nutrient inputs increase primary and secondary productivity, with their influence propagating throughout food webs, generating a wide range of ecosystem responses (Polis et al., 1997; Sanchez-Pinero & Polis, 2000). Invertebrates are the most abundant and diversified animal group worldwide, comprising 80% of all known eukaryote species (Brusca & Brusca, 2003). They occupy a wide range of ecological niches, making them crucial components of food webs and fulfilling key functions vital for maintaining ecosystem integrity and delivering ecosystem services (Wilson, 1987; Kotze et al., 2022). For example, invertebrates influence primary production through seed dispersal, pollination and herbivory, and act as ecosystem engineers by forming and modifying habitats through bioturbation and bioerosion (Prather et al., 2013). Investigating how invertebrates respond to nutrient subsidies is important to gain insight into the impacts of allochthonous nutrient inputs on ecosystem functioning and service delivery.

Seabirds forage at sea and transfer marine nutrients to land at their breeding and roosting sites, mainly as guano deposits (Grant et al., 2022). Guano provides a natural nutrient subsidy for island and coastal ecosystems worldwide (De La Peña-Lastra, 2021) and indirectly boosts food webs around seabird colonies by enriching primary producers. Seabirds also provide direct nutrient subsidies in terrestrial systems through consumers that feed on seabird tissues, carcasses, eggs, or discarded marine prey (Kolb et al., 2011). Seabird nutrient subsidies influence the abundance, diversity and behavior of terrestrial and aquatic invertebrate consumers (Kolb et al., 2011; Young et al., 2011). However, research to date has predominantly focused on temperate or polar regions. Many tropical communities are severely threatened by climate change and local stressors, and important questions remain about how tropical ecosystems will respond to biodiversity loss (Clarke et al., 2017). Tropical areas have higher environmental complexity and species diversity, which may result in different ecological responses to nutrient inputs. A global meta-analysis on the effects of seabird nutrient subsidies on invertebrates reveals that only 6% of studies have been conducted in tropical regions (Van Der Vegt & Bokhorst, 2023). This underrepresentation limits our ability to draw firm conclusions about global patterns of seabird effects (Grant et al., 2022) and to fully understand how seabird nutrient subsidies influence invertebrate communities in biodiversity-rich tropical coastal areas.

Mangroves, which can host huge nesting seabird colonies, are a crucially important coastal habitat, acting as carbon sinks, connecting land and sea habitats, providing nurseries for marine species, protecting tropical coastlines, and supporting the livelihoods of coastal communities (Worthington et al., 2020). Mangroves support unique and diverse invertebrate assemblages, particularly crustaceans and mollusks. These groups play major ecological roles in mangrove ecosystem functioning (Ferreira et al., 2024), including carbon and other nutrient cycling, sediment bioengineering (Cannicci et al., 2008), mangrove growth regulation (Lee, 2008), and act as food resources for numerous vertebrates (Nagelkerken et al., 2008; Sandoval et al., 2022). Nesting and roosting seabirds can contribute substantial quantities of nutrient-rich guano to mangrove forests (Irick et al., 2015; McFadden et al., 2016). Nutrient enrichment of mangrove habitats influences invertebrate community structure and trophic relationships (Valiela et al., 2004; Feller & Chamberlain, 2007). Onuf et al. (1977) showed that seabird-derived nutrients increased mangrove leaf nutritional quality, resulting in increases in biomass of folivorous insects and herbivory rates.

Similarly, fertilization experiments have shown that nutrient enrichment can lead to either increased or decreased consumption of mangroves, depending on the feeding guild and behavior of the herbivores (Feller, 1995; Feller et al., 2007; Feller & Chamberlain, 2007), suggesting that nutrient enrichment causes a shift in resource use. However, these studies solely focused on mangroves as a food source. In mangrove habitats, consumers can access various additional primary food sources, such as sediment organic matter (SOM), macroalgae and benthic microalgae (BMI; Nagelkerken et al., 2008). The effects of nutrient enrichment on these various sources and the consequences on resource use in mangrove invertebrate food webs remain poorly explored. Furthermore, invertebrates occupy multiple trophic levels in mangroves, yet nutrient enrichment studies have investigated the effects mainly on primary consumers (Feller et al., 2013). Research in other coastal invertebrate food webs shows that nutrient subsidies are incorporated at multiple trophic levels (Silva et al., 2022), and nutrient enrichment increases consumer sizes (Hemmi and Jormalainen, 2002) and alters community trophic structure (Vizzini et al., 2016; Wimp et al., 2019). Whether this response is consistent for multilevel and functionally important mangrove invertebrate communities, such as gastropods and crabs, remains to be examined. Such investigations are essential to understanding the functioning of naturally subsidized mangrove ecosystems.

Here, we investigate how seabird nutrient subsidies impact the macroinvertebrate food web in the mangrove forests of Aldabra Atoll (Seychelles). Following previous analyses confirming seabird nutrient enrichment of this mangrove ecosystem (Appoo et al., 2024), we aim to assess the trophic response of the macroinvertebrate community to seabird-derived nutrients. We use stable isotopes of nitrogen ($\delta^{15}\text{N}$) and carbon ($\delta^{13}\text{C}$) and total nitrogen concentration (%N) of basal food sources and macroinvertebrate consumers sampled in mangroves with and without nesting seabirds. In food webs, there is a stepwise increase in $\delta^{15}\text{N}$ per trophic level (Post, 2002), resulting in high $\delta^{15}\text{N}$ values in high-trophic level marine predators, like seabirds. After guano deposition, volatilization of ammonia results in further enrichment of $\delta^{15}\text{N}$ in guano, causing elevated $\delta^{15}\text{N}$ values in seabird-subsidized systems (Kazama, 2020). In contrast, $\delta^{13}\text{C}$ values vary little among trophic levels, closely reflecting values of organic matter at the base of food webs (Post, 2002). Carbon derived from marine sources exhibits higher $\delta^{13}\text{C}$ than terrestrial sources. Due to their coastal location, mangrove communities can display $\delta^{13}\text{C}$ gradients ranging from terrestrial (depleted) to marine (enriched) values (Bouillon et al., 2011). Therefore $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values can demonstrate the functioning of ecosystems by showing nutrient or energy flow in food webs, identifying the sources of nutrients and organic matter assimilated by consumers, and characterizing trophic niches and interactions (Layman et al., 2012). Specifically, we aim to determine whether seabird-derived nutrients increase the nitrogen composition of mangrove food web components at multiple trophic levels. At seabird sites, we expect the availability of enriched food sources will lead to (i) larger sizes of macroinvertebrate consumers and shifts in their resource use, as indicated by (ii) broader isotopic niches and (iii) higher contributions of enriched resources to consumer diets, compared to non-seabird sites.

2. METHODS

2.1. Study area

Aldabra Atoll (9°24' S, 46°20' E), in the southern Seychelles, is a large raised coral atoll (total area 365 km²) in the Western Indian Ocean (Appendix S1: Figure S1). The atoll comprises four main islands (total land area 155 km²) surrounding a shallow lagoon. The atoll hosts 78% of the total mangrove area in Seychelles (ca. 1700 ha; 11% of Aldabra's land area; Walton et al., 2019). Aldabra's mangroves occur along the lagoon shores and islets, with *Rhizophora mucronata* as the most dominant mangrove

species, followed by *Ceriops tagal*, *Bruguiera gymnorhiza*, and *Avicennia marina* (Macnae, 1971). The mangroves are influenced by semi-diurnal tides ranging from 2–3 m amplitude (Farrow & Brander, 1971). Aldabra has a semi-arid climate with mean annual temperatures of 24–28 °C, mean annual rainfall of 975 mm and two distinct seasons (Haverkamp et al., 2017); the wet season during Nov–Apr influenced by the north-west monsoon winds, and the dry season during May–Oct influenced by the south-east trade winds.

Aldabra's mangroves host large nesting seabird populations in single and mixed-species colonies, comprising great frigatebirds *Fregata minor*, lesser frigatebirds *F. ariel* and red-footed boobies *Sula sula* (Burger & Betts, 2001). Their distribution coincides with the absence of feral cats; there are fewer breeding seabirds on the largest island of Grande Terre, the only island with a feral cat population. Seabirds occur year-round in Aldabra's mangroves due to multiple breeding peaks, long breeding cycles and roosting patterns of non-breeding individuals. Nesting frigatebirds and red-footed boobies contribute around 41.4 and 40.9 tonnes of nitrogen and phosphorus per year, respectively, to Aldabra's mangroves, enriching mangrove food webs (Appoo et al., 2024). Human influence on the atoll is limited to the presence of a small research station with 10–20 permanent staff. Aldabra's remoteness and protection as a Strict Nature Reserve and UNESCO World Heritage Site have ensured that the mangroves and seabird colonies are relatively undisturbed.

2.2. Field sampling

Sampling occurred between November 2022 and March 2023 during the breeding period of all three seabird species. We collected samples at 10 sites distributed along the lagoon shores around the atoll, ensuring a minimum distance of 1 km between each site. We selected sites based on the breeding seabird distribution, with five sites with low (<20 nests) nesting activity and five sites with high nesting activity (250–700 nests; Appendix S1: Figure S1).

We sampled the main basal food sources in mangroves (Nagelkerken et al., 2008), taking into account the feeding behavior of the consumers (Phillips et al., 2014); green mangrove leaves, epiphytic macroalgae, SOM and BMI (see below). At each site, samples of basal resources were collected in eight random quadrats, each measuring 5 x 5 m and spaced at least 50 m apart along the mangrove fringe (total site length 400m). Within each quadrat, we collected between one and three samples of each basal resource. *Rhizophora mucronata* comprise 79% of mangrove trees at our surveyed sites

(Appoo et al., 2024), making it the dominant mangrove food source. We collected young, fully expanded green *R. mucronata* leaves exposed to the sun. Six leaves were sampled from at least three individual trees and pooled to form one composite sample per quadrat. Epiphytic macroalgae (Chlorophyta) were collected randomly on *R. mucronata* roots using forceps. SOM was collected by inserting a PVC corer ($\varnothing = 22$ mm) into the top 2-cm sediment layer. Collection of BMI was not possible without SOM or other organic matter contamination; therefore we used average stable isotope values compiled from mangroves in semi-arid and arid regions (see below).

