Impacts of Invasive Species on Tropical Seabird Populations on Tetiaroa Atoll, French Polynesia

Eve McKinley Hallock

A thesis
submitted in partial fulfillment of the
requirements for the degree of

Master of Science

University of Washington
2025

Committee:

Sarah J. Converse
Beth Gardner
P. Dee Boersma

Program Authorized to Offer Degree:
School of Environment and Forest Sciences

University of Washington

Abstract

Impacts of Invasive Species on Tropical Seabird Populations on Tetiaroa Atoll, French Polynesia
Eve M. Hallock

Co-Chairs of the Supervisory Committee:
Sarah J. Converse
USGS Washington Cooperative Fish and Wildlife Research Unit
School of Aquatic and Fisheries Sciences & School of Environmental and Forest Sciences
Beth Gardner
School of Environmental and Forest Sciences

Seabird populations provide crucial ecological services to their environments, yet their populations are declining globally due to invasive species, climate change, habitat loss and degradation, over-fishing, and pollution. Although they are keystone species and bio-indicators of coral island health, tropical seabirds remain understudied. Their reproductive success is influenced by an array of biotic and abiotic factors, particularly in coral island (atoll) ecosystems where low-lying nesting habitats are vulnerable to anthropogenic and environmental disturbances. In Chapter 1, we modeled daily nest survival of Brown Boobies (*Sula leucogaster*) on Tetiaroa Atoll, Society Islands, French Polynesia, using a Bayesian framework. We analyzed data from 903 nests monitored between 2021 and 2024 across three motus (islets) that differed in exposure to invasive rats before and during a rat-eradication effort. Our daily nest survival model included motu-specific intercepts, a before-after-control-impact design to assess effects of rat suppression, and covariates representing ocean swell height, El Niño-Southern Oscillation conditions, colonial nest density, and an avian disease outbreak event. We found no evidence that rat presence negatively affected daily nest survival, which may indicate that rats are less of a threat to Brown Booby reproduction when compared to other seabird species. Higher ocean swells were associated with lower daily nest survival probability, while positive Southern

Oscillation Index values, indicative of La Niña conditions, were associated with higher daily nest survival probabilities. These findings suggest that oceanic variability, rather than rat presence, was the dominant driver of nest success during the study period, suggesting the importance of accounting for risks posed by a changing climate and rising sea levels when developing seabird conservation strategies on atolls. In Chapter 2, we investigated terrestrial habitat associations of four seabird species on Tetiaroa, the Red-footed Booby (*Sula sula*), Brown Noddy (*Anous stolidus*), Black Noddy (*Anous minutus*), and White Tern (*Gygis alba*). We conducted 824 avian point counts with multiple observers at 110 sites between 2022 and 2024. A variety of vegetation variables were measured at each site, including the abundance of mature native broadleaf trees and previously cultivated coconut palm (*Cocos nucifera*), which is considered invasive and may be harmful to atoll ecosystem functioning. We fit species-specific *N*-mixture models to the avian point count data, using a zero-inflation Poisson distribution to model abundance, and habitat variables in both the zero-inflated and abundance components. Estimated Red-footed Booby abundance was higher in areas closer to the shoreline, with greater amounts of the coastal shrub, *Heliotropium arboretum,* and native broadleaf trees including *Pisonia grandis*, and in areas with more open space in the herbaceous layer. Abundance was lower with greater amounts of invasive *Cocos nucifera* trees. We found estimated abundance of Brown Noddies was lower in areas with greater amounts of *Pandanus tectorius* trees. Estimates of Black Noddy abundance and probability of White Tern presence were higher with greater amounts of native broadleaf trees. Our findings provide information on habitat associations of these seabird species, which can be used to inform terrestrial restoration projects on Tetiaroa and other atolls.

Table of Contents

List of Tables

List of Figures

Acknowledgements

This thesis would not have been possible without my graduate advisors, Drs. Beth Gardner and Sarah Converse. I am grateful to have been a member in both of their labs these past years, and I thank them both for their patience and for introducing me to and guiding me in the world of quantitative ecology and model building. They have spent countless hours on all aspects of these projects, and I will always be impressed by how much they do in a day in their lives as professors, researchers, and managers. My committee member, Dr. Dee Boersma, has been nothing but welcoming, supportive, and inspiring, and the world of seabird conservation owes so much gratitude to her.

I am lucky to have met the most incredible scientific role models while living on Tetiaroa. Dr. Jayna DeVore was always there when I needed a mentor or when I needed to laugh, and I cannot begin to describe the extent of what I have learned from her. Jayna, I will always cherish our time walking the motu together, and just know that I tell everyone I meet about cane toads, leeches, Tuamotu Sandpipers, sea hares, crabs, amongst other creatures because of you. The research and mentoring that she and Dr. Simon Ducatez are doing in the field of conservation ecology revived the hope in me that had been waning. Dr. Sebastian Steibl is an endless source of inspiration, motivation, and advice. He raises the bar for the study of atoll ecology with the most impressive breadth of literary knowledge, passion for understanding places' histories and futures, and exploration of every abiotic and biotic pathway in a system. I thank Dr. Jean-Yves Hiro Meyer for his mentorship in avian ecology and botany of Polynesia. No one is more knowledgeable or passionate about the conservation of these islands than him. Thank you for identifying every plant that stumped me, (even grasses and freshly germinated seedlings), for

showing me the Reed Warblers and orchids, and for making my birthday in the field special. Thank you all for showing me who an ecologist should be.

I also want to thank the fellow Master's students with whom I shared Tetiaroa's motu and ecostation: Miléna, my partner in crime who kept me grinning and laughing, Solène, the sweetest person on any side of the Pacific, my roommate Antoine, Charlotte, Sara, Mathilde, Julie, and Clementine. Meeting them and so many others made it all worth doing: Tihoni, Lusiano, Antonin, Paola, Joan, Anne-Laure, Teva B., Margaux, Guillaume, Arnaud, Kahaina, Théo, Mareva, Teva S., Margot, Tuterai, Vairupe, Virginie, Vahine, Romain, Hina, Anaïs, Gustave, Temakehu, Herehia, Della, and Tumi. Thank you to those at SOP Manu and Biosécurité PF who shouldered my avian disease outbreak worries and who corresponded with me through the darkest period of my work. Baudouin Des Monstiers, Miléna Philip, and Solène Fabre Barroso led incredible rat and yellow crazy ant eradication crews, and I thank all the people who spent long hours macheteing and hauling gear through the forest to make these conservation plans happen. Thank you most of all to Hinano and Frank Murphy, for their generosity, support, interest, and never-ending passions in furthering science and culture. Māuruuru roa. Thank you all for making Tetiaroa feel like my home; it broke my heart to leave. Te hina'aro nei au e na'amāuruuru ia outou pa'atoa nō tō outou mana'o turu.

I must also acknowledge the first place and people who taught me about atolls. Sarah Glover and Dr. Alex Wegmann welcomed me to Palmyra Atoll in 2021, which truly changed my whole life. Thank you for introducing me to the most mesmerizing *Pisonia grandis* forest, to the same tropical seabirds I write about now, to the reef, coconut crabs, eels, mantas, Bristle-thighed

Curlews, and so much more. I hope you know that I use everything you taught me, and Palmyra is still always on my mind.

Back on the continent, I cannot say enough about my family and friends who kept me going, especially Emelia, Janne, Aubrey, Anya, and my parents. I would not have gotten very far without them. Thank you to my forestry school cohort in Seattle: Marcela, Nate, Fern, Leo, Dylan, Amelia K.-G., Lety, and more, without whom my life would have been much grayer. They are the most driven, friendly, caring, intelligent, and empathetic biologists, and I am so excited to see what they all do next. When I was feeling nervous and alone at Pacific Seabird Group Conferences, I met supportive mentors like Kim Nelson and Doug Forsell and kind students like Carina, Cassidy, and Lauren. Thank you all for encouraging me to stay the course when I needed to hear it most.

I had a diligent team of undergraduate interns who spent a total of 1,182 hours processing over 15 million game camera photos of 294 Brown Booby nests. I thank Zara, Mads, Yinuo, Alex, Alexander, Amit, Ananya, Asta, Avery, Boricia, Bridget, Charli, Christina, Daniel, Elijah, Emily, Erin B., Erin W., Ezra, Gabe, Iris, Isabel, Jack, Jessica, Joaquin, Juliana, Katherine, Leah, Leo, Lily, Lucia, Luciana, Maia, Megan C., Megan F., Mikaela, Moses, Netanya, Nicole, Niko, Rachel, Sofia B., Sofia C., Sophia, Suzu, and Theo. Through the vast tediousness, I hope they enjoyed watching the daily and nightly lives of these birds as much as I did, and graciously ignored any unflattering photos of me captured by the nest cameras. Thank you most of all to Alexandra Coenen, who spent many hours helping me compile, convert, and correct the resulting outputs. Alex, I loved our mini seabird adventures, both on Protection Island and Tetiaroa, and I know your career in avian ecology will be so bright.

I te mau manu o te moana, te fenua, e te ra'i. Finally, I would also like to thank the birds themselves, before they get reduced to data rows run through a machine. In his book, The Seabird's Cry: The Lives and Loves of the Planet's Great Ocean Voyagers, Adam Nichols described seabirds as "the only animals at home on the sea, in the sea, in the air, and on land"; it will always be an honor to share any of their realms, if only fleetingly[1]. I had never met a biologist of any kind until 2017, on an island in the Gulf of Maine, Drs. Liz Craig and Kristin Covino inspired me in more ways than they will ever know. It was there that I first understood what it is like to walk through a dense seabird colony. This has been described as witnessing nature as its rawest and most brutal form – piercingly loud, all-encompassing pain and chaos occurring in every direction, overwhelming the senses and drowning out the elements. While this is true, these places are also full of such intensely beautiful life. The concept that first drew me to field biology from the humanities was Jakob von Uexküll's theory of *Umwelt*, the species-specific sensory manner of perceiving the subjective world[2]. In a seabird colony, it is easy to find bold examples. One can never feel or know, but can still witness every sound, smell, and sight of another species' cycle of life. In 1697, the pirate, William Dampier, described the Booby as "Water-fowl, somewhat less than a Hen,…her Feet are flat like a Ducks feet. It is a very simple Creature, and will hardly go out of a Man's way"[3]. This description makes it clear to me that he,

---

[1] Nicolson, A. (2018). *The Seabird's Cry: The Lives and Loves of the Planet's Great Ocean Voyagers*. Henry Holt and Co.

[2] von Uexküll J. (1934/2010). *A Foray into the Worlds of Animals and Humans with a Theory of Meaning*. Minneapolis, MN: University of Minnesota Press.

[3] Dampier, W. (1697). *A new voyage round the world*. London: James Knapton.

like most people, never spent time with them as individuals, day after day, for months on end, watching them build their nests, raising their young, catching their fish, greeting one another with call and dance, enduring sickness and loss, commuting to and from the sea. It is true that certain birds never flushed due to my presence, but perhaps this can be explained by a curious, or protective, or even trusting nature. Since I believe that *Umwelt* is central to living beings, I cannot attest to understand the complexities of a seabird's mind. I can say that I am truly glad to have met and known each of them in the way that I did, beyond lenses of data collection or birdwatching, but as other living creatures with unique personalities, and lives far from simple.

Ia maita'i te tai'ora'a.

Chapter 1: Ecological Dynamics of Seabird Populations On Tetiaroa Atoll, French Polynesia

1.1 Introduction

Seabirds are one of the most threatened groups of vertebrates globally, due to a variety of anthropogenic and environmental factors (Dias et al., 2019). While seabirds forage in marine environments, they require land for nesting and roosting, and in turn provide a critical ecosystem service. Areas near seabird colonies are more productive both above and below the waterline due to deposition of seabird guano (Graham et al., 2018). This fertilization can promote coral and algae growth and, in some cases, serve as a primary nutrient source for terrestrial vegetation (Anderson & Polis, 1999; Kurle et al., 2008). Declines in seabird populations can alter this nutrient cycling, causing cascading effects through both the terrestrial and marine systems (Benkwitt et al., 2021; Graham et al., 2018).

Given threats to seabirds, both on land and at sea, a better understanding of seabird ecology is critical to assess status and evaluate potential conservation actions. In the tropical Pacific, relatively little is known about seabird populations. There are existing archaeological records of bones and extensive cultural resources across the Pacific that are helpful for understanding extant and historical species compositions (Steadman, 1989; Thibault & Cibois, 2017). However, long-term data on behavior, breeding ecology, demography, range, diet, and threats are time intensive and expensive to collect due to the remoteness of many islands. Sparse terrestrial surveys have been completed, and even fewer at-sea surveys have been conducted. Overall, the lack of long-term, intensive ecological studies of seabirds in this region results in a substantial gap in our knowledge.

Islands in the tropical Pacific, like islands around the world, are experiencing major transformations in their ecosystems and economies due to climate change, sea-level rise, and other anthropogenic disturbances (Steibl et al., 2024a). Atolls (low-lying, ring-shaped series of coral islets) are especially vulnerable to certain of these disturbances and have been notably impacted by invasive species and habitat degradation (Young et al., 2017; Steibl et al., 2024a). Although atolls are global biodiversity "cool spots" for most taxa, they are hotspots for tropical seabirds (Thaman, 2008; Steibl et al., 2024b). Over 50 seabird species breed across at least 200 islands in the tropical Pacific, with an estimated 31.2 million individuals nesting on Indo-Pacific atolls, which accounts for ~25% of all tropical seabirds in the world (Berr et al., 2023; Steibl et al., 2024b).