We sampled three of the most abundant macroinvertebrate consumers in this system. Mangrove periwinkle snails of the genus *Littoraria* are ubiquitous in Aldabra's mangroves (Taylor, 1971) and are generalist herbivores, consuming mangrove tissues, fungi, micro- and macroalgae and lichen on mangroves (Christensen et al., 2001; Lee et al., 2001; Alfaro, 2008). Three *Littoraria* spp. individuals were collected randomly in each quadrat on mangrove trees from different substrates, including leaves, roots, and trunks. Sesarmid crabs, *Leptarma leptosoma*, are abundant on *R. mucronata* on Aldabra (Macnae, 1971), feeding primarily on green mangrove leaves but also consuming algae and sediment (Dahdouh-Guebas et al., 1999; Bouillon et al., 2002). We collected 15 individuals randomly on mangroves in each site. As a secondary consumer, we sampled the portunid omnivorous crab *Thalamita crenata* on intertidal mudflats adjacent to mangrove forests. *Thalamita crenata* is a generalist predator and scavenger, consuming mainly macroinvertebrates such as mollusks and crustaceans but also algae and plant detritus (Cannicci et al., 1996; Dahdouh-Guebas et al., 1999). Adjacent to each site (< 50m from mangrove fringe), we sampled 7–10 *T. crenata* crabs, except for one seabird site where the crabs were absent. We collected a total of 987 samples of basal food sources (seabird sites n=253, non-seabird sites n=258) and macroinvertebrate consumers (seabird sites n=231 and non-seabird sites n=245). Details of sample sizes for each site and sample type are provided in Appendix 1: Table S1 and S2. Additionally, we collected guano from active nests of frigatebirds (n=27) and red-footed boobies (n=32) at seabird sites as the main source of seabird-derived nutrients. All samples were kept cool on ice during daytime field sampling until arrival at laboratory in the evening.

2.3. Sample processing and isotope analysis

Plant samples were rinsed with fresh water. For each *Littoraria* spp. individual, we measured the shell height using calipers (± 1 mm) and sampled their foot muscle. We measured crab carapace width using

calipers (± 1 mm) and collected body muscle from sesarimid crabs and limb muscle from portunid crabs. All samples were dried in an oven at 60 °C for at least 48 hrs. Samples were powdered using a ball mill and subsamples were weighed and placed in tin capsules. $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values were measured using an Isoprime 100 Isotope Ratio Mass Spectrometer with international standards IAEA-600, USGS-41 and IAEA-CH6, at the stable isotope facility at Lancaster University (Lancaster, UK). Epiphytic macroalgae and SOM samples were analyzed separately for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. Before $\delta^{13}\text{C}$ analysis, dry subsamples were rinsed repeatedly with 10% v/v HCl to remove carbonates, washed with distilled water and dried again. Results are expressed in delta notation in ppm (‰) following the equation:

$$\delta^{13}\text{C} \text{ or } \delta^{15}\text{N} = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} \right) - 1 \quad (1)$$

where $R = {}^{13}\text{C}/{}^{12}\text{C}$ or ${}^{15}\text{N}/{}^{14}\text{N}$, using Vienna Pee Dee Belemnite as the standard value for carbon and atmospheric nitrogen for nitrogen. Accuracy based on internal standards was within 0.1 ‰ SD for $\delta^{13}\text{C}$ and 0.2 ‰ SD for $\delta^{15}\text{N}$. Selected samples were run in triplicate to ensure accuracy of readings further. Variations in tissue lipid content can influence $\delta^{13}\text{C}$ values; therefore, we used mathematical normalization methods to standardize the lipid content of samples following Post et al., (2007). For basal plant samples, equations were applied according to carbon content (%C), while invertebrate samples were normalized if C:N ratios were > 3.5 . The equations used were:

$$\text{plants } < 40 \% \text{ C: } \delta^{13}\text{C}_{\text{normalized}} = \delta^{13}\text{C} - 3.02 + 0.09 \times \% \text{ C} \quad (2)$$

$$\text{plants } > 40 \% \text{ C: } \delta^{13}\text{C}_{\text{normalized}} = \delta^{13}\text{C} - 5.84 + 0.14 \times \% \text{ C} \quad (3)$$

$$\text{aquatic animals: } \delta^{13}\text{C}_{\text{normalized}} = \delta^{13}\text{C} - 3.32 + 0.99 \times \text{C:N} \quad (4)$$

2.4. Data analysis

2.4.1. Isotopic and nitrogen composition of food web components

We produced a $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ biplot comprising all food web components at seabird and non-seabird sites. To verify whether $\delta^{15}\text{N}$ enrichment through seabird nutrient subsidies resulted in a higher %N of food web components, we assessed the linear relationships between $\delta^{15}\text{N}$ and %N using Spearman rank correlations. We tested the influence of nesting seabird presence on $\delta^{13}\text{C}$ using linear mixed models for each food web component using the 'lmer' function from R package *lme4* (Bates et al., 2015). Models included seabird status as a fixed effect and site as a random effect. We performed

diagnostics on model residuals to verify normality, homogeneity of variance and independence using the 'plot' function from the R package *car* (Fox and Weisberg, 2019).

2.4.2. Consumer size

We tested the influence of seabird nutrient subsidies on consumer size by assessing the linear relationships between $\delta^{15}\text{N}$ and consumer size using Spearman rank correlations. For each consumer, we then performed parametric or non-parametric *t*-tests, as appropriate, to assess differences in consumer size between seabird and non-seabird sites.

2.4.3. Consumer isotopic niche space

We compared consumer isotopic niches between seabird and non-seabird sites by plotting the isotopic niche space of each consumer and their standard ellipse areas based on maximum likelihood estimates. We computed ellipses containing 95% of the data (SEA) and 40% of the data corrected for small sample size (SEA_c) and convex hulls using functions 'createSiberObject' and 'groupmetricsML' from R package *SIBER* (Jackson et al., 2011). We assessed the % niche overlap, measured as the proportion of overlap between standard ellipses of consumers. To account for uncertainty in the data, we also estimated the Bayesian standard ellipse areas (SEA_B) for each consumer using Monte Carlo Simulation with 10⁴ iterations, using functions 'siberMVN' and 'siberEllipses'. We determined the probability that SEA_B posterior distributions are smaller (or larger) between seabird and non-seabird sites for each consumer.

2.4.4. Resource contributions to consumer diet

We estimated the relative contribution of different resources to consumers at seabird and non-seabird sites using Bayesian stable isotope mixing models with R package *MixSIAR* (Stock & Semmens, 2016). For herbivorous littorinid gastropods and sesarmid crabs, we included BMI, mangrove leaves, epiphytic macroalgae and SOM as potential food sources. For omnivorous portunid crabs, potential resources were BMI, mangrove leaves, epiphytic macroalgae, littorinid gastropod and sesarmid crabs. Guano can also be consumed directly and was included as a food source for consumers at seabird sites. We ran separate models for each consumer and status and applied mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values (\pm SD) of each food source according to their seabird status. Aldabra is a semi-arid oceanic atoll (Farrow, 1971), therefore BMI stable isotope values applied were average for mangroves in arid and semi-arid regions;

$\delta^{13}\text{C} = -15.7 \pm 3.0 \text{ ‰}$ and $\delta^{15}\text{N} = 2.0 \pm 1.9 \text{ ‰}$ suggested by Medina-Contreras et al., (2023), compiled from various sources (Hsieh et al., 2002; Shahraki et al., 2014; Akbari Noghabi et al., 2022). Trophic enrichment factors (mean \pm SD) used varied depending on the consumer. For littorinid gastropods, we applied $\delta^{13}\text{C} = 5.3 \pm 0.3 \text{ ‰}$, $\delta^{15}\text{N} = 4.2 \pm 0.2 \text{ ‰}$ (Teoh et al., 2018), and for sesarmid crabs, $\delta^{13}\text{C} = 5.4 \pm 0.9 \text{ ‰}$, $\delta^{15}\text{N} = 3.9 \pm 0.5 \text{ ‰}$ (Sandoval et al., 2022), from trophic discrimination experiments of gastropods and crabs feeding on mangroves, respectively. For portunid crabs, we used $\delta^{13}\text{C} = 1.3 \pm 0.3 \text{ ‰}$ commonly assumed by McCutchan et al., (2003) and $\delta^{15}\text{N} = 3.4 \pm 1.0 \text{ ‰}$ (Post, 2002) according to their high-protein diet (Le et al., 2017). Models were fitted using 3 chains and 'very long' Markov Chain Monte Carlo lengths using the function 'run_model', and convergence were checked based on the Gelman-Rubin and Geweke diagnosis using the function 'output_JAGS'.

3. RESULTS

3.1. Isotopic and nitrogen composition of food web components

At seabird sites, littorinid gastropods had the highest $\delta^{15}\text{N}$ values, while SOM had the lowest $\delta^{15}\text{N}$ values. In contrast, at non-seabird sites, portunid crabs exhibited the highest values of $\delta^{15}\text{N}$ and mangrove leaves had the lowest (Figure 1). At both seabird and non-seabird sites, portunid crabs were the most enriched in $\delta^{13}\text{C}$ (most marine group), while mangrove leaves were the most depleted in $\delta^{13}\text{C}$ (most terrestrial group).

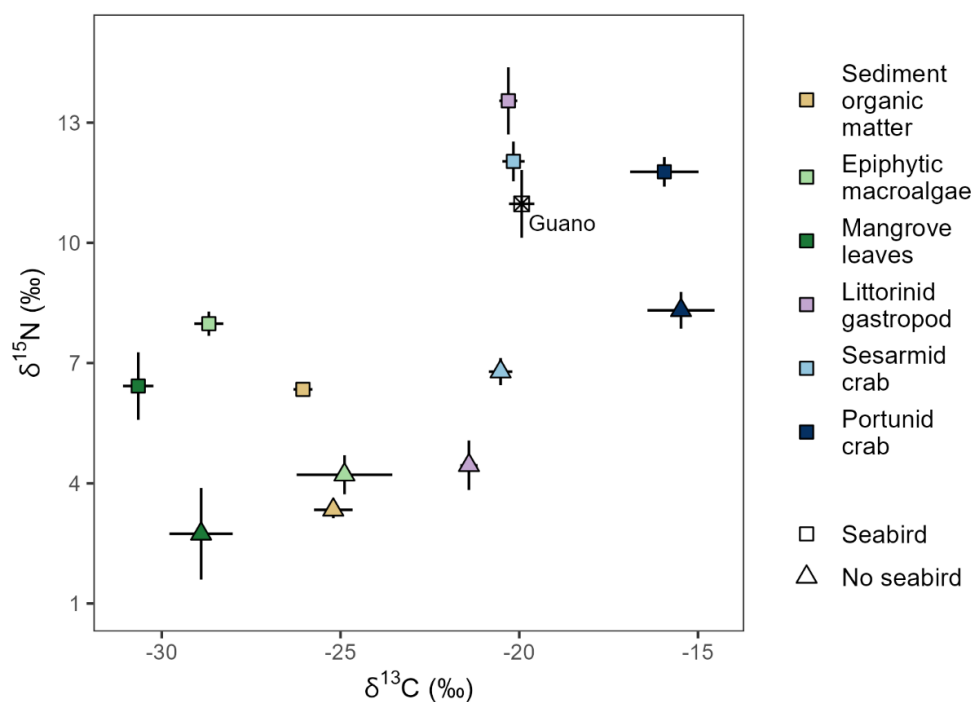


Figure 1. Biplot of normalized $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (means and 95% confidence intervals) of seabird guano, basal sources and consumers at seabird and non-seabird sites.