The overarching goal of my thesis is to contribute to a better understanding of the ecology of seabirds in the tropical Pacific to improve future conservation efforts. My work is centered on Tetiaroa, a coral atoll in the Society Islands of French Polynesia. Tetiaroa, like many islands, was invaded by rats, including black (*Rattus rattus*) and Polynesian (*Rattus exulans*) rats (Figure 1.1). An effort to eradicate rats from the atoll provides an important backdrop for my thesis research, though rats are by no means the only challenge that seabirds face on Tetiaroa. In Chapter 1, I describe an effort to better understand drivers of hatching success in Brown Boobies (*Sula leucogaster*), a large, ground-nesting seabird which is the only ground-nester that continued to nest in areas of Tetiaroa invaded by rats. Second, I investigated effects of habitat structure on intensity of use by four additional seabird species: Red-footed Boobies (*Sula sula*), Black Noddies (*Anous minutus*), Brown Noddies (*Anous stolidus*), and White Terns (*Gygis alba*). These species are either exclusively (Red-footed Boobies, Black Noddies, White Terns) tree nesters or nest both on the ground and in trees (Brown Noddies) and thus provide context to understand other threats to atoll ecosystems, such as the loss of native forests.

1.2 Study Site

Tetiaroa Atoll, a small (3,366 ha) coral atoll in French Polynesia (17°00′S, 149°34′W), situated 50 km north of Tahiti and Moʻorea, constitutes one of the best protected reserves in the Society Islands. It has 12 motu (islets) of varying sizes and habitats and one main lagoon in the center (Figure 1.1). Mā'ohi navigators were likely the first to discover the atoll around the 11th century A.D., along with the nearby high islands of Tahiti and Moʻorea (Molle unpublished, 2022). For several centuries thereafter, it was primarily used by high status groups from the Society Islands for various religious and exclusive social practices, with a resident population fluctuating in the hundreds and possibly reaching a maximum of 3,000 (Molle unpublished, 2022). In the 1760s, Europeans arrived on Tahiti during the Pōmare dynasty, the last reigning line of monarchs who controlled most of what is now French Polynesia, including Tetiaroa. In 1904, Dr. Johnston Walter Williams established a copra plantation on Tetiaroa, clearing native forest on the seven largest motu to plant coconut palm (*Cocos nucifera)* for coconut oil production, resulting in the monoculture zones that remain today (Molle et al., 2019). In the 1960's, the American actor Marlon Brando purchased Tetiaroa and began his development of the atoll, which resulted in the creation of the Brando Resort on Onetahi, and a nature reserve encompassing the other 11 motu.

The atoll's vegetation was mapped by Marie-Hélène Sachet and Francis Raymond Fosberg, updated by Jean-François Butaud, and remapped using lidar (light detection and ranging) methods by Benoit Stoll in 2017 (Sachet & Fosberg, 1983; Butaud, 2006; Stoll et al., 2023). Vegetative habitats include two main forest types: native forest dominated by either *Pisonia grandis* or *Pandanus tectorius* with secondary species such as *Guettarda speciosa* and *Cordia subcordata,* and former interior copra plantations dominated by invasive *Cocos nucifera* (Stoll et al., 2023). Coastal vegetation often lines the motu perimeters, and includes *Heliotropium arboreum, Pemphis acidula, Suriana maritima,* and *Scaevola taccada*. *Casuarina equisetifolia* and *Calophyllum inophyllum*, tree species introduced by early voyagers, are also scattered throughout the atoll (Sachet & Fosberg, 1983).

As has occurred on many islands, several biological invasions have occurred on Tetiaroa (Figure 1.1; Russell et al., 2011). Polynesian rats (*Rattus exulans*) were likely spread by Polynesian voyagers to the Society Islands by 600 AD and were introduced to Tetiaroa at least 400 years ago (Atkinson, 1985). Despite their smaller size, they have been recorded as predators of large seabirds such as Great Frigatebirds (*Fregata minor*) and Laysan Albatross (*Diomedea immutabilis*) (Atkinson, 1985). Black rats (*Rattus rattus*) are larger than Polynesian rats, and were likely brought to the atoll by Europeans during the copra farming period up to 100 years ago. Both rat species, along with Norway rats (*Rattus norvegicus*), are thought to be responsible for the extinctions of Tahitian Rail (*Rallus pacificus*) and Tahitian Sandpiper (*Prosobonia leucoptera*) across the Society Islands (Atkinson, 1985; Thibault, 1973), and both Polynesian and black rats are potential predators of breeding seabirds on Tetiaroa (Russell et al., 2011). Cats (*Felis catus*) were introduced to Tetiaroa in an attempt to control rats (Thibault, 1976) and were removed by 2009. Yellow crazy ants (*Anoplolepis gracilipes*) were likely introduced during hotel landscaping around 20 years ago.

A large-scale rat eradication effort, led by Island Conservation and Tetiaroa Society personnel, has gone through a multitude of stages. In 2009, a rat eradication was attempted on the inhabited motu, Onetahi, and in 2018, rats were eradicated from Reiono (Samaniego et al., 2020), home to the remaining native *Pisonia grandis* forest. The most extensive atoll-wide round of rodenticide was deployed from June to July 2022 (Ringler et al., 2023). Given the documented negative effects of rats on seabird reproductive success globally, rats are predicted to have impacts on ground-nesting seabird species, such as terns and noddies (family Laridae), and potentially the ground-nesting Brown Booby on Tetiaroa (Harper & Bunbury, 2015; Jones et al., 2008).

1.3 Literature Cited

Anderson, W. B., & Polis, G. A. (1999). Nutrient fluxes from water to land: seabirds affect plant nutrient status on Gulf of California islands. *Oecologia*, 118, 324-332.

Butaud, J.-F. (2006). Inventaire fl oristique et défi nition des enjeux de conservation de l'atoll de Tetiaroa. Direction de l'Environnement, Papeete.

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

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

Dias, M. P., Martin, R., Pearmain, E. J., Burfield, I. J., Small, C., Phillips, R. A., Yates, O., Lascelles, B., Borboroglu, P. G., & Croxall, J. P. (2019). Threats to seabirds: A global assessment. *Biological Conservation*, *237*, 525–537. https://doi.org/10.1016/j.biocon.2019.06.033

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

Jones, H. P., Tershy, B. R., Zavaleta, E. S., Croll, D. A., Keitt, B. S., Finkelstein, M. E., & Howald, G. R. (2008). Severity of the effects of invasive rats on seabirds: a global review. *Conservation Biology*, *22*(1), 16-26

Kurle, C.M., Croll, D.A., Tershy, B.R. (2008). Introduced rats indirectly change marine rocky intertidal communities from algae- to invertebrate-dominated, *Proc. Natl. Acad. Sci.* U.S.A. 105 (10) 3800-3804, https://doi.org/10.1073/pnas.0800570105

Molle, G., Hermann, A., Lagarde, L., & Stoll, B. (2019). The Long-Term History of Teti'aroa (Society Islands, French Polynesia): New archaeological and ethnohistorical investigations. *Research Report*, *10*(2).

Ringler, D., Griffiths, R., Murphy, F., des Monstiers, B., & Russell, J. C. (2023). Rat biosecurity surveillance and response following eradication on a tropical atoll. *Human-Wildlife Interactions*, *17*(2), 174-186.

Russell, J. C., Faulquier, L., & Tonione, M. A. (2011). Rat invasion of Tetiaroa atoll, French Polynesia. *Island invasives: eradication and management. Gland, Switzerland: IUCN*, 118-123.

Sachet, M. H. and Fosberg, F. R. (1983). An ecological reconnaissance of Tetiaroa Atoll. Atoll Research Bulletin No. 275. *The Smithsonian Institution*, Washington D. C. 88

Samaniego, A., Griffiths, R., Gronwald, M., Holmes, N. D., Oppel, S., Stevenson, B. C., & Russell, J. C. (2020). Risks posed by rat reproduction and diet to eradications on tropical islands. *Biological Invasions*, *22*(4), 1365–1378. https://doi.org/10.1007/s10530-019-02188-2

Steadman, D. W. (1989). Extinction of birds in eastern Polynesia: a review of the record, and comparisons with other Pacific island groups. *Journal of Archaeological Science* 16(2):177–205. https://doi.org/10.1016/0305-4403(89)90065-4

Steibl, S., Kench, P. S., Young, H. S., Wegmann, A. S., Holmes, N. D., Bunbury, N., Teavai-Murphy, T. H., Davies, N., Murphy, F., & Russell, J. C. (2024a). Rethinking atoll futures: Local resilience to global challenges. *Trends in Ecology & Evolution*, *0*(0). https://doi.org/10.1016/j.tree.2023.11.004

Steibl, S., Steiger, S., Wegmann, A. S., Holmes, N. D., Young, H. S., Carr, P., & Russell, J. C. (2024b). Atolls are globally important sites for tropical seabirds. *Nature Ecology & Evolution*, *8*(10), 1907-1915.

Stoll, B., Tuheiava, P., Badie, M., & Oliveira, L. D. (2023). Cartographie lidar des biotopes terrestres, marins et intertidaux de l'atoll de Tetiaroa. *Spatial Analysis and GEOmatics*. https://conbio.onlinelibrary.wiley.com/doi/10.1111/cobi.13630

Thaman, R. (2008). Atolls–the "biodiversity cool spots" vs "hot spots": A critical new focus for research and conservation. *Micronesica*, *40*, 33–61.

Thibault, J.C. (1973). Remarques sur l'appauvrissement de l'avifaune Polynésienne. *Bull. Étud. Océanien*. 15: 262-270.

Thibault, J.-C. (1976). L'avifaune de Tetiaroa (Archipel de la Société. Polynésie française). L'Oiseau et la Revue française d'ornithologie 46: 29-45.

Thibault, J.-C., & Cibois, A. (2017). Birds of eastern Polynesia: A biogeographic atlas (First edition). *Lynx Edicions*.

Young, H. S., Miller-ter Kuile, A., McCauley, D. J., & Dirzo, R. (2017). Cascading community and ecosystem consequences of introduced coconut palms (*Cocos nucifera*) in tropical islands. *Canadian Journal of Zoology*, *95*(3), 139–148. https://doi.org/10.1139/cjz-2016-0107

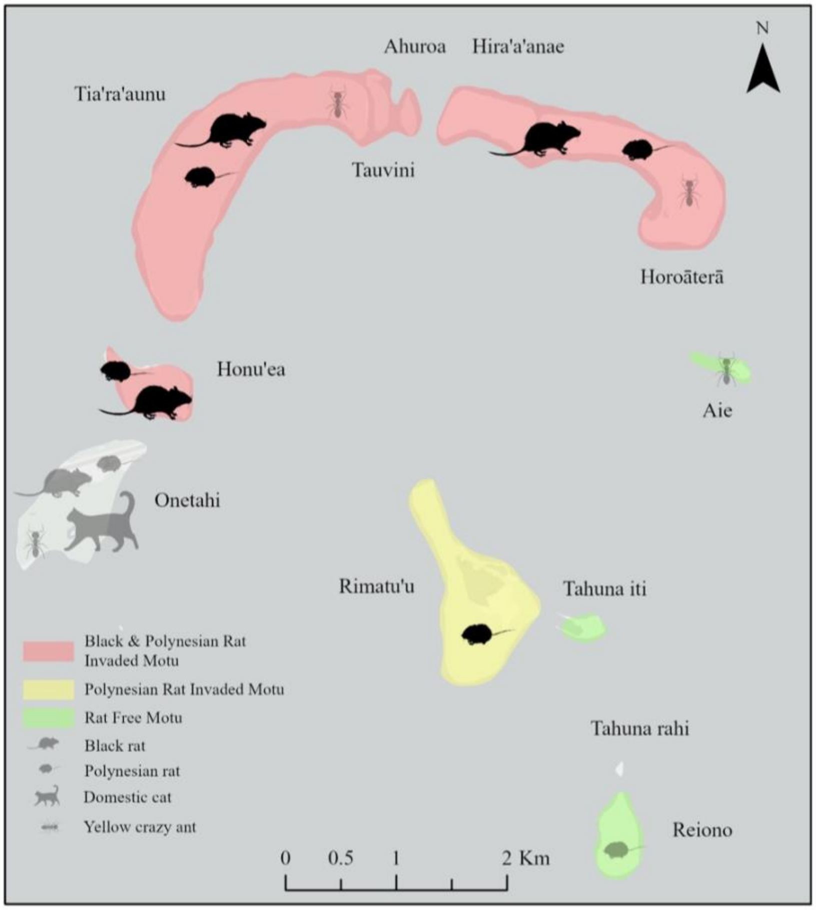

Figure 1.1 Map of Tetiaroa's faunal invasion history. Cats (*Felis catus*) and both rat species were eradicated from Onetahi in 2009. Polynesian rats (*Rattus exulans*) were successfully eradicated from Reiono in 2018. Black rats (*Rattus rattus*) have not been reported anywhere on the atoll post-2024. Polynesian rats persist in the northern motu as of 2025. Yellow crazy ants (*Anoplolepis gracilipes*) were eradicated from Aie, Horoāterā, Tia'ra'aunu, and Onetahi in 2022 – 2023.