%N increased with $\delta^{15}\text{N}$ for all basal sources, with SOM and epiphytic macroalgae showing the highest increase (SOM: $r_s = 0.57$, $p < 0.0001$, $n = 239$, epiphytic macroalgae: $r_s = 0.62$, $p < 0.0001$, $n = 192$, mangrove leaves: $r_s = 0.44$, $p < 0.0001$, $n = 80$; Figure 2a). We observed similar positive correlations between %N and $\delta^{15}\text{N}$ for littorinid gastropods ($r_s = 0.36$, $p < 0.0001$, $n = 240$) and sesarmid crabs ($r_s = 0.38$, $p < 0.0001$, $n = 150$), but not for portunid crabs ($r_s = -0.09$, $p = 0.44$, $n = 86$; Figure 2b). $\delta^{13}\text{C}$ did not differ between seabird and non-seabird sites for all food web components (Appendix S1: Figure S2).

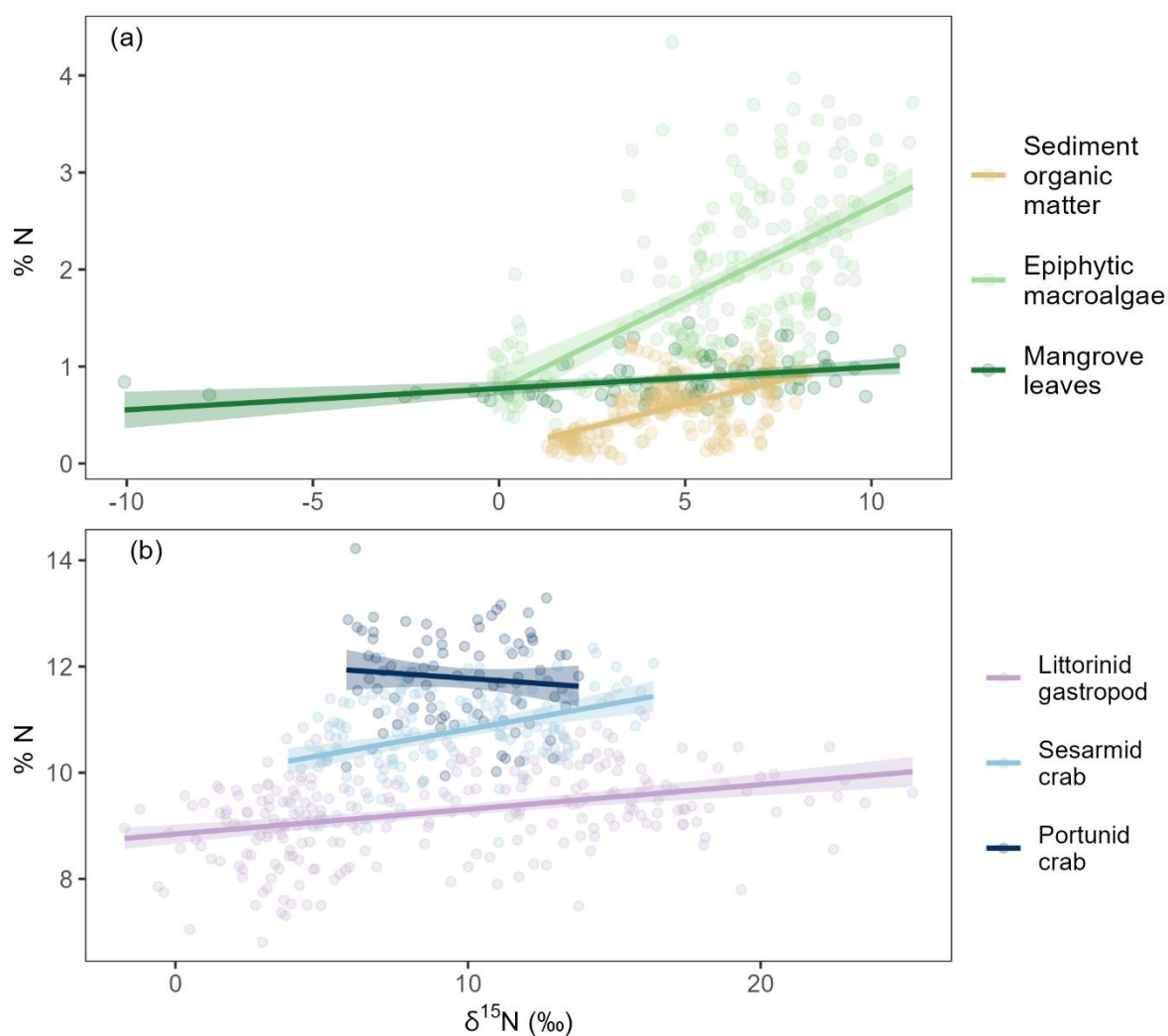


Figure 2. Linear relationships between %N and $\delta^{15}\text{N}$ for (a) basal resources and (b) consumers. Points represent raw data and shaded areas represent 95% confidence intervals. All linear relationships were significant except for portunid crabs.

3.2. Consumer size

We found no correlation between $\delta^{15}\text{N}$ and size (shell height) of littorinid gastropod ($r_s = -0.2$, $p = 0.76$, $n = 240$) and no difference in shell height between seabird and non-seabird sites ($W = 7575$, $p = 0.49$; Figure 3a, 3b). However, size (carapace width) increased with higher $\delta^{15}\text{N}$ values for both sesarmid ($r_s = 0.38$, $p < 0.0001$, $n = 150$; Figure 3c) and portunid crabs ($r_s = 0.28$, $p = 0.01$, $n = 86$; Figure 3e). Sesarmid and portunid crabs were both larger at seabird than non-seabird sites (respectively, $W = 3525$, $p = 0.007$; $t = 2.97$, $df = 83$, $p = 0.004$; Figure 3d, 3f).

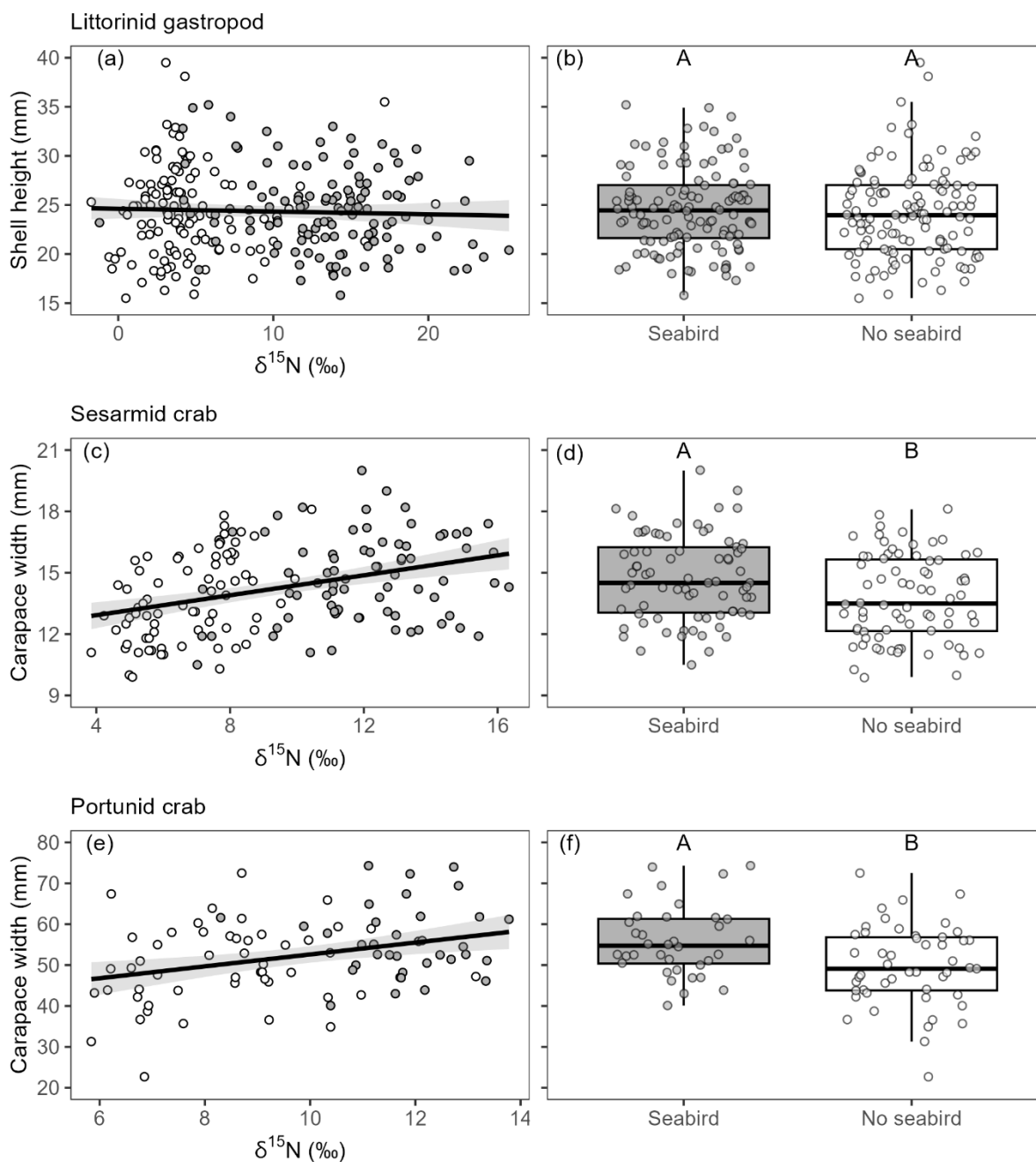


Figure 3. Linear relationships between size of consumers and $\delta^{15}\text{N}$ for (a) littorinid gastropods, (c) sesarmid crabs and (e) portunid crabs. Shaded areas represent 95% confidence intervals. Sizes of (b) littorinid gastropods, (d) sesarmid crabs and (f) portunid crabs at seabird and non-seabird sites. Boxplots display median and interquartile range. Different letters denote significant ($p < 0.05$) differences between means. Filled and open points represent raw data for seabirds and non-seabird sites, respectively.

3.3. Consumer isotopic niche space

Niche overlap differed between seabird and non-seabird sites, mainly between littorinid gastropods and sesarmid crabs (Figure 4a, 4b). The proportion of overlap between their isotopic niches (indicated by SEA_C ellipses) was higher at seabird sites (28.1%) compared to non-seabird sites (14.7%). Overlap in isotopic niches between littorinid gastropods and portunid crabs, as well as between sesarmid and portunid crabs, was only observed with their SEA ellipses (Figure 4a, 4b). The proportion of overlap between littorinid gastropods and portunid crabs was similar at seabird (12.9%) and non-seabird sites (13.0%). For sesarmid and portunid crabs, overlap was slightly higher at seabird sites (20.3%) than at non-seabird sites (17.2%).

The isotopic niche width of littorinid gastropods and sesarmid crabs at seabird sites shifted upwards along the $\delta^{15}N$ axis compared to non-seabird sites (Appendix S1: Figure S3). For portunid crabs, the isotopic niche width at seabird sites contracted along the $\delta^{13}C$ axis compared to non-seabird sites. Isotopic niche size, indicated by SEA_B , of littorinid gastropods was larger (probability = 0.99) at seabird sites (median, 95% credibility intervals: 19.2 ‰², 16.0–2.9 ‰²) compared to non-seabird sites (14.3 ‰², 11.8–16.9 ‰², Figure 4c, 4d). Sesarmid crabs also had larger isotopic niches (probability = 0.92) at seabird sites (8.41 ‰², 6.55–10.3 ‰²) than at non-seabird sites (6.61 ‰², 5.20–8.22 ‰²). In contrast, the isotopic niche size of portunid crabs was smaller (probability = 0.99) at seabird sites (9.81 ‰², 6.88–13.4 ‰²) compared to non-seabird sites (16.3 ‰², 12.1–21.3 ‰²).

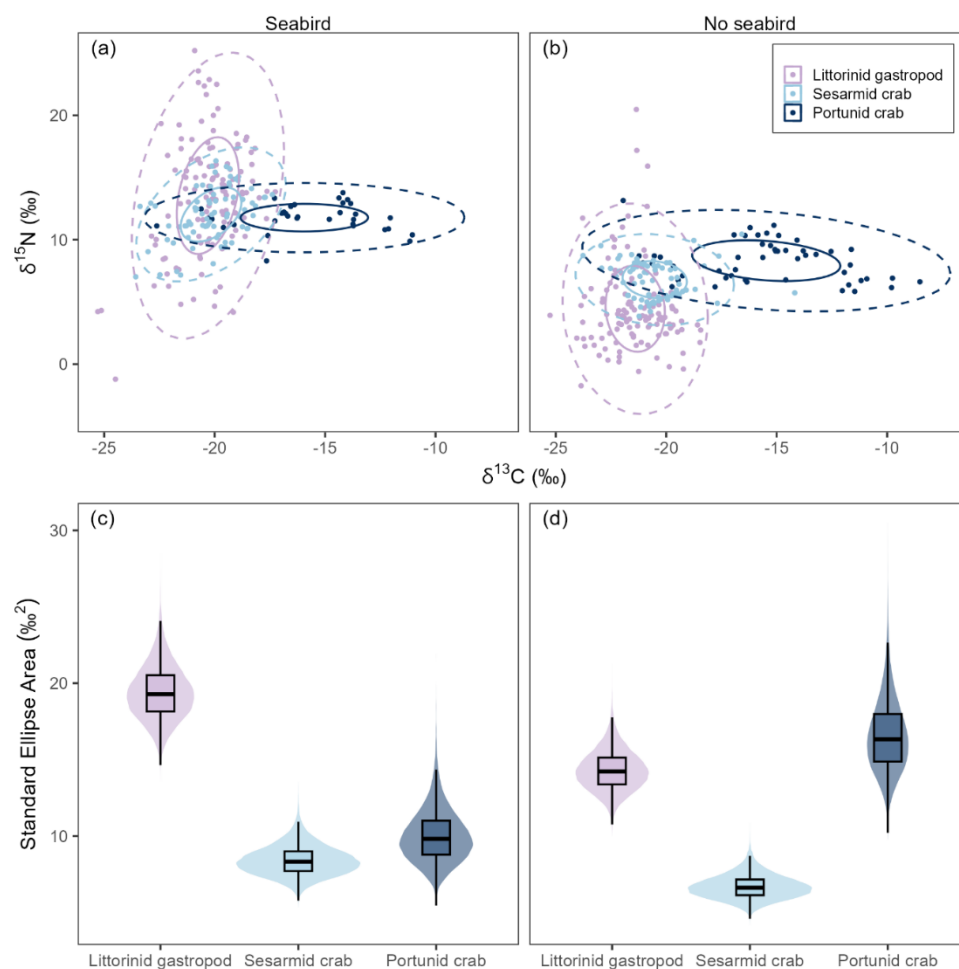


Figure 4. Isotopic niche space showing niche overlap between macroinvertebrate consumers at (a) seabird and (b) non-seabird sites. Solid and dashed lines represent standard ellipse areas containing 40% (SEA_c) and 95% of the data (SEA_B), respectively. Isotopic niche sizes, represented by Bayesian standard ellipse areas (SEA_B) of macroinvertebrate consumers at (c) seabird and (d) non-seabird sites. Violin plots show data distribution; boxplots display median and interquartile range.

3.4. Resource contributions to consumer diet

There were marked differences in the relative contribution of food resources to consumers between seabird and non-seabird sites. For littorinid gastropods, the dominant food resources were epiphytic macroalgae (35%, 0.4–61%) and guano (34%, 26–44%) at seabird sites, and mangrove leaves (77%, 64–85%) and BMI (14%, 6.7–22%) at non-seabird sites (Figure 5a). For sesamid crabs, the main food resources were epiphytic macroalgae (29%, 2.7–58%) and guano (28%, 19–40%) at seabird sites, and mangrove leaves (41%, 20–68%) and SOM (36%, 2.2–72%) at non-seabird sites (Figure 5b). For portunid crabs, the main food resources were BMI and sesamid crabs, comprising higher proportions

at non-seabird sites (BMI: seabird = 38%, 29–48%, non-seabird = 51%, 36–73%; sesarmid crab: seabird = 20%, 0.8–48%, non-seabird = 34%, 7.7–53%; Figure 5c).

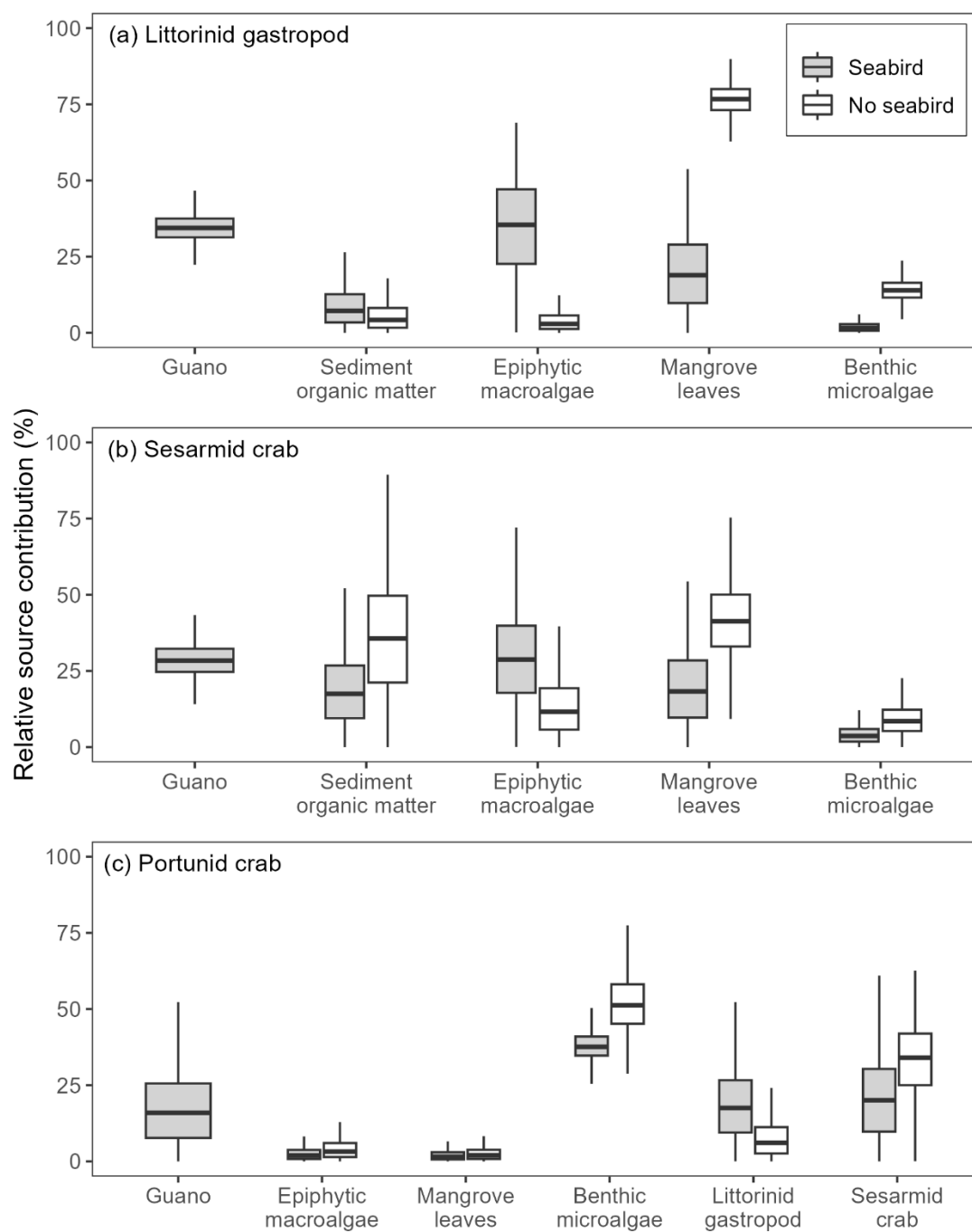


Figure 5. Isotope mixing model estimates of relative contributions of different resources to the diet of (a) littorinid gastropods, (b) sesarmid crabs and (c) portunid crabs, at seabird and non-seabird sites. Boxplots display median and interquartile range.

4. DISCUSSION

We show that seabird nutrient subsidies strongly influence mangrove macroinvertebrate trophic relationships. Seabird-derived nutrient enrichment increased the nitrogen content of basal food sources and primary consumers, as well as the sizes of herbivorous and omnivorous crabs at seabird sites. In mangroves with nesting seabirds, herbivorous gastropods and crabs switched to enriched resources, leading to greater isotopic niche sizes and niche overlap compared to mangroves without nesting seabirds. Our results provide broad insights into how seabird nutrient subsidies can influence mangrove ecosystem processes and service delivery.