Chapter 2: Drivers of Brown Booby (*Sula leucogaster*) Hatching Success in the Tropical Pacific

This work was coauthored with Beth Gardner, Amelia J. DuVall, Jayna L. DeVore, and Sarah J. Converse. At the time of publication of this thesis, it was not in review at a journal.

2.1 Abstract

Seabird reproductive success is influenced by an array of biotic and abiotic factors, and in atoll ecosystems, low-lying nesting habitats are vulnerable to anthropogenic and environmental disturbances. We modeled daily nest survival of Brown Boobies (*Sula leucogaster*) on Tetiaroa Atoll, Society Islands, French Polynesia, using a Bayesian framework. We analyzed data from 903 nests monitored between 2021 and 2024 across three motu (islets) that differed in exposure to invasive rats before and during a rat-eradication effort. Our daily nest survival model included motu (islet)-specific intercepts, a before-after-control-impact (BACI) design to assess effects of rat suppression, and covariates representing ocean swell height, El Niño-Southern Oscillation conditions, colonial nest density, and a disease outbreak period. We found no evidence that rat presence negatively affected daily nest survival; instead we found some evidence of a positive effect of rat presence. We further found that higher swells were associated with lower daily nest survival probability (-0.31, CRI = -0.42, -0.19), while positive Southern Oscillation Index values, indicative of La Niña conditions, were associated with higher daily nest survival probabilities (0.25, CRI = 0.12, 0.38). Neither nest density nor a disease outbreak in 2023 had discernible effects on nest survival. Hatching success, estimated by compounding daily survival over a 47-day incubation period, ranged from approximately 0.16 to 0.88 across modeled environmental scenarios. Our surprising result regarding rat effects may have been due to some unmodeled

confounding factor, or may indicate that rats do not pose a meaningful threat to Brown Booby nests at our study site. Our findings suggest that oceanic variability, rather than rat presence, was the dominant driver of nest success during the study period, suggesting the importance of accounting for risks posed by a changing climate when developing seabird conservation strategies on tropical atolls.

2.2 Introduction

Seabirds forage in marine environments but require terrestrial habitats for nesting and roosting, thereby serving as indicators for the marine environment (Piatt et al., 2007) and providing important ecosystem services in terrestrial environments (Ellis, 2004; Duda et al., 2020). For example, areas near seabird colonies are more productive both above and below the waterline due to deposition of seabird guano (Graham et al., 2018). However, many seabird species are in decline throughout the world, due to a variety of factors including invasive species, fisheries bycatch, and environmental change (Dias et al., 2019). These declines in seabird populations can alter nutrient cycling and cause cascading effects through both terrestrial and marine ecosystems (Benkwitt et al., 2021; Kurle et al., 2008). Given threats to seabird populations and the essential role they play in both marine and terrestrial habitats, it is important to evaluate threats to their populations.

Breeding seabirds often nest in high densities on relatively small breeding islands, rendering these populations highly susceptible to nest predators and disease. Invasive species impacts have been documented for at least 165 seabird species (Dias et al., 2019), which include the persistent threat of non-native mammals that have spread to coastlines and islands worldwide (Philippe-

Lesaffre et al., 2023). Rats are a ubiquitous problem for seabirds, affecting at least 75 species, and are responsible for several extirpations and population declines (Jones et al., 2008).

While invasive predators have received a great deal of attention, other anthropogenic terrestrial threats can impact seabird nesting sites, such as invasive vegetation, development, mining, agriculture, military activities, and pollution (Pagenaud et al., 2022, Steibl et al., 2024a). Human disturbances at breeding colonies, ranging from visitation to targeted hunting, can decrease species diversity, breeding success, and even lead to abandonment of colonies (Dias et al., 2019; Berr et al., 2023a). At sea, anthropogenic threats such as bycatch and overfishing impact seabird survival, and foraging and breeding success are driven by variable conditions in the ocean surrounding breeding sites (Dias et al., 2019). Climate change and extreme weather events have already impacted at least 96 seabird species (Dias et al., 2019). These events are predicted to increase in frequency and intensity with climate change-driven sea-level rise, however some at-risk low-lying areas, such as atolls may prove somewhat resilient when natural sediment accretion processes are unimpeded (Steibl et al., 2024a). Higher swell heights can also impact breeding outcomes through wave inundation of nests (Reynolds et al., 2015).

Large-scale oceanic conditions, such as the El Niño – Southern Oscillation (ENSO), drive ocean productivity (Ancona et al., 2011; Schreiber & Schreiber, 1984), with impacts on seabird diet in both temperate and warm waters globally (Ancona et al., 2012). During warmer El Niño conditions, nutrient upwelling slows, leading to a decline in ocean productivity, diminished availability of forage fish (Schreiber, 2002), and changes in prey size, composition, and abundance (Ancona et al., 2012). These conditions influence breeding outcomes via changes in the physical condition of breeding birds or due to their reduced ability to provide food for nestlings (Schreiber, 2002).

Many seabird species nest on low-lying atolls, which provide important habitat for seabird populations (Berr et al., 2023b; Steibl et al., 2024b). Seabirds regularly forage several hundred kilometers away from their atoll breeding grounds (Young et al., 2015), bringing back pelagic nutrient resources in the form of guano (Steibl et al., 2024b), which promotes terrestrial primary production (Fosberg, 1994), as well as coral reef productivity (Benkwitt et al., 2021). Thus threats, such as invasive rats, can cause ecological damage to tropical atolls through seabird depredation and resulting population reduction (Graham et al., 2018; Benkwitt et al., 2021). In addition, ground nesting seabirds on low-lying islands in particular are susceptible to ocean swells that periodically sweep over beaches and travel inland, inundating vegetation and soil and flooding nests (Reynolds et al., 2015).

The Brown Booby (*Sula leucogaster*) nests on atolls throughout the tropics and provides an opportunity to study drivers and threats to reproduction. They are plunge-divers and eat flying fish, squid, and other mid-sized forage fish (Nelson, 1978), and are found in three ocean basins, with colonies on hundreds of islands as well as along continental coastlines (Carboneras et al., 2016). Brown Boobies nest on the ground in small, relatively low-density colonies, either on cliff ledges or underneath vegetation on sandy and rocky substrate when on flat land (Ospina-Alvarez, 2008). Breeding pairs usually lay two eggs but most often raise only one chick, due to siblicide, parental ejection, or other factors (Nelson, 1978). Brown Boobies are listed as least concern, though declining, on the IUCN Red List (iucnredlist.org; accessed 15 May 2025). However, historic populations could have been as much as 90% larger (Steadman, 1989; Woodworth et al., 2021).

In studies across a variety of avian taxa, nest depredation is often cited as the primary cause of reproductive failure (Lima, 2009), which is also shown in results of colonial seabird nest monitoring (Byerly et al., 2021). However, predators are not generally well documented for any Brown Booby population, with published data on black rat egg depredation available from only three islands (Harper & Bunbury, 2015). Hundreds of rat eradication projects have been successfully completed globally; some seabird colonies have reported population growth and recovery in response (Jones et al., 2008). However, data are limited, responses vary, and some eradications are the topic of controversy, which indicates the need for further investigation of the impacts of rats (Towns et al., 2006). To better understand the factors driving hatching success of Brown Boobies, we followed nests on Tetiaroa Atoll, French Polynesia. On this atoll, Brown Boobies nest in areas with and without rats. A rat eradication effort was undertaken on Tetiaroa during our monitoring period, thus providing a before-after-control-impact design to explore the impact of rats on nesting success. We examined nest outcomes in relation to rat exposure along with other environmental factors that may affect hatching success, including wave inundation, the Southern Oscillation Index (an index of ENSO conditions), colony density, and a disease outbreak observed in seabirds on the atoll during our study period.

We evaluated several hypotheses through this work. We hypothesized that Brown Boobies, which evolved without mammalian predators, experience substantial declines in hatching success when these predators are present due to a combination of disturbance and nest depredation, and thus we predicted that hatching success of Brown Boobies would be lower in the presence of rats. Second, we hypothesized that on low-lying nesting islands, wave inundation is a substantial source of nest loss, thus we predicted that we would observe lower hatching success during periods of high ocean swells. Third, we hypothesized that at-sea productivity drives hatching success of Brown Boobies due to lower incubation constancy when food conditions are poor; thus, we predicted that we would observe lower hatching success during periods of low ocean productivity. Fourth, we hypothesized that colonial seabirds benefit from intra-colony behavioral responses to threats, and so we predicted that we would observe lower hatching success in areas with lower Brown Booby nest density.

2.3 Methods

2.3.1 Study System

Tetiaroa Atoll is a small low-lying coral atoll in French Polynesia (17°00′S, 149°34′W), situated 50 km north of Tahiti and Mo‘orea (Figure 1.1). The atoll consists of 12 motu (islets) of varying sizes, habitats, and with and without black and Polynesian rats (Figure 1.1). Terrestrial habitats include two main forest types: native forest dominated by either *Pisonia grandis* or *Pandanus tectorius* with secondary species such as *Guettarda speciosa* and *Cordia subcordata,* and former interior copra plantations dominated by invasive *Cocos nucifera* (Stoll et al., 2023). Rat eradication occurred on one motu, Reiono, in 2018 and an extensive atoll-wide round of rodenticide was deployed from June-July 2022 (Ringler et al., 2023).

Brown Boobies (a‘o, Tahitian; Richter-Gravier, 2019) nest predominantly on three of Tetiaroa’s motu: Tahuna iti, Tia’ra’aunu, and Horoāterā (Figure 2.1). Tia’ra’aunu and Horoāterā are in the north of the atoll and Brown Bobbies nest largely in the reef-facing coastal vegetation (i.e., *Heliotropium arboreum*) there. Tahuna iti has the highest density of Brown Boobies, and is situated near the center of the lagoon. *Pemphis acidula* and *Pisonia grandis*, as well as a wide array of native grasses and ground plants, are found there, creating more diverse microhabitats and colony characteristics relative to the northern motu.

2.3.2 Nest Monitoring

To understand the drivers of Brown Booby hatching success, we did intensive nest searching and monitoring. We followed individual nests between July and December 2021, January and October 2022, and April and November 2023 to determine the fate of these nests. During a Brown Booby GPS tracking project on Tahuna iti in 2024, we followed 5 additional nests (each with a tagged parent). During these periods, nests were visited every 8 – 9 days on average, during which we spent one full day searching each motu with known colonies (Tahuna iti, Tia'ra'aunu, and Horoāterā). Two additional motu (Tauvini and Hira'a'anae) were also searched nearly every week. We searched all other shoreline areas once per month, except on the inhabited motu of Onetahi, but no nests were discovered outside the five motu noted above. We flagged and numbered new nests and recorded the contents and status of all existing nests. We tracked nests on an interactive map in the mobile mapping application Gaia GPS (www.gaiagps.com; Louisville, Colorado, USA) and took photos to assist with relocating and identifying nests upon reencounter.

Because of the challenge of following chicks of a ground-nesting bird, due to the ease with which chicks can leave the nest, we considered nests as successful when eggs hatched and did not model the chick or fledgling stages. Thus, each nest's history was terminated on the day when the nest was first known to have either hatched or failed. Eggs that remained in nests past the date of possible viability (53 days) we assumed died on the date when they were certain to have reached ≥53 days old, based on the date of discovery. Nests that went unmonitored for more than 42 days (i.e., when members of the field team departed Tetiaroa) were censored at the last observation. Nests that were observed only once were removed from the analysis. Encounter histories were built for each nest, starting at discovery date and ending with known failure or hatch date.

Additionally, we outfitted a subset of nests ($n = 294$) with game cameras set to take photos every 30 seconds to 15 minutes, depending on monitoring effort. Nests with relatively fresh eggs were prioritized for cameras, to ensure that nests could be tracked throughout development. We reviewed all photos using Timelapse2 (Greenberg et al., 2019) to determine nest successes and failures, and causes of egg mortality. Unique IDs, nest dates, rat activity, number of eggs hatched, and cause of nest failure were noted. Causes of documented nest failure were recorded as undetermined, rat depredation, land or hermit crab depredation, other, siblicide, egg ejection by adult, abandonment, non-viability (infertility or embryo death), and wave inundation.

2.3.3 Covariate Data

We developed an array of covariates associated with our hypotheses and other factors that could influence the success of nests across different motu. We were able to model the effect of rats using a before-after-control-impact (BACI) analysis. Rat eradication was attempted across much of Tetiaroa from June 9, 2022 to July 31, 2022, but was not completely successful. Rat populations were sharply suppressed, and ongoing efforts to eliminate Polynesian rats continue, so we refer, for simplicity, to pre- and post-suppression periods. To account for the BACI design, we established two covariates. First, we established a before-treatment indicator variable, assigned to all nest monitoring dates, equal to 1 if the nest monitoring date occurred pre-rat suppression (prior to July 31, 2022) or a 0 if the nest monitoring date was post-rat suppression. Second, we created a rat indicator variable where a 1 was assigned to each nest based on whether the location had rats (Tia’ra’aunu and Horoāterā) pre-rat suppression, and a 0 otherwise (post-rat suppression or if the nest was located on Tahuna iti at any time).