Nesting seabirds contribute substantial nitrogen to Aldabra's mangroves, enriching all food web components (Appoo et al., 2024). The positive relationships between $\delta^{15}\text{N}$ enrichment and %N confirmed that seabird subsidies enhance the nutrition of basal food sources. This effect was 1.5 times stronger in SOM and epiphytic macroalgae than in mangrove leaves, probably because most seabird guano in mangroves is deposited directly onto the sediment at low tide or into the water at high tide, elevating seawater and sediment nutrient concentrations (Appoo et al., 2024). The higher nitrogen content in epiphytic macroalgae compared to mangroves is likely due to their faster nutrient uptake from the water column (Hong et al., 2019). Elevated $\delta^{15}\text{N}$ values also correlated with increased nitrogen in littorinid gastropods and sesarimid crabs but not in portunid crabs. Seabird-derived nutrient enrichment is usually highest for primary consumers compared to secondary consumers (Kolb et al., 2011). Similar results in terrestrial invertebrates suggest that subsidy enrichment of higher trophic levels may not be reflected in tissues due to nutrient use for more complex metabolic processes (Obrist et al., 2022). Littorinid gastropods exhibited the highest $\delta^{15}\text{N}$ values at seabird sites, which can be due to sample contamination of their foot muscle from passing through guano on mangrove substrates. However, an increase in %N linked to seabird-derived nutrient enrichment is plausible. Similar effects have been documented in other mollusks, such as the periwinkle *Littorina brevicula* and mussel *Mytilus* spp. or *Septifer* sp. near seabird colonies on Rishiri Island (Kazama, 2020), and the common limpet *Patella vulgata* and acorn barnacle *Semibalanus balanoides* at seabird colonies on the Farne Islands (Healing et al., 2024). The absence of $\delta^{13}\text{C}$ differences between seabird and non-seabird sites indicates minimal influence of seabirds on organic matter inputs in mangrove food webs, consistent with findings from other terrestrial and coastal food webs (Choy et al., 2010; Gagnon et al., 2013).

Sesarmid and portunid crabs were ca. 6% and 11% larger, respectively, at seabird sites. Crab growth is facilitated by the assimilation of high quality resources (Thongtham & Kristensen, 2005; Kristensen et al., 2017). Higher food quality also increases the molting frequency and reproductive effort of mangrove crabs, supporting secondary productivity (Micheli, 1993; Riley et al., 2014). By increasing nitrogen content in basal food sources and primary consumers, we show that seabird nutrient subsidies contribute to larger sizes of herbivorous and omnivorous mangrove crabs. Links between larger sizes of consumers and seabird nutrient enrichment of food sources have also been documented in lizards (Richardson et al., 2019) and herbivorous reef fish (Benkwitt et al., 2021). Crabs are important components of mangrove fisheries worldwide (Rönnbäck, 1999), and they are often regulated by catch-size limits (Glaser and Diele, 2004). Research in coastal wetlands shows that nutrient subsidies increase fisheries' landings of mobile invertebrates. Nutrient inputs enrich food sources and increase the growth and reproduction of exploited mangrove species, thereby enhancing fisheries yields (Breitburg et al., 2009). Although additional data on crab abundance would allow stock assessment, our results provide a preliminary indication that seabird nutrient subsidies can promote mangrove crab fishery productivity.

Additionally, crab fisheries' productivity and landings correlate positively with mangrove coverage (Manson et al., 2005; Aburto-Oropeza et al., 2008; Carrasquilla-Henao et al., 2013). On Aldabra, seabird nutrient subsidies boost mangrove forest nutrient status (Appoo et al., 2024), and increases in mangrove extent coincide with seabird colonies (Constance et al., 2021). By improving mangrove forest health, seabird nutrient subsidies can indirectly enhance not only mangrove crab fisheries but also other income-generating activities like ecotourism and critical services such as coastal protection, suggesting that seabird populations can play an important role in promoting mangrove ecosystem service delivery (Plazas-Jiménez and Cianciaruso, 2020). In contrast, we found no relationship between seabird nutrient subsidies and size of littorinid gastropods. This may be due to differences in species composition of littorinids sampled across sites. Moreover, littorinid gastropod growth depends on the secretion of calcium carbonate and is associated with shell morphology (form and thickness; Riascos & Guzman, 2010): fast-growing littorinid snails have thin, spherical shells to accommodate larger body mass, while slower-growing individuals have thick, cone-shaped shells (Kemp & Bertness, 1984). Improving the taxonomic resolution of littorinid gastropods, as well as

collecting additional data on shell allometry or tissue dry weight, would help determine any seabird nutrient subsidy effect on gastropod sizes.

Seabird nutrient subsidies had similar impacts on the isotopic niches and resource contributions of the two macroinvertebrate herbivores. At seabird sites, littorinid gastropods and sesarmid crabs exhibited broader isotopic niches, shifting towards more enriched $\delta^{15}\text{N}$, and had greater overlap, attributed to their similar resource use. Epiphytic macroalgae and guano constituted >50% of their relative resource contributions, in stark contrast to their relative resource contributions at non-seabird sites, where littorinid gastropods consumed 77% mangrove leaves, and sesarmid crabs 41% mangrove leaves and 36% SOM. The preference for epiphytic macroalgae as a resource for the two herbivores at seabird sites is likely related to the higher nutritional content of epiphytic macroalgae as a result of enrichment by seabird nutrient subsidies (Kolb et al., 2010). Littorinid gastropods and sesarmid crabs play important roles in recycling mangrove nutrients and organic matter (Ferreira et al., 2024). The shift in resource use suggests that seabird nutrient enrichment can potentially reduce mangrove consumption and nutrient cycling by littorinid gastropods and sesarmid crabs. Additional data on invertebrate abundance, community composition and mangrove herbivory rates are needed to explore this link. Mangrove herbivory might be increased for other feeding guilds; leaf-eating insects in seabird-subsidized mangroves in Florida had higher feeding rates, which led to greater losses of mangrove biomass (Onuf et al., 1977), indicating increased recycling of mangrove carbon by this group of herbivores. Furthermore, our study sites are nitrogen-limited (Appoo et al., 2024) and fertilization experiments have demonstrated that nitrogen enrichment increases mangrove herbivory in such environments (Feller et al., 2007). Improving the taxonomic resolution of littorinid gastropods and epiphytic macroalgae samples would reduce potential sources of error related to taxonomic differences between sites and strengthen our results. In addition, expanding our study to include more herbivore feeding guilds would provide a more holistic overview of the impacts of seabird nutrient subsidies on mangrove nutrient cycling.

Food resources for portunid crabs at seabird sites comprised comparable relative proportions of benthic microalgae (37%), sesarmid crabs (20%), guano (17%) and littorinid gastropods (16%). In contrast, at non-seabird sites, portunid crabs consumed mainly benthic microalgae (51%). The niche overlap of portunid crabs with mangrove-dwelling macroinvertebrates was also slightly higher at seabird sites compared to non-seabird sites. Together, this suggests that at seabird sites, portunid crabs

foraged closer to the mangroves, where resources were of higher quality due to seabird-derived nutrients. Conversely, in the absence of seabirds, portunid crabs likely foraged further away from the mangroves, indicated by their larger isotopic niche, which shifted towards more enriched $\delta^{13}\text{C}$ values (reflecting a marine carbon signature, as opposed to depleted $\delta^{13}\text{C}$ values associated with terrestrial carbon). Additionally, mixing model results suggests that at non-seabird sites, portunid crab diet primarily consisted of prey feeding on BMI, such as shrimps, hermit crabs and fiddler crabs commonly found in the intertidal zone (Cannicci et al., 1996; Le et al., 2017). This suggests that at non-seabird sites, portunid crabs likely have a reduced role in the mangrove food web dynamics and contribute more to the intertidal food web. Our analysis included global averages of benthic microalgae isotopic ratios from semi-arid mangroves, and direct measurements are needed to strengthen our findings.

Consistent with our results, studies in Mediterranean coastal ponds subsidized by seabird guano show that invertebrate communities shift their resource use towards enriched sources, and the authors suggest that seabird nutrient enrichment leads to high trophic redundancy and simplification of food webs (Vizzini et al., 2016). High trophic redundancy may also indicate high functional redundancy, i.e., more species with similar functional roles (Agusto, 2021). Theoretical predictions reveal that food webs with high trophic and functional redundancy are more resilient, meaning that if one species were to go extinct, their trophic or functional role would be maintained by other species within the same feeding guild (Borrvall et al., 2000; Sanders et al., 2018). In our study, two macroinvertebrate herbivores with different feeding guilds (surface grazer and folivore) switched to similar trophic habits at seabird sites, suggesting the potential for similar shifts of other species within the same feeding guilds. This implies that seabird nutrient subsidies may contribute to functional redundancy of macroinvertebrate fauna and, consequently, the trophic resilience of mangrove food webs. This is particularly important in the Western Indian Ocean, where mangrove invertebrate communities exhibit low functional redundancy and high functional vulnerability (Cannicci et al., 2021). Additional assessments including more trophic guilds, along with mangrove invertebrate abundance and diversity are needed to explore and validate this link.

5. CONCLUSION

Invertebrate assemblages underpin mangrove health, functioning and ecosystem services. Our study provides insights into the impacts of seabirds within mangroves by shedding light on the trophic

response of functionally important macroinvertebrate fauna to seabird guano contributions. Seabird nutrient subsidies enhance the nutritive value of basal food sources and increase sizes of mangrove crabs, suggesting that seabird populations can promote mangrove crab fisheries' productivity and benefit the provisioning of mangrove ecosystem services. Enrichment of basal resources caused a shift in resource use among primary and secondary mangrove macroinvertebrate consumers, altering trophic interactions with potential consequences on mangrove ecosystem processes. Further studies addressing higher trophic levels, such as mangrove fish communities, are needed to elucidate the extent of the effects of seabird nutrient subsidies on tropical coastal food webs and fisheries.

ACKNOWLEDGEMENTS

We thank the Seychelles Islands Foundation for providing administrative and logistical support during the fieldwork, especially Frauke Fleischer-Dogley, Ervin Ally, Elma Balette, Sebastien Cowin, Nikita Pothin, Michelle Jones, Annabelle Cupidon, Guilly Mellie, Anna Koester and Francis Solomon. J.A was supported by a doctoral fellowship from the Reunion Island Regional Council. Funding was provided by the African World Heritage Fund to J.A, PADI Foundation to J.A, and Bertarelli Foundation as part of the Bertarelli Programme in Marine Science to N.A.J.G. Fieldwork and ethical approval was provided by the Seychelles Bureau of Standards (permit number A0157).

AUTHOR CONTRIBUTIONS

Conceptualization: J.A, N.G, S.J, N.B. Methodology: J.A, N.B. Data collection: J.A, C.J. Formal analysis: J.A. Writing (Original Draft): J.A. Writing (Review): N. G, C.J, S.J, N.B.

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SUPPLEMENTAL INFORMATION

Table S1. Number of samples collected by type and site.

	Mangrove leaves <i>Rhizophora mucronata</i>	Epiphytic macroalgae	Sediment organic matter	Littorinid gastropod <i>Littoraria</i> spp.	Sesarmid crab <i>Leptarma leptosoma</i>	Portunid crab <i>Thalamita crenata</i>
Seabird						
S1	8	24	24	24	15	0
S2	8	20	24	24	15	10
S3	8	24	24	24	15	10
S4	8	22	24	24	15	9
S5	8	3	24	24	15	7
No seabird						
N1	8	22	24	24	15	10
N2	8	24	24	24	15	10
N3	8	24	24	24	15	10
N4	8	11	24	24	15	10
N5	8	18	23	24	15	10

Table S2. Mean \pm SD of $\delta^{15}\text{N}$ and normalized $\delta^{13}\text{C}$ values of different components of macroinvertebrate food webs in mangroves with and without nesting seabirds.

	Seabird			No seabird		
	n	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	n	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$
Mangrove leaves <i>Rhizophora mucronata</i>	40	6.43 \pm 2.63	-30.7 \pm 1.33	40	2.74 \pm 3.57	-28.9 \pm 2.77
Epiphytic macroalgae	93	7.98 \pm 1.47	-28.7 \pm 2.0	99	4.21 \pm 2.45	-24.9 \pm 6.71
Sediment organic matter	120	6.34 \pm 0.93	-26.1 \pm 1.46	119	3.34 \pm 1.14	-25.2 \pm 2.97
Littorinid gastropod <i>Littoraria</i> spp.	120	13.5 \pm 4.64	-20.3 \pm 1.40	120	4.45 \pm 3.42	-21.4 \pm 1.32
Sesarmid crab <i>Sesarma leptosoma</i>	75	12.0 \pm 2.16	-20.2 \pm 1.36	75	6.79 \pm 1.47	-20.5 \pm 1.44
Portunid crab <i>Thalamita crenata</i>	36	11.8 \pm 1.09	-15.9 \pm 2.84	50	8.32 \pm 1.62	-15.5 \pm 3.30

Figure S1. Location of sampling sites within mangroves of Aldabra Atoll (Seychelles) in the Western Indian Ocean. Seychelles EEZ outlined (dashed line) and names of Aldabra's four main islands are given. Photos showing (A) nesting lesser frigatebirds and (B) red-footed booby, (C) littorinid gastropods and (D) portunid crab *Thalamita crenata* on Aldabra. Photos © SIF, Jennifer Appoo.

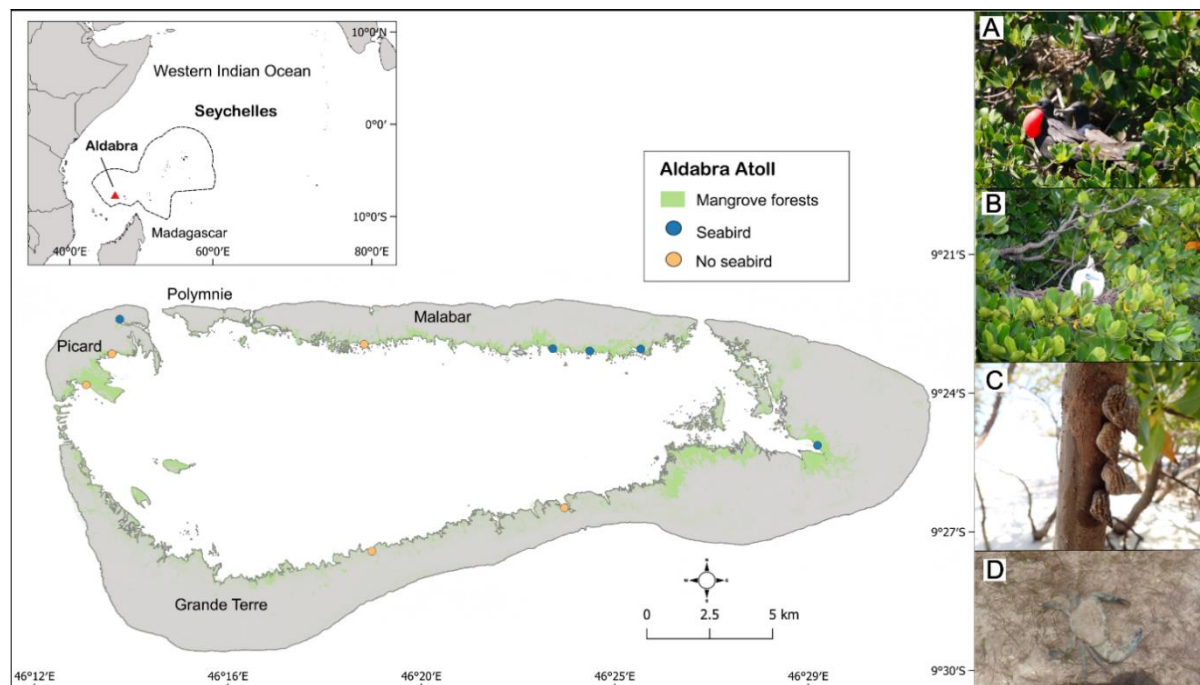


Figure S2. Linear mixed models result for each food web component showing effect size estimates of nesting seabirds on normalized $\delta^{13}\text{C}$. Factor level represented by model intercept (dashed grey line) correspond to nesting seabird presence = yes. Error bars represent 95% confidence intervals around estimates.

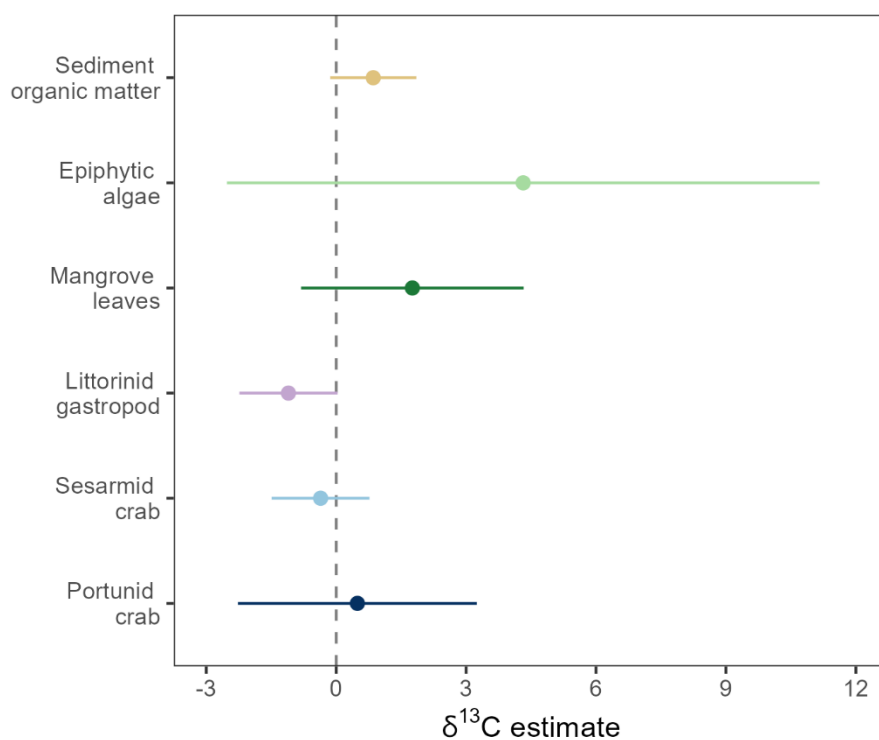
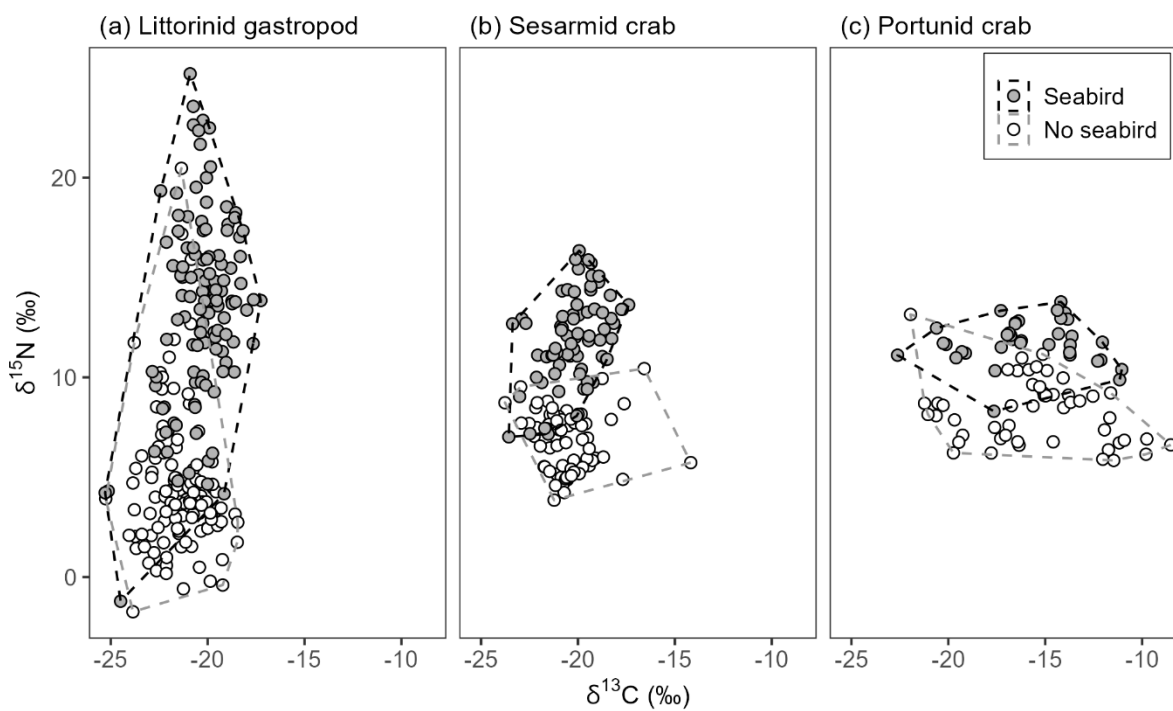


Figure S3. Convex hull area showing the isotopic niche width of macroinvertebrate consumers at seabird and non-seabird sites.



CHAPTER 6

General Discussion

6.1. Overview and key findings

Focussing on the tropical Western Indian Ocean (WIO) seabird assemblage and using seabird islands in Seychelles, the aim of this thesis was to assess the impacts of seabird nutrient subsidies on tropical oceanic islands. To achieve this overarching aim, I explored nutrient dynamics of different components of the seabird subsidy transfer, including the nutrient vector (seabirds), the nutrient subsidy (guano), the nutrient transfer (flow) and the nutrient recipients (impacts), through four main objectives and across four data chapters.

- Objective 1 (nutrient vector): In Chapter 2, I characterized the isotopic signatures of tropical seabirds by examining the drivers of seabird isotopic structure. The results showed distinct spatial and seasonal patterns of nitrogen isotope signatures of seabird colonies from across the tropical WIO, with higher values observed in seabirds breeding at low latitudes and during the austral winter monsoon.
- Objective 2 (nutrient subsidy): Chapters 3 and 4 provide a quantitative and qualitative assessment of tropical seabird guano. I assessed guano isotopic and nutrient concentrations for seabirds breeding on Farquhar and Aldabra atolls, respectively, and estimated their annual nutrient deposition rates. Seabird colonies contributed a total of 86.6 N tonne.yr⁻¹ and 67.2 P tonne.yr⁻¹ on Farquhar, and 41.9 N tonne.yr⁻¹ and 40.9 P tonne.yr⁻¹ on Aldabra. Seabird nutrient deposition on Farquhar was driven by biomass and breeding characteristics, with higher nutrient quantities estimated from sooty tern than red-footed booby and brown noddy colonies.
- Objective 3 (nutrient transfer): To evaluate the pathways of seabird-derived nutrient transfer across the land-sea interface of tropical seabird islands, I examined the flow of seabird-derived nutrient from island to nearshore-marine environments on Farquhar (Chapter 3), and from mangroves to adjacent habitats on Aldabra (Chapter 4). On Farquhar, nutrient transfer from seabird colonies to soil, coastal vegetation and seagrass occurred year-round, regardless of

seabird breeding period. On Aldabra, seabird-derived nutrients were transferred trophically from primary producers to secondary macroinvertebrate consumers, and horizontally from mangroves to adjacent coastal habitats through tidal flow.