We quantified the potential inundation risk to nests using projected global wave data made from WAVERYS multi-year wave reanalysis (Law-Chune et al., 2021). WAVERYS takes into account oceanic currents from previous physical oceanography models, data from historical altimetry missions, and directional wave spectra from the satellite Sentinel 1 SAR. We extracted the daily maximum sea surface primary swell wave significant heights (in meters) that corresponded with each date during our nest monitoring period (available from the E.U. Copernicus Marine Service Information, accessed December 2024, https://doi.org/10.48670/moi-00022).

We characterized oceanic conditions using the Southern Oscillation Index (SOI), a measure of differences in air pressure occurring between Tahiti and Darwin, Australia, calculated using the Ropelewski and Jones (1987) method (available at the Physical Sciences Laboratory, accessed January 2025, NOAA https://psl.noaa.gov/data/timeseries/month/SOI/). Positive SOI values correspond with La Niña cycles characterized by cooler ocean temperatures with more upwelling and a general increase in ocean productivity; while negative SOI values relate to El Niño cycles with warmer ocean temperatures, less nutrient upwelling, and declines in ocean productivity (Ancona et al., 2012).

Nest density was calculated as the number of active nests within a 15-m radius of each nest. For a neighboring nest to be counted as active, it had to have been initiated within 30 days of a target nest's initiation date.

A mass mortality event began in April 2023 and likely impacted all seabird species on Tetiaroa. While the exact origin and cause of these deaths was never determined, we observed a rapid increase in seabird mortalities from mid-April to early June 2023. We created a binary indicator variable for the disease outbreak, where all nest monitoring dates were assigned a value of 1 for this variable if the monitoring date was during the disease outbreak (April 10 to June 5, 2023) and 0 otherwise.

2.3.4 Daily Nest Survival Modeling

Modeling nest survival daily was first proposed by Mayfield (1961, 1975) to account for the lower probability of finding nests that fail early, resulting in a potential positive bias in the estimated probability of nest success. If probability of success can be estimated at a finer time scale, such as a day, then overall success can be estimated by raising the daily rate to the power of the number of days in the nesting period. A variety of improvements have been developed since Mayfield's work, largely around developing model likelihoods that do not require assumptions about when a nest failed or succeeded during the final monitoring interval (Rotella et al., 2000; Dinsmore et al., 2002). Bayesian implementations of daily nest survival models have also been described (Royle & Dorazio, 2008; Converse et al., 2013).

We modeled the state of nest *i* at observation t, for $t = 1\colon T_i$, as

$$y_{i,t} \sim Bernoulli\left(S_{i,t-1} * y_{i,t-1}\right)$$

where $y_{i,t}$ = 1 if the nest is alive and 0 otherwise. The probability of daily survival $S_{i,t}$ is multiplied by the state at the previous observation, $y_{i-1,t}$, to prevent the resurrection of failed nests.

Because the number of days between monitoring occasions was unequal, we then modeled the survival probability as:

$$S_{i,t} = S.d_{i,d}^{days_{i,t}}$$

where $days_{i,t}$ is the number of days between observation *t* and observation *t*+1 for nest *i*, and $S.d_{i,d}$ is the probability of surviving one day. We then modeled daily nest survival as a function of daily covariates, with a logit link:

$$logit(S.d_{i,d}) = \beta_{motu}[motu_i] + \beta_{before} * I.before_{i,d} + \beta_{rats} * I.rats_{i,d} + \beta_{swell} * swell_{i,d} + \beta_{SOI} * SOI_{i,d} + \beta_{density} * density_i + \beta_{disease} * I.disease_{i,d}$$

where modeled effects included a motu-specific intercept, β_{motu}, for the three motu included in the analysis; β_{before}, the effect of a nest-day occurring before rat suppression; β_{rats}, the effect of a nest occurring on a motu with rats; β_{swell}, the effect of ocean swells; β_{SOI}, the effect of SOI;

$\beta_{density}$, the effect of nest density; and $\beta_{disease}$, the effect of the disease outbreak. Data include $motu_i$, the motu where nest *i* occurred; $I.before_{i,d}$, an indicator for whether day d for nest *i* occurred before the rat suppression period; $I.rats_{i,d}$, an indicator for whether day d for nest *i* occurred before the rat suppression period on a motu with rats; $swell_{i,d}$, the swell height on day d for nest *i*; $SOI_{i,d}$, the SOI on day d for nest *i*; $density_i$, the number of active nests around nest *i*; and $I.disease_{i,d}$, an indicator for whether day *d* for nest *i* occurred during the disease outbreak.

We built daily nest survival models in a Bayesian framework. All analyses were conducted in R, (R Core Team 2024, version 4.4.2) using the NIMBLE package (NIMBLE Development Team, version 1.3.0). All continuous covariates were standardized by *Z*-scoring. We specified relatively uninformative priors for all parameters, Normal (0, SD = 10) on the logit scale. We ran the model for 25,000 iterations across each of three Markov chains and discarded the first 5,000 iterations from each chain as burn-in, resulting in 60,000 posterior samples used for inference. Convergence was assessed both visually and using the Gelman–Rubin $\hat{R}$ statistic (Gelman & Rubin, 1992), with potential scale reduction factors $\hat{R} \leq 1.01$ for all monitored parameters. Code and data are available on GitHub at https://github.com/EveMHallock/Tetiaroa_BRBO.

To predict overall hatching success, we assumed an incubation period of 47 days. Based on this assumption, we developed predictions by raising daily survival probabilities to 47 for various scenarios of interest.

2.4. Results

We located and monitored 1,067 Brown Booby nests, of which *n* = 903 nests were included in the analysis after data cleaning (Table 2.1). The nests were distributed primarily across the reef side of Horoāterā and Tia'ra'aunu, which were occupied by rats before suppression efforts, and in higher densities across the north-eastern section of Tahuna iti, which was never invaded by rats (Figure 2.1). We found differences in overall nest success by motu with Tahuna iti having higher daily nest survival than Tia'ra'aunu and Horoāterā (Table 2.2).

Our results provided mixed evidence for our hypotheses. After accounting for the elements of the before-after-control-impact design, through inclusion of motu pre-suppression effects, we found no support for lower daily nest survival in the presence of rats. On the contrary, we found some evidence of a positive effect of rats (logit-scale coefficient = 0.44; 95% credible intervals (CRI) = -0.05, 0.91; Table 2.1, Figure 2.2). Indeed, predicted hatching success increased post-suppression at the rat-free motu, while it declined at the two motu that had been occupied by rats (Figure 2.3).

We did find strong evidence to support our hypothesis regarding wave inundation, with a negative relationship between ocean swells and daily nest survival (-0.31, 95% CRI = -0.42, -0.19; Table 2.2, Figure 2.2). Predictions for Tahuna iti, pre-eradication, with all other continuous covariates at their means, indicated that hatching success would decrease from around 0.53 at the mean swell height (over the period of monitoring) to around 0.36 at 2 SD above the mean swell height (Figure 2.4).

We also found strong evidence in favor of our hypothesis regarding ocean productivity. Model results indicated a positive relationship between SOI and daily nest survival (0.25, 95% CRI = 0.12, 0.38; Table 2.2, Figure 2.2), indicating higher nest survival during ENSO cool phases. Predicted hatching success on Tahuna iti (pre-eradication) increased from 0.51 at the mean SOI value to 0.72 at 2 SD above the mean SOI value (Figure 2.5).

We found no support for our hypothesis regarding nest density. The effect of nest density was not distinguishable from 0 (0.00, 95% CRI = -0.10, 0.09; Table 2.2, Figure 2.3), indicating no impact on hatching success as nest density changed. Finally, despite our expectation that the disease outbreak between April and June 2023 would reduce hatching success, we found no discernible effect on hatching success (0.07, 95% CRI = -0.22, 0.37; Table 2.2; Figure 2.3).

From the subset of 294 nests that were monitored with time-lapse game cameras as well as in-person surveys, 129 successfully hatched, 163 failed at the egg stage, and 2 nests had undetermined outcomes. 48 nests failed as egg(s) after 53 days, indicating that the egg(s) were no longer viable. We observed 114 nests that failed as viable eggs: 32 nests pre-rat suppression and 82 post-rat suppression (Table 2.3). Of the 32 nests that failed as viable eggs prior to rat suppression, the leading observed causes were ejection of the egg by the adult Booby (n = 9) and rat depredation (n = 9), followed by wave inundation (n = 7). Of the 82 nests observed post suppression, leading observed causes were ejection of the egg by an adult Booby (n = 29), wave inundation (n = 16), and crab predation (n = 13). All observed causes, as well as information on non-viable eggs and chick observed mortalities, can be found in Table 2.2 and Figure 2.6.

2.5 Discussion

2.5.1 Drivers of Brown Booby Hatching Success

This study provides new insights into drivers of Brown Booby hatching success. While we hypothesized that rat presence would negatively impact nest survival, rats were associated with an uncertain, yet positive effect on hatching success. This unexpected outcome highlights the need for investigating factors not fully captured in our model, as well as additional years of monitoring data. With game cameras, we captured nine nests that failed due to rat depredation and three that were scavenged by rats (after eggs had been sitting in the nest for >53 days without hatching; Table 2.3; Figure 2.6). While these observations suggest that rats are having some impact (35% of observed nest failures prior to rat suppression on motu with rats), when compared with other causes of failure, such as wave inundation, the impact appears minimal. In our daily nest survival model results, we found a strong influence of oceanic conditions, including ocean swells and SOI, on reproductive success. Despite substantial observed seabird mortality during a disease outbreak, we found no discernible effect of the disease on hatching success, indicating that other environmental factors occurring over the same time period may have been more influential. These results underline the importance of long-term seabird monitoring and considering many biotic and abiotic factors, particularly in the context of investigating invasive species and climate change.

A key component of our study was the inclusion of rat suppression as a factor influencing nest survival. While Sulids have much thicker eggshells than smaller seabirds, which could limit rat depredation, rodents have proven to be a critical threat to even larger seabirds, such as albatrosses (Diomediadae) (Harper & Bunbury, 2015). Rats may not be as prevalent or effective in depredating Brown Booby eggs as anticipated, potentially due to the Brown Booby's large size and thick eggshells, which could provide some level of protection (Atkinson, 1985). There are several confounding effects that may also have driven the unexpected result related to rats. Parental attentiveness, potential interaction effects between the two rat species, food resources available to rats, or the timing of rat activity may mitigate the risk of depredation. We did not have data on rat densities and relied on a binary indicator variable of rat presence, which may have been too coarse and thereby masked more localized effects of rats.

Atkinson (1985) has suggested that some island chains that lack endemic mammals have apparently experienced relatively lower rates of avifauna extirpation after rat invasion because of the influence of native land crabs, particularly in an equatorial zone between 15°N and 20°S (Atkinson, 1985). Tetiaroa has numerous species of native land and intertidal crab species, including large, long-lived coconut crabs (*Birgus latro*), brown land crabs (*Cardisoma carnifex*), and strawberry hermit crabs (*Coenobita perlatus*). We observed each of these species depredating and scavenging eggs and ejected chicks of Brown Boobies during our study, and most cases occurred in the post-rat suppression period on Tia'ra'aunu and Horoāterā (19 total nests were depredated or scavenged by crabs; Figure 2.6). Suppression of rats could lead to increases in crab populations, which occurred on Palmyra Atoll post-rat eradication (Nigro et al., 2017). One investigation of the potential impacts of native crabs on nesting Brown Boobies was conducted on Belmonte Island, and results there indicated that salty lightfoot crabs (*Grapsus grapsus*) scavenged, rather than depredated, eggs and small chicks (Gianuca & Vooren, 2007). Similarly, Dodson & Fitzgerald (1980) observed minimal depredation of Sulid eggs on Clipperton Island, and noted that parents attending young chicks defended chicks against red land crabs (*Gecarcinus planatus*). Seabirds may have evolved defense mechanisms against depredation from land crabs, potentially conferring some benefit in the face of rat depredation risk (Atkinson, 1985; Jones et al., 2008).

Oceanic factors, including ENSO and swell height, play an important role in predicting hatching success, highlighting the effects of climate on nesting seabirds. Climatic conditions are thought to be a primary driver in shaping seabird reproductive success in the central Pacific (Schreiber & Schreiber, 1984; Schreiber, 2018), as shown by the positive relationship between SOI and nest survival in our model results. The cool phases of ENSO (La Niña), which are associated with higher productivity at sea, support higher availability of prey for seabirds, leading to increased chick survival, given that other conditions are suitable (Schreiber, 2002). On Johnston Atoll, Brown Boobies were found to be one of the least affected seabird species during the 2002-2003 El Niño phase, with relatively low numbers of chick mortalities, however numbers of nests did decline, and timing of breeding also shifted (Schreiber, 2018). It is common for the effect of reduced ocean productivity on demography to be delayed; however, we found an immediate effect of SOI on the hatching success of Brown Boobies. On Isla Isabel, Galapagos, researchers found that warmer local surface waters in the winter of the previous year were associated with lower local primary productivity, implying reduced availability of prey during El Niño (warm) phases, which led to decreased reproductive success of Red-footed Boobies (*Sula sula*; Ancona et al., 2011). They also found that SOI values from six months prior had a negative effect on fledging success, implying a delayed effect. While we found an effect without a lag, lagged effects could be investigated in future analyses.