- Objective 4 (nutrient recipients): I compared sites with and without seabirds to evaluate the impacts of seabird-derived nutrients on tropical island and coastal habitats and communities. On Farquhar, I examined the influence on nutrient status of island and seagrass habitats (Chapter 3). Seabird-derived nutrients maintained high foliar nitrogen levels in coastal plants year-round, indicating persistent enrichment of island habitats by tropical seabird colonies. On Aldabra, I investigated the effects on mangrove nutrient status and cycling (Chapter 4), and on mangrove macroinvertebrate food web (Chapter 5). Seabird-derived nutrients enrich mangroves and reverse their nutrient limitations. Seabird nutrient subsidies enrich basal food sources of mangrove macroinvertebrate consumers, resulting in larger mangrove crabs. Epiphytic macroalgae were more enriched (higher nitrogen content) compared to mangrove leaves, and comprised higher resource contributions to primary macroinvertebrate consumers at seabird sites.

6.2. Research contributions, context and implications

My thesis has made the following main contributions to seabird nutrient cycling and island-ocean connectivity science:

6.2.1. Ecological indicators and references in tropical seabird systems

Chapter 2 provides an understanding of isotopic dynamics of seabirds in the tropical WIO. The study revealed a latitudinal gradient in seabird isotopic signatures, which has been documented in other predatory fishes, such as tropical tunas and swordfish (Ménard et al., 2007; Lorrain et al., 2015; Zudaire et al., 2015; Dhurmeea et al., 2020), but not previously in seabirds in this region. As marine top predators, seabirds integrate information of food web dynamics and exhibit clear responses to environmental variability, making them powerful bioindicators of marine health and ecosystem changes (Piatt and Sydeman, 2007). By synthesising isotopic compositions of multiple seabird species from 2003 to 2023, we provide essential isotopic references to monitor marine ecosystem status (Gagne et al., 2018) in a region undergoing rapid climatic change (Roxy et al., 2016). More importantly, the results

give preliminary insights that seabird blood nitrogen isotope values could serve as a proxy for monitoring changes in marine environmental conditions in the WIO. Building on this, Chapters 3 and 4 fill information gaps in guano isotopic, macro- and micro-nutrient values for previously unassessed seabird species, allowing estimates of tropical seabird nutrient deposition to be refined and scaled-up at regional or global scales (Otero et al., 2018; De La Peña-Lastra et al., 2022).

6.2.2. Magnitude and scale of nutrient connectivity in tropical seabird islands

My research has quantified the magnitude of nutrient fluxes on tropical seabird islands by assessing local-scale estimates of seabird nutrient deposition rates in Chapter 3 and 4. Seabird nutrient contributions on Goëlettes (Farquhar Atoll; Chapter 3), estimated at 2,421.6 N kg.ha⁻¹.yr⁻¹ and 1,815.3 P kg.ha⁻¹.yr⁻¹, are among the highest estimates for a tropical seabird island (Heron Island, Australia: 587.5 N kg.ha⁻¹.year⁻¹, 118.8 P kg.ha⁻¹.yr⁻¹ [Staunton Smith and Johnson, 1995]; Guarita, Brazil: 1950.5 N kg.ha⁻¹.yr⁻¹; Redonda, Antigua and Barbuda: 173.4 N kg.ha⁻¹.yr⁻¹, Siriba, Brazil: 221.08 N kg.ha⁻¹.yr⁻¹ [Linhares and Bugoni, 2023]). This finding emphasizes the role of seabirds as key nutrient providers and drivers of productivity in nutrient-limited atoll environments.

Mangroves maintain connectivity between terrestrial and coastal habitats such as seagrass and coral reefs. Research on biological connectivity and nutrient flow in mangroves with adjacent habitats has largely focussed on ontogenetic movements of reef fish communities (Buelow and Sheaves, 2015). By tracing the flow of seabird-derived nutrients in Aldabra's mangroves (Chapter 4), my research showed the spatial scale of nutrient connectivity maintained by tropical seabirds, linking oceanic systems, mangroves and adjacent lagoon habitats. In the Indian Ocean, red-footed boobies and frigatebirds can forage at mean maximum distances of 112 km (Trevail et al., 2023) and 944 km (Weimerskirch et al., 2010) from their breeding colonies, respectively. Collectively, this illustrates that biological connectivity facilitated by seabirds in mangroves is far more extensive than fish-facilitated connectivity (Buelow and Sheaves, 2015). Furthermore, the vertical transfer of seabird-derived nutrients within food webs had never been documented previously within mangrove ecosystems. My research showed the transfer and incorporation of seabird-derived nutrients across multiple trophic levels, from primary producers to secondary macroinvertebrate consumers. By demonstrating vertical nutrient connectivity, this study showed how seabirds exert bottom-up control in mangrove food webs.

6.2.3. Influence of seabird nutrient subsidies on tropical coastal habitats and communities

Seagrass and mangroves are essential components of the coastal ecosystem mosaic, but have been under-represented in seabird nutrient subsidy research, which has focussed primarily on coral reefs so far. Moreover, seabird nutrient enrichment of seagrass and mangroves had previously only been assessed in species found in Caribbean and Central America (Herbert and Fourqurean, 2008; Adame et al., 2015; McFadden et al., 2016). My research is the first to examine seabird connectivity links in these habitats in the Indo-Pacific region, and specifically on the influence of seabird-derived nutrients on the seagrass *Thalassodesmion ciliatum* (Chapter 3) and the mangrove *Rhizophora mucronata* (Chapter 4). This research can contribute to understanding seagrass and mangrove species-specific responses to seabird nutrient subsidies.

Chapter 5 documents the response of mangrove gastropods and crabs to seabird nutrient enrichment, revealing potential consequences on mangrove nutrient cycling. This study showed that seabirds reduced the contribution of mangrove leaves to macroinvertebrate herbivore diet, contrasting with Onuf et al. (1977) who showed that seabird-derived nutrients increased insect herbivory in Florida's mangrove. This demonstrates the variability in mangrove herbivore responses to seabird nutrient subsidies. In addition, by enriching basal resources, seabirds increase the size of mangrove crabs, which are key components of mangrove fisheries. This indicates how seabirds can contribute to mangrove-derived services, and can help refine the economic valuation of seabird nutrient contributions in tropical coastal ecosystems to support seabird and mangrove conservation (Plazas-Jiménez and Cianciaruso, 2020).

Low-lying tropical islands, such as atolls, are highly vulnerable to global climate change impacts such as sea-level rise and increased storm surges. On atolls where they nest, seabirds promote healthy native vegetation communities, which stabilize sediment and promote sediment accretion processes (Steibl et al., 2023). Chapter 3 demonstrated that tropical seabirds provide nutrients to coastal vegetation year-round, while Chapter 4 showed that mangrove-nesting seabirds promote healthy mangrove forests. Mangroves play a critical role in protecting coastlines from erosion and storm surges. Collectively, these findings further demonstrate how tropical seabird communities contribute to

sediment accretion and atoll stability, thereby enhancing atoll resilience to global change (Steibl et al., 2023).

The research in this thesis also has direct practical implications for policy and conservation management:

6.2.4. Sooty egg tern harvesting in Seychelles

Seychelles hosts over three million sooty terns, which have been harvested commercially for their eggs over the past century (Feare et al., 2007). This exploitation is highly unsustainable, with recent counts showing population declines in all of Seychelles' sooty tern colonies since the 1960s (ICS unpubl. data) and research predicting the extinction of harvested colonies within the next few decades (Inch et al., 2024). Chapter 3 estimated nutrient quantities delivered by sooty terns on Farquhar Atoll, showing that due to their high biomass, sooty terns are an essential tropical seabird species in nutrient provisioning. This highlights their important role in subsidizing nutrient-poor atoll environments and provides key data to predict the potential ecological impacts of colony extinctions on tropical seabird islands and nearshore environments. This study provides critical evidence to support and extend (ideally permanently) the current ban of sooty tern egg harvesting in Seychelles (Skerrett, 2021).

6.2.5. Invasive mammal predator eradication on Aldabra

Studies comparing seabird islands with and without rats are offering unprecedented insights into the benefits of invasive mammal eradications for whole-ecosystem restoration and timescale of ecosystem recovery (Benkwitt et al., 2021; Graham et al., 2024). Seabird populations on Aldabra are heavily impacted by introduced rats and cats, and an eradication is being planned (Harper et al., 2015). Chapters 4 and 5 show that seabird populations in mangrove areas promote good nutrient status and health of mangroves, enhancing diverse mangrove functions and services. These findings provide support for the eradication and suggest that mangrove ecosystem health and services can now be added to the list of expected positive outcomes. Moreover, this research documents seabird-derived nutrient levels across Aldabra's mangroves, providing essential pre-eradication nutrient baselines to assess ecosystem-level changes post-eradication (Pascoe et al., 2021).

6.3. Specific recommendations

From the research presented in this thesis, 11 specific recommendations for management and conservation of tropical seabird islands can be derived (Table 6.1). These recommendations address research (recommendations 1, 2 and 9), policy (3 and 10), monitoring (7 and 8), and conservation (4, 5, 6, 10 and 11) and are assigned a prioritisation level to guide implementation. Seabird nutrient subsidies are impacted by human activities at various stages of the subsidy pathway (c.f. Table 1.1). Hence, for management and conservation actions to be effective, it is essential to target efforts at different stages, from the nutrient donor system (open ocean), to the nutrient transfer pathway and the nutrient recipient system (seabird islands; Buckner et al., 2017).

Table 6.1. Policy, research, monitoring and conservation recommendations for tropical seabird islands based on evidence presented in this thesis. Regional and national relevance refers to seabird islands in the tropical WIO and Seychelles, respectively. Three stages of subsidy pathway are considered: donor system (open ocean), transfer pathway and recipient system (seabird islands).