We found that wave inundation, as represented by the maximum swell height, had a negative effect on nest survival, with higher wave heights associated with reduced nest survival probabilities. On camera, we observed 29 nests that were swept away (~10% of nests monitored with cameras; Figure 2.6). This result suggests that extreme weather events, such as those caused by ocean swells, may increase the likelihood of nest failure, potentially due to nest disturbance or flooding. For a subset of nests (*n* = 656), we measured the distance from the nest to the coastal vegetation line and found that nests on Tahuna iti were 3.5 – 4.5 times further inland on average than nests on Horoāterā and Tia'ra'aunu. This suggests that there may be differences in nest susceptibility to inundation by motu that are not fully captured in our model. Perhaps without rat predators and in suitable habitat, Brown Boobies could nest further inland, providing protection from swells.

In the context of climate change, it is uncertain how sea level rise and extreme weather events will impact Brown Boobies on Tetiaroa. Tidal data from Papeete, Tahiti shows that the sea level rose an estimated 20 cm between 1955 and 2023 (Becker et al., 2012), which is above the global mean rate, suggesting that nearby atolls like Tetiaroa could be at risk for land loss. However, the frequency of tropical cyclones in the South Pacific is predicted to decrease (Walsh et al. 2012). On Midway Atoll, sea level rise, storm surges, and wave-driven flooding impact seabird nesting success (Reynolds et al., 2015). Projections from a passive modeling approach (without additional wave-driven effects) indicated that, with 2 m sea level rise, up to 15% of Laysan Albatross (*Phoebastria immutabilis*), 18% of Black-footed Albatross (*Phoebastria nigripes*), and 13% of Bonin Petrel (*Pterodroma hypoleuca*) nests would be inundated on Midway Atoll (Reynolds et al., 2015). Projections from their model that included wave-driven effects were far more dire. Furthermore, the land on atolls is frequently dynamic and unstable, with motu size and location evolving over time (Stoll et al. 2025). Several smaller motu on Tetiaroa have been in near constant flux (Stoll et al. 2025), including Tahuna iti. For the Brown Boobies nesting on Tahuna iti, this instability could become more severe with climate change, impacting their main breeding area on Tetiaroa. Models that project sea-level rise on top of current motu landmass shifting could help predict how many nests will face inundation.

The long-term effects of rat eradication can take time to unfold; landscape changes and increases in populations of native species are sometimes not detected until years after invasive species removal is completed (Philippe-Lesaffre et al., 2023; Saunier et al., 2024). On Tromelin Island, Masked Booby (*Sula dactylatra*) and Red-footed Booby populations showed significant increases 15 – 17 years post-rat eradication (Saunier et al., 2024). However, for the first six years post-eradication, researchers observed population decreases and suggested that the lag time was partially due to the relatively delayed age to maturity and the philopatric nature of Sulid species, which influences new breeder recruitment (Saunier et al., 2024). On Surprise Island, New Caledonia, researchers used over 20 years of surveys to detect post-eradication changes. They also predicted that Brown Boobies would respond positively to rat eradication, but their results showed a slight but steady decline in estimated breeding pairs up to four years after eradication (Philippe-Lesaffre et al., 2023). Given environmental stochasticity, it would be useful to include more years of data to evaluate whether the observed effects are truly due to rats or environmental variation on Tetiaroa that we did not capture in our model.

2.5.2 Conservation Implications

Island ecosystems, including tropical atolls, are disproportionately affected by the intersecting crises of invasive species and climate change. Seabirds, as important nutrient transporters and ecosystem sentinels, are central to the functioning and resilience of many atoll ecosystems (Graham et al., 2018; Steibl et al., 2024c) Our findings add new empirical evidence in understanding seabird responses to invasive species and environmental change. While invasive mammals, particularly rats, are widely recognized as critical threats to island-nesting seabirds, our findings indicate that, for Brown Boobies on Tetiaroa, oceanic conditions were more influential drivers of hatching success during the study period. The strong negative effects of wave inundation and the positive association with La Niña conditions underscore the vulnerability of ground-nesting seabirds to climate-driven ocean dynamics. As sea levels rise and storm intensity fluctuates around the world, nesting habitat suitability on low-lying islands or coastlines may decline even in the absence of other threats. Invasive species removal remains a key conservation goal, and long-term population monitoring will be essential to detect potential delayed responses to rat eradication and to understand how climate change interacts with restoration efforts on atoll ecosystems like Tetiaroa.

2.6 Acknowledgments

Funding was provided by the USDA Bridging the Gap Fellowship through the University of Washington School of Environmental and Forest Sciences. Funding was also provided by the Tetiaroa Society, and the Seeley, Bailey, and Alexander families. Additional support was provided by the Washington Cooperative Fish and Wildlife Research Unit. We thank Dee Boersma and Julia Parrish, and numerous volunteers who participated in fieldwork and data

processing. Nest monitoring was conducted under University of Washington Institution Animal Care Protocol #4448-01 and under French Polynesian research permits.

2.7 Literature Cited

Ancona, S., Calixto-Albarrán, I., & Drummond, H. (2012). Effect of El Niño on the diet of a specialist seabird, *Sula nebouxii*, in the warm eastern tropical Pacific. *Marine Ecology Progress Series*, *462*, 261–271. https://doi.org/10.3354/meps09851

Ancona, S., Sánchez-Colón, S., Rodríguez, C., & Drummond, H. (2011). El Niño in the Warm Tropics: local sea temperature predicts breeding parameters and growth of blue-footed boobies. *Journal of Animal Ecology*, 80(4), 799-808.

Anderson, W. B., & Polis, G. A. (1999). Nutrient fluxes from water to land: seabirds affect plant nutrient status on Gulf of California islands. *Oecologia*, 118, 324-332.

Atkinson, I. A. E. (1985). The spread of commensal species of *Rattus* to oceanic islands and their effects on island avifaunas. Pages 35–81 in P. J. Moors, editor. Conservation of island birds: case studies for the management of threatened island species. International Council for Bird Preservation, Cambridge, United Kingdom

Becker, M., Meyssignac, B., Letetrel, C., Llovel, W., Cazenave, A., & Delcroix, T. (2012). Sea level variations at tropical Pacific islands since 1950. *Global and Planetary Change*, *80–81*, 85–98. https://doi.org/10.1016/j.gloplacha.2011.09.004

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

Berr, T., Millon, A., Dumas, P., Guehenneuc, P., Perez, F., De Méringo, H., Baudat-Franceschi, J., Le Corre, M., & Vidal, É. (2023a). Human visitation disrupts natural determinants of breeding seabird communities on coral reef islands. *Global Ecology and Conservation*, *48*, e02732. https://doi.org/10.1016/j.gecco.2023.e02732

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

Byerly, P. A., Zaluski, S., Nellis, D., & Leberg, P. L. (2021). Colony characteristics influence nest survival of Caribbean Roseate Terns. *Ornithological Applications*, *123*(1), duaa069. https://doi.org/10.1093/ornithapp/duaa069

Carboneras, C., Christie, D. A., Jutglar, F., Garcia, E. F. J., & Kirwan, G. M. (2016). Brown Booby (*Sula leucogaster*). In *Handbook of the Birds of the World Alive* (J. del Hoyo, A. Elliott, J. Sargatal, D. A. Christie, and E. de Juana, Editors). Lynx Edicions, Barcelona.

Converse, S. J., Royle, J. A., Adler, P. H., Urbanek, R. P., & Barzen, J. A. (2013). A hierarchical nest survival model integrating incomplete temporally varying covariates. *Ecology and Evolution*, *3*(13), 4439–4447. https://doi.org/10.1002/ece3.822

Dias, M. P., Martin, R., Pearmain, E. J., Burfield, I. J., Small, C., Phillips, R. A., Yates, O., Lascelles, B., Borboroglu, P. G., & Croxall, J. P. (2019). Threats to seabirds: A global assessment. *Biological Conservation*, *237*, 525–537. https://doi.org/10.1016/j.biocon.2019.06.033

Dinsmore, S.J., White, G.C. & Knopf, F.L. (2002), Advanced Techniques For Modeling Avian Nest Survival. *Ecology*, *83*: 3476-3488. https://doi.org/10.1890/0012-9658(2002)083[3476:ATFMAN]2.0.CO;2

Dodson, J. J. & G. J. Fitzgerald. (1980). Observations on the breeding biology of the boobies (Sulidae) at Clipperton Islands, eastern Pacific. *Nat. Can.* 107:259-267.

Duda, M. P., Glew, J. R., Michelutti, N., Robertson, G. J., Montevecchi, W. A., Kissinger, J. A., Eickmeyer, D. C., Blais, J. M., & Smol, J. P. (2020). Long-term changes in terrestrial vegetation linked to shifts in a colonial seabird population. *Ecosystems*, *23*(8), 1643–1656. https://doi.org/10.1007/s10021-020-00494-8

Ellis, J. (2005). Marine Birds on Land: A Review of Plant Biomass, Species Richness, and Community Composition in Seabird Colonies. *Plant Ecol 181*, 227–241. https://doi.org/10.1007/s11258-005-7147-y

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

Fosberg, F.R. (1994). Comments on atoll phosphate rock. *Atoll Res. Bull.* 396, Smithson. Inst. Sch. Press, Washington, DC

Gelman, A., & Rubin, D. B. (1992). Inference from iterative simulation using multiple sequences". *Statistical Science*. *7*(4), 457–472.

Gianuca, D., & Vooren, C. M. (2007). Abundance and behavior of the sally lightfoot crab (*Grapsus grapsus*) in the colony of the brown booby (Sula leucogaster) in the Sao Pedro and Sao Paulo Archipelago. *Investigaciones Marinas*, *35*(2). https://doi.org/10.4067/S0717-71782007000200012

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

Greenberg, S., Godin, T. & Whittington, J. (2019) User Interface Design Patterns for Wildlife-Related Camera Trap Image Analysis. *Ecology and Evolution,* (*9*)2, 13706-13730.

Harper, G. A., & Bunbury, N. (2015). Invasive rats on tropical islands: their population biology and impacts on native species. *Global Ecology and Conservation*, 3, 607–627. https://doi.org/10.1016/j.gecco.2015.02.010

Jehle, G., Yackel Adams, A. A., Savidge, J. A., & Skagen, S. K. (2004). Nest Survival Estimation: A Review of Alternatives to the Mayfield Estimator. *The Condor*, *106*(3), 472–484. https://doi.org/10.1093/condor/106.3.472

Jones, H. P., Tershy, B. R., Zavaleta, E. S., Croll, D. A., Keitt, B. S., Finkelstein, M. E., & Howald, G. R. (2008). Severity of the effects of invasive rats on seabirds: a global review. *Conservation Biology*, *22*(1), 16-26.

Kurle, C.M., Croll, D.A., & Tershy, B.R. (2008). Introduced rats indirectly change marine rocky intertidal communities from algae- to invertebrate-dominated, Proc. Natl. Acad. Sci. U.S.A. 105 (10) 3800-3804, https://doi.org/10.1073/pnas.0800570105

Law-Chune, S., Aouf, L., & Dalphinet, A. (2021). WAVERYS: a CMEMS global wave reanalysis during the altimetry period. *Ocean Dynamics. 71*, 357–378. https://doi.org/10.1007/s10236-020-01433-w

Lima, S. L. (2009). Predators and the breeding bird: Behavioral and reproductive flexibility under the risk of predation. *Biological Reviews*, *84*(3), 485–513. https://doi.org/10.1111/j.1469-185X.2009.00085.x

Mayfield, H. F. (1961). Nesting Success Calculated From Exposure. *The Wilson Bulletin*, *73*(3).

Mayfield, H. F. (1975). Suggestions for Calculating Nest Success. *The Wilson Bulletin*, *87*(4), 456–466.

Molle, G., Hermann, A., Lagarde, L., & Stoll, B. (2011). The Long-Term History of Teti'aroa (Society Islands, French Polynesia): New archaeological and ethnohistorical investigations. *Research Report*, *10*(2).

Nelson, J. B. (1978). *The Sulidae: Gannets and Boobies* (1st ed.). University of Aberdeen.

Nigro, K.M., Hathaway, S.A., Wegmann, A.S., Miller-ter Kuile, A., Fisher, R.N. and Young, H.S. (2017). Stable isotope analysis as an early monitoring tool for community-scale effects of rat eradication. *Restor Ecol*, 25: 1015-1025. https://doi.org/10.1111/rec.12511

NIMBLE Development Team. (2024). NIMBLE: MCMC, Particle Filtering, and Programmable Hierarchical Modeling. doi:0.5281/zenodo.1211190. R package version 1.3.0, https://cran.r-project.org/package=nimble.

Ospina-Alvarez, Andres. (2008). Coloniality of Brown Booby (*Sula leucogaster*) in Gorgona National Natural Park, Eastern Tropical Pacific. *Ornitologia Neotropical.* 19: 517–529.

Pagenaud, A., Ravache, A., Bourgeois, K., Mathivet, M., Bourguet, É., Vidal, É., & Thibault, M. (2022). Nest-site selection and its influence on breeding success in a poorly-known and declining seabird: The Tahiti petrel *Pseudobulweria rostrata*. *PLOS ONE*, *17*(4). https://doi.org/10.1371/journal.pone.0267408

Philippe-Lesaffre, M., Thibault, M., Caut, S., Bourgeois, K., Berr, T., Ravache, A., Vidal, E., Courchamp, F., & Bonnaud, E. (2023). Recovery of Insular Seabird Populations Years after Rodent Eradication. *Conservation Biology*. https://doi.org/10.1111/cobi.14042.

Piatt, J. F., Sydeman, W. J., & Wiese, F. (2007). Introduction: A modern role for seabirds as indicators. *Marine Ecology Progress Series*, *352*, 199–204. https://doi.org/10.3354/meps07070

R Core Team (2023). R: A Language and Environment for Statistical Computing_. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.

Reynolds M.H., Courtot K.N., Berkowitz P., Storlazzi C.D., & Moore J. (2015). Will the Effects of Sea-Level Rise Create Ecological Traps for Pacific Island Seabirds? *PLOS ONE* *10*(9). https://doi.org/10.1371/journal.pone.0136773

Richter-Gravier, Raphael. (2019). Manu Narratives of Polynesia: A Comparative Study of Birds in 300 Traditional Polynesian Stories. PhD Thesis. *University of Otago, L'Université de la Polynésie Française*.

Ringler, D., Griffiths, R., Murphy, F., des Monstiers, B., & Russell, J. C. (2023). Rat biosecurity surveillance and response following eradication on a tropical atoll. *Human-Wildlife Interactions*, *17*(2), 174-186.

Rotellam, J. J., Taper, M. L., & Hansen, A. J. (2000). Correcting Nesting-Success Estimates for Observer Effects: Maximum-Likelihood Estimates of Daily Survival Rates With Reduced Bias. *The Auk*, *117*(1), 92–109. https://doi.org/10.1093/auk/117.1.92

Royle, J. A., & Dorazio, R. M. (2008). Hierarchical modeling and inference in ecology: the analysis of data from populations, metapopulations, and communities. *Academic Press*, San Diego, USA.

Russell, J. C., Faulquier, L., & Tonione, M. A. (2011). Rat invasion of Tetiaroa atoll, French Polynesia. *Island invasives: eradication and management. Gland, Switzerland: IUCN*, 118-123.

Sachet, M. H. & Fosberg, F. R. (1983). An ecological reconnaissance of Tetiaroa Atoll. Atoll Research Bulletin No. 275. *The Smithsonian Institution*, Washington D. C. 88

Saunier, M., Amy, M., Baumann, M., Bignon, F., Cartraud, A., d'Orchymont, Q., Gazal, J., Goguelat, A., Lemenager, M., Marinesque, S., Orlowski, S., Manuelian, P. E., & Le Corre, M. (2024). Long-term monitoring highlights the positive responses of the seabird community to rat eradication at Tromelin Island, Western Indian Ocean. *Conservation Science and Practice*, *6*(2), e13083. https://doi.org/10.1111/csp2.13083

Schreiber, E. A. (2002). Climate and weather effects on seabirds. *Biology of marine birds*, *741*.

Schreiber, E. A. (2018). Breeding Biology and Ecology of the Seabirds of Johnston Atoll, Central Pacific Ocean: Results of a Long-Term Monitoring Project 1984-2003. 10.13140/RG.2.2.25362.91846.

Schreiber, R. W., & Schreiber, E. A. (1984). Central Pacific seabirds and the El Niño southern oscillation: 1982 to 1983 perspectives. *Science*, *225*(4663), 713-716.

Steadman, D. W. (1989). Extinction of birds in eastern Polynesia: a review of the record, and comparisons with other Pacific island groups. *Journal of Archaeological Science* 16(2):177–205. https://doi.org/10.1016/0305-4403(89)90065-4

Steibl, S., Kench, P. S., Young, H. S., Wegmann, A. S., Holmes, N. D., Bunbury, N., Teavai-Murphy, T. H., Davies, N., Murphy, F., & Russell, J. C. (2024a). Rethinking atoll futures: Local resilience to global challenges. *Trends in Ecology & Evolution*, *0*(0). https://doi.org/10.1016/j.tree.2023.11.004

Steibl, S., Steiger, S., Wegmann, A. S., Holmes, N. D., Young, H. S., Carr, P., & Russell, J. C. (2024b). Atolls are globally important sites for tropical seabirds. *Nature Ecology & Evolution*, *8*(10), 1907-1915.

Steibl, S., Bunbury, N., Young, H. S., & Russell, J. C. (2024c). A Renaissance of Atoll Ecology. *Annual Review of Ecology, Evolution, and Systematics*, *55*(Volume 55, 2024), 301–322. https://doi.org/10.1146/annurev-ecolsys-102722-013447

Stoll, B., Fischer, T., Daniellot-Dejoux, J., Hopuare, M., & Murphy, F. (2025). Tetiaroa diachronic geomorphology 1955 -2023 Monitoring the shoreline and vegetation cover of tropical atoll in the climate change context. *Journal of Interdisciplinary Methodologies and Issues in Sciences*, *12*(2). https://doi.org/10.46298/jimis.14063

Stoll, B., Tuheiava, P., Badie, M., & Oliveira, L. D. (2023). Cartographie lidar des biotopes terrestres, marins et intertidaux de l'atoll de Tetiaroa. *Spatial Analysis and GEOmatics*. https://conbio.onlinelibrary.wiley.com/doi/10.1111/cobi.13630

Thaman, R. (2008). Atolls–the "biodiversity cool spots" vs "hot spots": A critical new focus for research and conservation. *Micronesica*, *40*, 33–61.

Thibault, J. C. (1976). L'avifaune de Tetiaroa (Archipel de la Société. Polynésie française). L'Oiseau et la Revue française d'ornithologie 46: 29-45.

Thibault, J. C., & Cibois, A. (2017). Birds of eastern Polynesia: A biogeographic atlas (First edition). *Lynx Edicions*.

Towns, D.R., Atkinson, I.A.E. & Daugherty, C.H. (2006). Have the harmful effects of introduced rats on islands been exaggerated? *Biological Invasions 8*, 863–891. https://doi.org/10.1007/s10530-005-0421-z

Walsh, K. J. E., McInnes, K. L., & McBride, J. L. (2012). Climate change impacts on tropical cyclones and extreme sea levels in the South Pacific—A regional assessment. *Global and Planetary Change*, *80–81*, 149–164. https://doi.org/10.1016/j.gloplacha.2011.10.006

Young, H. S., Maxwell, S. M., Conners, M. G., & Shaffer, S. A. (2015). Pelagic marine protected areas protect foraging habitat for multiple breeding seabirds in the central

Pacific. *Biological Conservation*, *181*, 226–235.
https://doi.org/10.1016/j.biocon.2014.10.027

Table 2.1 The distribution over years and motu of 1,067 Brown Booby nests monitored on Tetiaroa Atoll from 2021-2024. After data cleaning, 903 of these nests were included in the model of daily nest survival. Note that these data represent what was observed during surveys, not model results.

Motu	Year	Nests Monitored	Nests Censored	Number of Nests Observed with Hatched Eggs
Hira'a'anae[a]	2022	3	3	1
	2023	3	3	2
Tahuna Iti	2021	21	2	11
	2022	145	17	89
	2023	152	45	78
	2024	5	0	1
Tia'ra'aunu	2021	13	2	8
	2022	129	6	61
	2023	145	35	43
Tauvini[a]	2022	1	1	1
	2023	2	2	1
Horoāterā	2021	8	1	4
	2022	219	12	113
	2023	221	35	75

[a] Because only a small number of nests were monitored on these motu, they were not included in the analysis of nest survival.

Table 2.2 Estimated coefficients (posterior mean, standard deviation, and 95% credible interval) from daily nest survival model for Brown Boobies on Tetiaroa Atoll, French Polynesia. Motu-specific intercepts (Tahuna Iti, Tia’ra’aunu, Horoātera̅) represent baseline logit-scale daily survival probabilities. Fixed effects include covariates for pre-eradication period, rat presence, primary swell height (standardized), Southern Oscillation Index (SOI; standardized), nest density (standardized), and a binary indicator for disease outbreak. The rightmost column provides the posterior probability that the effect has the same sign as the mean, i.e., the probability that the effect is positive (if the mean is positive) or negative (if the mean is negative). Parameters with 95% CRIs excluding zero include swell height (negative effect) and SOI (positive effect).

Parameter	Mean	SD	95% CRI	Probability that effect has same sign as mean
Tahuna Iti	4.54	0.14	4.26, 4.83	NA
Tia’ra’aunu	3.66	0.10	3.46, 3.86	NA
Horoātera̅	3.69	0.12	3.47, 3.92	NA
Pre-Eradication	-0.26	0.23	-0.71, 0.20	0.87
Rats	0.44	0.25	-0.05, 0.91	0.96
Swells	-0.31	0.06	-0.42, -0.19	1.00
SOI	0.25	0.07	0.12, 0.38	1.00
Density	0.00	0.05	-0.10, 0.09	0.54
Disease	0.07	0.15	-0.22, 0.37	0.67

Table 2.3 Observed causes of nest failure for 176 Brown Booby nests monitored with game cameras across Tetiaroa Atoll, summarized by site, time period (relative to rat eradication effort), and failure stage. Each row summarizes the number of observed failures attributed to different causes: egg removal by adult Booby (kicking or tossing with bill), crab depredation (when viable) or scavenging (when nonviable), other (one egg depredated by a Swamp Harrier, likely chick starvation, or likely abandonment), rat depredation and scavenging, wave inundation, and undetermined cause not caught on camera. Time period refers to the timing of atoll-wide rat-eradication efforts. Nests with known fail dates ≤ July 31, 2022 were grouped into the pre-suppression treatment, and nests monitored after this date were grouped into the post-suppression treatment. Outcomes are categorized by when the nest failed: viable egg (<53 days in nest), nonviable egg (>53 days in nest), or hatched chick stage.

Motu	Time Period	Nest Stage at Failure	Booby	Crabs	Other	Rats	Unknown	Waves	Total
Hira’a’anae[a]	Post-Suppression	Viable Egg	0	0	0	0	1	0	1
Tahuna Iti	Pre-Suppression	Hatched Chick	0	0	2	0	0	0	2
		Nonviable Egg	2	0	0	0	2	0	4
		Viable Egg	3	0	0	0	3	0	6
	Post-Suppression	Hatched Chick	0	0	0	0	0	2	2
		Nonviable Egg	8	1	0	0	2	1	12
		Viable Egg	6	1	0	0	9	2	18
Horoāterā	Pre-Suppression	Hatched Chick	0	0	1	0	0	1	2
		Nonviable Egg	3	0	0	2	3	0	8
		Viable Egg	4	0	1	6	2	3	16
	Post-Suppression	Hatched Chick	0	0	4	0	0	1	5
		Nonviable Egg	2	3	1	0	2	0	8
		Viable Egg	14	3	1	0	6	9	33
Tia’ra’aunu	Pre-Suppression	Hatched Chick	0	0	0	0	0	1	1
		Nonviable Egg	2	0	1	1	2	0	6
		Viable Egg	2	0	1	3	0	4	10
	Post-Suppression	Hatched Chick	0	0	1	0	0	0	1
		Nonviable Egg	2	2	0	0	6	0	10
		Viable Egg	9	9	1	0	7	5	31
Total			57	19	14	12	45	29	176

[a] Because only a small number of nests were monitored on these motu, they were not included in the analysis of nest survival.