Relevance	Recommendation	Explanation	Priority	Subsidy pathway stage
Global	1. Further research on influence of seabird nutrient subsidies on tropical islands, particularly on coastal ecosystem mosaics.	<p>- Our understanding of the scale of influence of seabird nutrient subsidies in tropical systems is still in its infancy. In mangroves, further research should quantify the impacts of seabird nutrient enrichment on macroinvertebrate biomass and functions (e.g., leaf and litter consumption rates, propagule and seedling predation, sediment biogeochemistry) to understand consequences on mangrove forest structure (Cannicci et al., 2008).</p> <p>- The role that seabird-derived nutrients play in mangrove-to-seagrass-coral reef connectivity is not yet understood (Chapter 4 & 5). Biologging of reef communities could be used to assess how they use mangrove habitats with nesting seabirds and quantify their spatial movements to adjacent seagrass and coral reefs, and to determine their ecological responses to seabird-derived nutrient enrichment.</p> <p>- The impacts on seagrass ecosystems remain under-investigated (Chapter 3). Research should explore how seabird-derived nutrients influence seagrass</p>	High	Recipient system

Relevance	Recommendation	Explanation	Priority	Subsidy pathway stage
		<p>morphological and physiological properties (Thomsen et al., 2022) and seagrass-derived services, such as carbon sequestration.</p> <p>- Seabird-derived nutrients can be exported beyond lagoon or atoll environments and have been detected up to 300m from shore (Benkwitt et al., 2021). Remote sensing technologies offer opportunities to document impacts at scale, e.g., to measure mangrove forest chemistry and map extent of nutrient flows out to sea.</p> <p>- Feedback loops whereby seabirds support their own populations should be explored. For example, by increasing marine productivity and fish biomass in nearshore-marine ecosystems, seabirds can increase prey availability for nearshore-foraging seabirds. Additionally, some pelagic fish use coastal habitats as nurseries. By promoting healthy coastal habitats, seabirds can indirectly influence their pelagic prey populations and foraging opportunities (Unsworth and Butterworth, 2021).</p>		
	<p>2. Quantify impacts of commercial fisheries on tropical seabird</p>	<p>Seabird nutrient cycling starts with seabirds foraging in the open ocean. Research efforts have focussed on understanding nutrient dynamics around breeding colonies and land-based threats to seabird populations. Consequently,</p>	High	Donor system

Relevance	Recommendation	Explanation	Priority	Subsidy pathway stage
	populations and nutrient flow.	our knowledge of factors affecting nutrient flow in marine environments, e.g., commercial fisheries, are comparatively limited. Industrial fisheries negatively impact seabirds via bycatch, competition and discards, but remain poorly studied for tropical seabirds. Biologging and predictive modelling are needed to assess seabird-vessel interactions and predict the consequences of depleted sub-surface predators and forage fish in tropical marine systems (Sydeman, 2017; Votier et al., 2023; Schoombie et al., 2024), to understand the impacts on tropical seabird populations and nutrient subsidies.		
	3. Develop IUCN Regional Red List Assessments for sooty terns.	Substantial long-term declines in sooty tern populations have been recorded in multiple oceanic regions, prompting calls for a re-evaluation of the global extinction risk of sooty terns, currently classified as 'least concern' (Feare et al., 2007; Hughes et al., 2017). Given the pan-tropical distribution of sooty terns, it's important to consider regional assessments, such as Regional Red Lists, to gain a more nuanced understanding of their conservation status and trends within specific ocean basins. Regional evaluations not only offer a more fine-scale insight into the species' situation, but also provide leverage for conservation policies at the local level, such as harvesting regulations (Chapter 3).	Low	NA

Relevance	Recommendation	Explanation	Priority	Subsidy pathway stage
Regional	4. Eradicate invasive alien predators from WIO seabird islands.	<p>Invasive alien predators, such as mice, rat, and cats, are among the biggest land-based threats to seabird populations, and occur widely across seabird islands in the tropical WIO (e.g., Aldabra, Chapter 4; Russell et al., 2016).</p> <p>Eradication of invasive alien predators leads to recovery of seabird populations and restoration of seabird-derived nutrient flows, resulting in widescale recovery of ecosystems, their functions and resilience (Graham et al., 2024; Dunn et al., 2024). Therefore, removing invasive alien predators and implementing biosecurity measures on tropical seabird islands are crucial actions (Russell and Holmes, 2015) and are highly effective climate adaptation strategies (Kappes et al., 2021).</p>	High	Recipient system
	5. Restore native terrestrial vegetation and mangroves on WIO seabird islands.	<p>Terrestrial habitats on many islands in the WIO consist of abandoned coconut plantations, which support few breeding seabirds (e.g., North Island, Farquhar Atoll, Chapter 3; Carr et al., 2021a). Rehabilitation of abandoned coconut plantations to native vegetation provides seabird breeding habitat and supports recovery of seabird populations and their nutrient subsidies (Hart et al., 2022). Similarly, mangrove restoration is likely to enhance seabird populations.</p> <p>Predictions shows that restoration of terrestrial native vegetation, following the</p>	High	Transfer

Relevance	Recommendation	Explanation	Priority	Subsidy pathway stage
		removal of invasive predators, maximizes the potential for seabird island ecosystem recovery (Carr, et al., 2021; Dunn et al., 2024). Moreover, restoration of terrestrial native vegetation, including mangroves, contribute to sediment accretion processes and stability of low-lying tropical islands (Steibl et al., 2023).		
	6. Reduce fishing quotas of industrial tuna fisheries.	Many tropical seabirds feed in association with surface-dwelling tunas during their foraging activities. Tuna drives seabird prey to the surface, making them available for seabirds (Jaquemet et al., 2004). Industrial fisheries in the WIO, dominated by purse-seiners and long-liners, primarily target tuna and tuna-like species. These tuna stocks have been consistently overfished and are nearing collapse (Heidrich et al., 2023), compromising seabird foraging opportunities and their nutrient fluxes. Reducing tuna fishing quotas will improve foraging conditions for seabirds (Ensanyar-Volle et al., 2023) while maintaining the sustainability and economic benefits of tuna fisheries for WIO nations, such as Seychelles.	High	Donor system
	7. Monitor seabird populations regularly.	Seabird population censuses are irregular on many remote or uninhabited islands in the WIO, leading to outdated population estimates or undocumented populations (Carr et al., 2021b). Accurate and regularly updated seabird	Medium	Transfer

Relevance	Recommendation	Explanation	Priority	Subsidy pathway stage
		<p>population estimates allow the documentation of changes following conservation actions, and improved estimates of nutrient deposition quantities (Chapter 3 & 4), which are important for assessing the impacts of seabird-derived nutrients (Votier et al., 2024). In addition, updated population estimates and distributions are needed to support IBA designations, which help target seabird conservation efforts effectively (Carr et al., 2021b; Skerrett, 2021).</p>		
	<p>8. Monitor seabird-derived nutrients to assess ecosystem change and recovery.</p>	<p>Nitrogen stable isotopes serve as a key ecological indicator to assess ecosystem-level changes of seabird islands (Pascoe et al., 2022). In the context of management actions, such as invasive predator eradications, monitoring seabird-derived nutrients before and after eradication is essential to determine whether whole-ecosystem recovery is occurring. This allows recovery goals to be evaluated, helps determine the timescales involved, provides feedback to guide management decisions, and can detect unforeseen outcomes (Benkwitt et al., 2021; Pascoe et al., 2021). Managers of seabird islands should therefore incorporate long-term monitoring of nitrogen stable isotopes (e.g., of a widespread taxon for each ecosystem considered) as an indicator for ecological</p>	<p>Medium</p>	<p>Recipient system</p>

Relevance	Recommendation	Explanation	Priority	Subsidy pathway stage
		change, following best practices and carefully designed field sampling protocols (Pascoe et al., 2022).		
	9. Strengthen collaborations for seabird island research and management.	Networks focussing on seabird research and island management, such as the Seychelles Seabird Group and the Indian Ocean Seabird Group, already exist in the region. These practitioner networks provide useful platforms to strengthen collaborations and maximise efforts and resources to protect and understand the functioning of seabird islands, for example; to develop collaborative studies, standardize monitoring protocols, extend monitoring coverage, share lessons learned and best practices, and advance seabird nutrient subsidy research (Burt et al., 2021).	Low	NA
National	10. Manage and protect seabird islands.	Logistical and economic challenges hinder the accessibility and management of remote seabird islands in island archipelago countries such as Seychelles. On unmanaged islands, poaching is a major threat, contributing to extinction of seabird colonies (Feare, 1978; Feare et al., 2007). Solutions that combine ecotourism with environmental protection can yield positive outcomes (Skerrett, 2021). Islands engaged in ecotourism activities support the permanent presence of field biologists, enabling surveillance of seabird colonies and providing	High	Recipient system

Relevance	Recommendation	Explanation	Priority	Subsidy pathway stage
		<p>monitoring and research opportunities (e.g., Farquhar Atoll, Chapter 3).</p> <p>Furthermore, alongside invasive alien species control, seabird re-establishment measures such as social attraction can be trialled at abandoned colonies to actively restore seabird populations and their nutrient fluxes (Feare et al., 2015).</p>		
	<p>11. Generate public awareness and sensitization on importance and role of seabirds.</p>	<p>To effectively protect seabird colonies, national-level sensitization is essential. In Seychelles, extensive public education programmes have been instrumental in sea turtle conservation, reversing centuries of exploitation. Similarly, dedicated environmental education initiatives are necessary to raise awareness about the significance of seabirds for tropical oceanic islands, emphasizing the harmful consequences of seabird poaching, invasive species and industrial fishing.</p>	Medium	NA

6.4. Concluding remarks: Conserve connectivity

Islands are threatened hotspots of biological, cultural and geophysical diversity (Kueffer and Kinney, 2017) and prioritizing their conservation is imperative to safeguarding global biodiversity and fulfilling humanity's goals for a sustainable future (Fernández-Palacios et al., 2021). Mobile animals are crucial for nutrient transport across ecosystem boundaries, with seabirds playing a particularly essential role in transferring nutrients from ocean to island environments (De La Peña-Lastra, 2021). This thesis explores the dynamics of seabird nutrient cycling in tropical oceanic islands. It investigates the functional role of seabirds on islands the tropical Western Indian Ocean, revealing seabirds as ecological indicators of marine environments in this region, as key nutrient providers in their breeding islands, as connectors of ocean-atoll-coastal ecosystems, as drivers of productivity of atoll habitats and communities, and as contributors to ecosystem-derived services of tropical coastal systems. Ultimately, this research furthers our understanding of the ecological and socio-economic importance of seabirds in tropical oceanic islands. Insights from this thesis underscore the importance of incorporating nutrient connectivity linkages into seabird island management practices. However, for management and conservation efforts to be most effective, it is important to implement actions at various stages of the seabird nutrient subsidy pathway. Connectivity underpins ecological resilience (Bernhardt and Leslie, 2013; Timpane-Padgham et al., 2017), so restoring and preserving nutrient connectivity in tropical seabird islands is critical for nature recovery in a changing climate. Further research should explore the roles of other key mobile animal groups involved in nutrient translocation to and within island and marine environments, such as sea turtles, crabs and reef sharks, to obtain a comprehensive understanding of animal-mediated nutrient cycling in tropical oceanic islands.

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