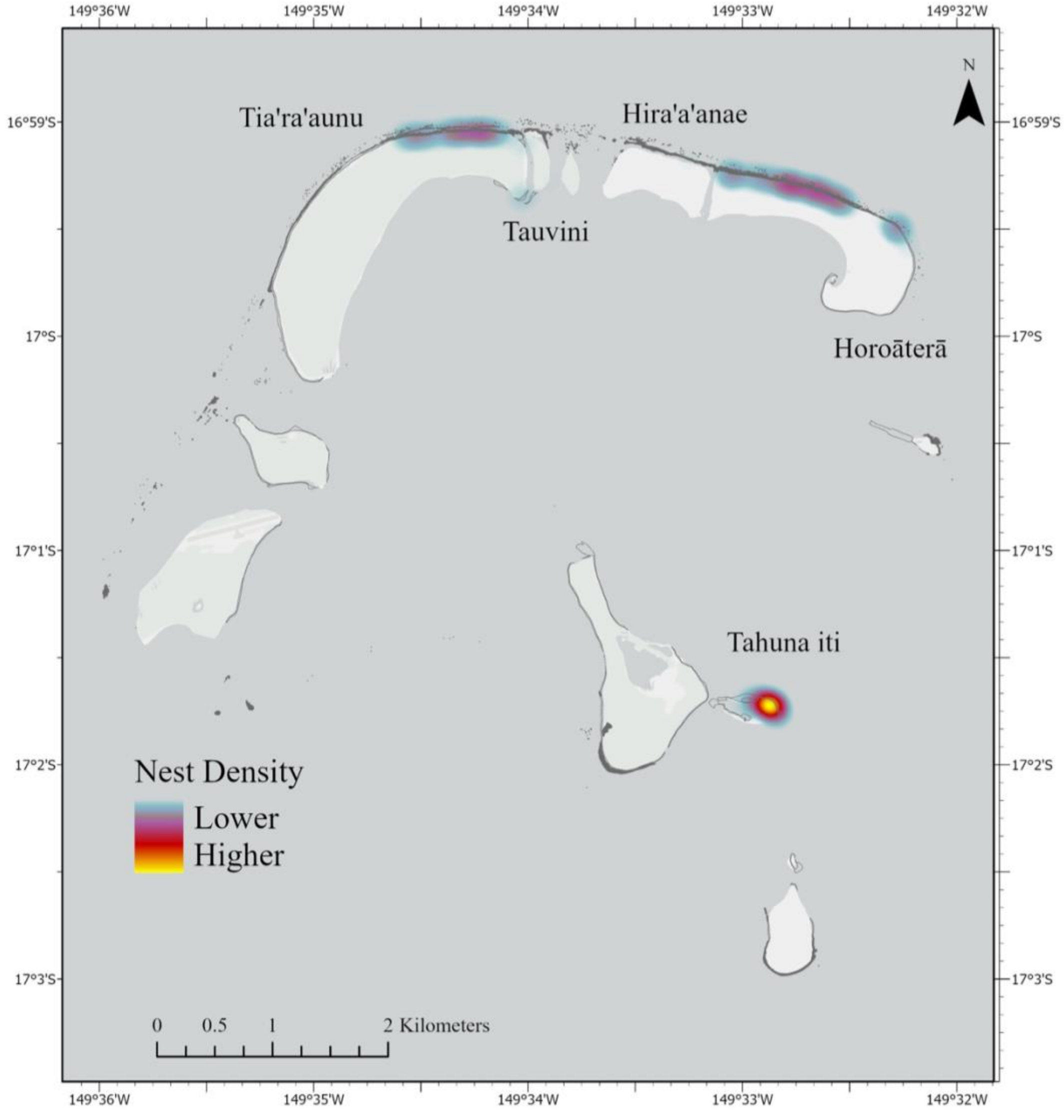

Figure 2.1 Heatmap of all 1,067 Brown Booby nests monitored from 2021 – 2024 on Tetiaroa Atoll, French Polynesia. Higher nest density areas included the northeastern side and interior of Tahuna iti, and northern reef-facing beaches of Tia’ra’aunu and Horoāterā.

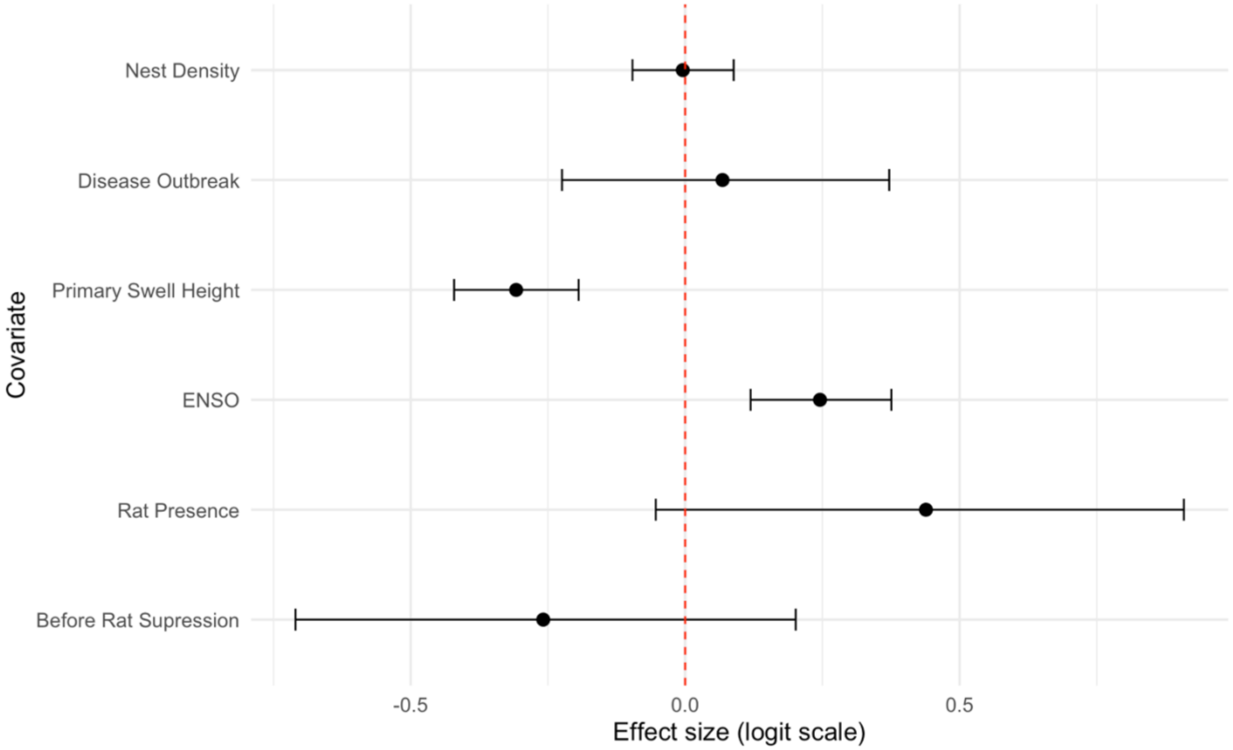

Figure 2.2 Posterior effect sizes of covariates on daily Brown Booby nest survival probability, shown on the logit scale. Points show posterior means and horizontal lines show 95% credible intervals for each covariate. Daily survival probability was modeled as a function of nest density, a disease outbreak (April–June 2023), primary swell wave height, El Niño-Southern Oscillation conditions (SOI), rat presence, and whether the monitoring date occurred before rat suppression. Covariates with credible intervals excluding zero were considered to have strong effects. Swell height had a strong negative effect, while SOI had a positive effect. Nest density and disease had no effect. Effects of rats and pre-suppression periods were both uncertain, however rats did have an overall positive effect.

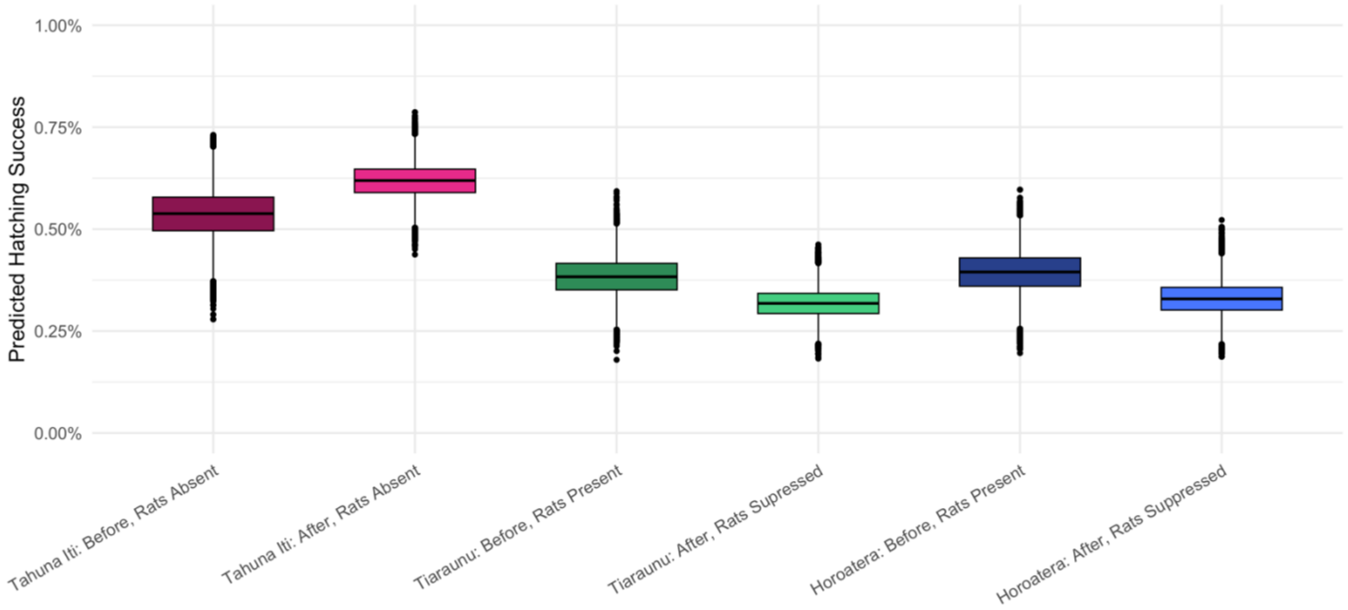

Figure 2.3 Predicted hatching success of Brown Booby nests across motu and rat management periods on Tetiaroa Atoll, 2021 – 2024. Boxes show the posterior probability of nest hatching success, computed as the cumulative product of daily survival probabilities over a 47-day incubation period. Predictions are presented for three motu, Tahuna Iti (rats absent), Tia’ra’aunu, and Horoāterā (both with rats present prior to July 2022), before and after rat suppression. Each scenario was generated by applying the inverse logit transformation to linear combinations of the motu-specific intercepts and relevant rat- and time-related covariates. For all predictions, continuous covariates (primary swell height, SOI, and nest density) were held at their mean values and the disease outbreak indicator was set to 0 (non-outbreak period). Predicted success increased post-suppression at Tahuna iti, but declined at Tia’ra’aunu and Horoāterā, despite rat suppression.

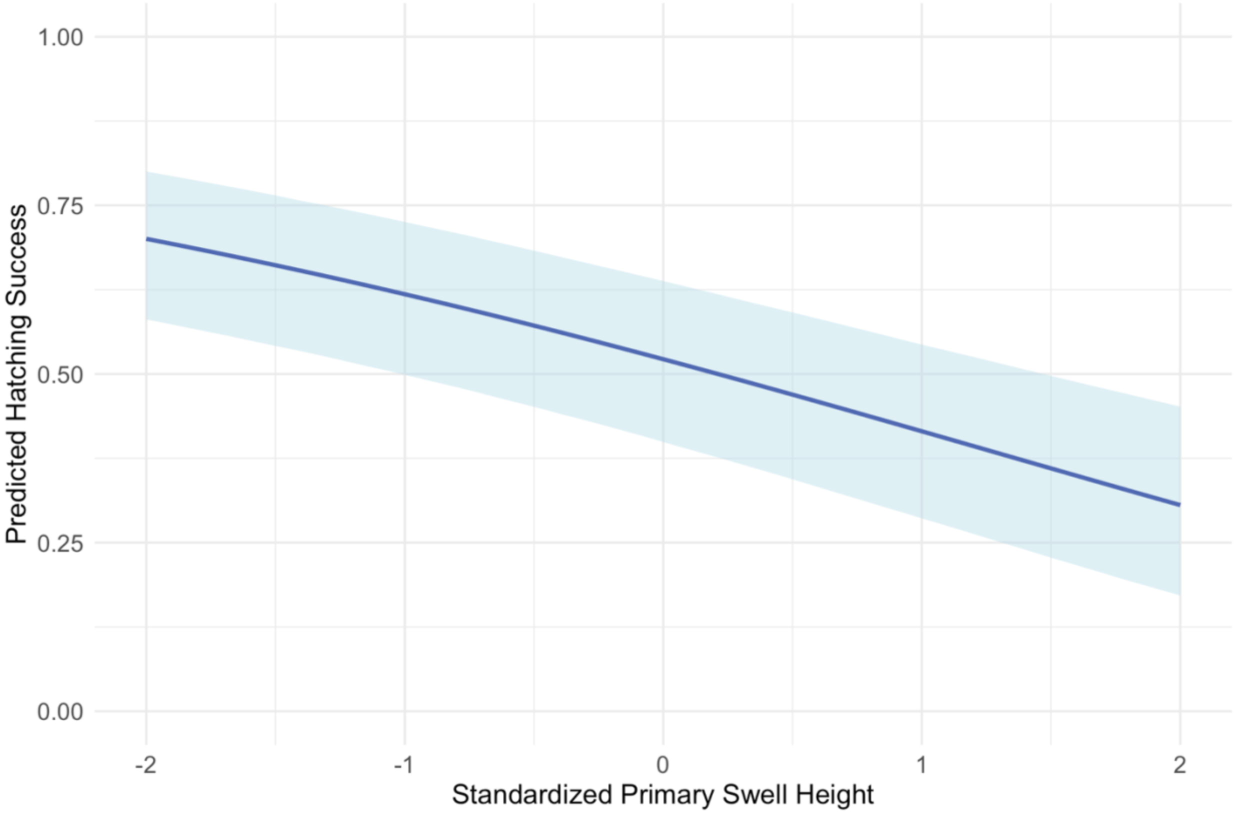

Figure 2.4 Predicted effect of primary swell height on hatching success of Brown Booby nests on Tetiaroa Atoll, French Polynesia, 2021 – 2024. Predicted hatching success was calculated as the cumulative survival probability over a 47-day incubation period, based on daily survival estimates from posterior draws of a Bayesian nest survival model. Values on the *x*-axis represent standardized swell height (in standard deviations). All other covariates, including SOI, nest density, and disease outbreak were held at their standardized means, and rat presence was set to 0. Predictions assume conditions on Tahuna Iti, prior to rat suppression. The shaded ribbon represents the 95% credible interval. Hatching success declined with increasing swell height, supporting the hypothesis that wave-driven inundation negatively affects nest survival.

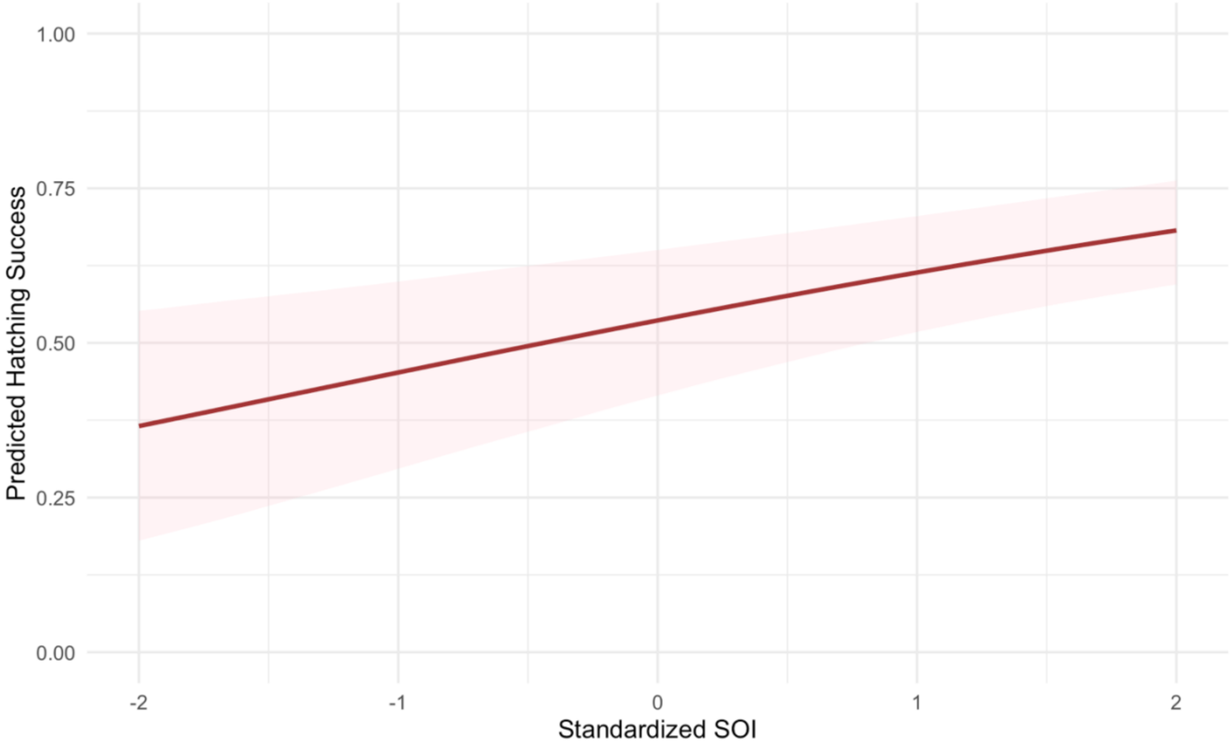

Figure 2.5 Predicted effect of Southern Oscillation Index on hatching success of Brown Booby nests on Tetiaroa Atoll, French Polynesia, 2021 – 2024. Hatching success was estimated by compounding daily survival probabilities over a 47-day incubation period, derived from a Bayesian nest survival model. The *x*-axis shows standardized SOI values, where positive values indicate La Niña-like (cooler, more marine productivity) conditions and negative values indicate El Niño-like (warmer, less marine productivity) conditions. All other covariates, including swell height, nest density, and disease outbreak were held at their standardized means, and rat presence was set to 0. Predictions reflect conditions on Tahuna iti prior to rat suppression. The shaded ribbon shows the 95% credible interval. Hatching success increased with higher SOI values, consistent with enhanced reproductive success during La Niña conditions.

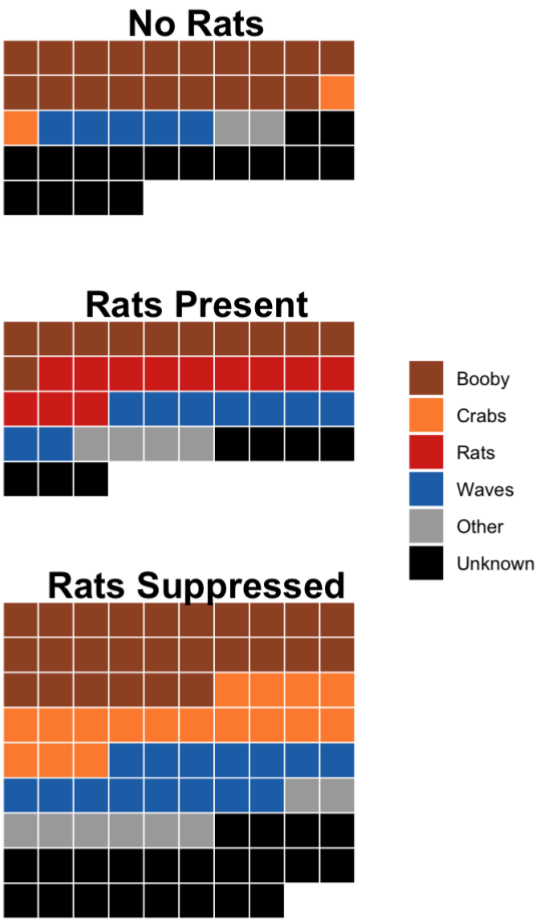

Figure 2.6 Mosaic plot of causes of egg removal caught on camera. One square represents one failed nest that we monitored. Causes of egg removal included: adult Booby egg ejection, crab depredation, rat depredation, nest flooding during inundation events, other, and undetermined. All 176 failures were plotted, which includes 13 nests that failed after hatching, 48 nests that failed as egg(s) after 53 days, and 115 nests that failed as viable eggs. Nests on Tahuna iti are in the top section labeled as "No Rats", while nests on Horoāterā and Tia'ra'aunu are grouped into the bottom two sections, before and after rat suppression.

Chapter 3: Terrestrial Habitat Use by Seabirds in the Tropical Pacific

This work was coauthored with Sarah J. Converse, Amelia J. DuVall, Jayna L. DeVore, and Beth Gardner. At the time of publication of this thesis, it was not in review at a journal.

3.1 Abstract

Terrestrial habitats are critical for breeding seabirds, but the terrestrial habitats used by tropical seabirds have not been well described. We investigated terrestrial habitat associations of four seabird species, the Red-footed Booby (*Sula sula*), Brown Noddy (*Anous stolidus*), Black Noddy (*Anous minutus*), and White Tern (*Gygis alba*) on Tetiaroa Atoll, Society Islands, French Polynesia. We conducted 824 avian point counts with multiple observers at 110 sites between 2022 and 2024 and measured a variety of habitat variables at each site. We fit species-specific *N*-mixture models to the avian point count data, using a zero-inflated Poisson distribution to model abundance. We included habitat variables in both the zero-inflation and abundance components of the model for each species. Estimated Red-footed Booby abundance was higher in areas closer to the shoreline, with greater amounts of the coastal shrub, *Heliotropium arboretum,* and native forest trees including *Pisonia grandis*, and in areas with more open space in the herbaceous layer. Abundance was lower with greater amounts of *Cocos nucifera* trees. We found Brown Noddy estimated abundance was lower in areas with greater amounts of *Pandanus tectorius* trees. Estimates of Black Noddy abundance and probability of White Tern presence were higher with greater amounts of native forest trees including *Pisonia grandis*. Our findings provide information on habitat associations of these seabird species, which can be used to inform conservation strategies on Tetiaroa and other atolls.

3.2 Introduction

Avian habitat use has been studied for over a century, and ornithologists have contributed substantially to the development of the ecological concept of habitat (Block & Brennan, 1993). However, knowledge of habitat relationships is highly uneven across avian groups, and the terrestrial habitat associations of tropical seabirds are not well understood. Atolls are tropical seabird hotspots that provide critical breeding and roosting sites (Sandin et al., 2022; Berr et al., 2023) for an estimated >30 million seabirds of 37 species (Steibl et al., 2024a). Many are home to the last *Pisonia grandis* forests in the world, as well as many other specialized salt-tolerant plants (Fosberg, 1949; Mueller-Dombois & Fosberg, 1998; Steibl et al., 2024b). In the Pacific, atolls have experienced a number of colonial and industrial anthropogenic pressures including development of *Cocos nucifera* (coconut palm) plantations, phosphate mines, military bases and bomb testing sites, and many are now undergoing other types of anthropogenic disturbances due to tourism (Molle et al., 2019; Steibl et al., 2024c). Each of these changes has directly impacted the native vegetation, but the extent to how seabird populations have been effected is poorly understood.

Invasive plants can cause dramatic community shifts and nutrient depletion (Young et al., 2017) in tropical forests. Across the Indian and Pacific Oceans, large swaths of many islands were once cleared and developed into *Cocos nucifera* plantations, now one of the most common vegetation types on tropical islands, covering almost 60% of all forested areas on Pacific atolls (Mueller-Dombois & Fosberg, 1998; von Brandis, 2012; Burnett et al., 2024). Coconut production is no longer commercially viable on most of these islands, as production has moved to mainland areas, leaving behind abandoned plantations that transition into dense monoculture stands (von Brandis, 2012; Carr et al., 2021). *Cocos nucifera* is now considered an invasive species in these areas (Young et al., 2017), and its global proliferation is reducing diversity of native flora, increasing mortality of native plant seedlings, depleting soils, affecting fresh ground water sources, and altering the nutrient cycling and fundamental ecosystem functioning of atolls through linked affects with breeding seabirds (Young et al., 2010; Young et al., 2014). Seabirds are known to use native flora species that are widespread across tropical atolls, such as *Pisonia grandis* (Young et al., 2010; Carr et al., 2021). This and other native tree species provide critical seabird nesting and roosting habitat, and can be outcompeted by fast-growing palms (Sachet & Fosberg, 1983; Mueller-Dombois & Fosberg, 1998). Young et al. (2010) speculate that *Cocos nucifera* may not provide suitable perches for roosting birds, and that rats (*Rattus* spp.) may nest and feed in *Cocos nucifera*, thus causing seabirds to avoid them. Declines in roosting seabird abundance result in declines in soil and leaf nutrient quality (Young et al., 2010) in the terrestrial environment and diminished nutrient leaching into coral reefs (Benkwitt et al., 2021; Graham et al., 2018).

Introduced predators, such as rodents, can have cascading effects on island ecosystems (Benkwitt et al., 2021; Graham et al., 2018). Islands often host several genera of invasive species, which can also interact with one another (Miller-ter Kuile et al., 2021). Rats can have direct negative effects on tropical seabirds; however, control of such introduced predators can lead to other habitat changes. The suppression and extinction of many plants across the tropical Pacific, including native broadleaf trees, is due in part to black rats (Meyer & Butaud, 2009; Miller-ter Kuile et al., 2021). Black rats are also known to directly consume *Cocos nucifera* (Harper & Bunbury, 2015), targeting pre-mature seeds in the canopy (Wegmann, 2009). When black rats

(*Rattus rattus*) are eradicated on islands with former *Cocos nucifera* plantations, juvenile palm recruitment can skyrocket due to reduced depredation of coconuts (Nigro et al., 2017), which can pose a major threat to native flora growth and recovery unless rapidly mitigated (Wolf et al., 2018). Palmyra Atoll in the Line Islands has begun to show changes in vegetation after black rat eradication (Young et al., 2010; Young et al., 2017; Wolf et al., 2018). Similarly, in the Chagos Archipelago, post–rat eradication comparisons of abandoned *Cocos nucifera* plantations and native forests provide evidence that seabirds are selecting native forest to breed (Carr et al., 2021). Thus, even when invasive mammal eradications are successful, vegetation management in previously

We investigated habitat associations of four breeding seabirds on Tetiaroa Atoll, French Polynesia. Former *Cocos nucifera* plantations are a dominant habitat type on Tetiaroa, taking up 2.69 of the limited 5.22 total square kilometers of land area, and 70.2% of the total forested area, most of which is occurring as a monoculture (Burnett et al., 2023). In addition, a major rat eradication effort was conducted during our study; thus, Tetiaroa provides a valuable natural laboratory for studying habitat change and seabird response in an atoll ecosystem. We conducted repeated point counts and measured a suite of habitat characteristics to better understand associations between habitat and abundance of four seabird species.

We focused our effort on three species that nest exclusively in trees – Red-footed Boobies (*Sula sula*; ua‘ao; Richter-Gravier, 2019), Black Noddies (*Anous minutus*; kīkiriri; Richter-Gravier, 2019), and White Terns (*Gygis alba*; ‘ītāta‘e; Richter-Gravier, 2019) – and one species that is a generalist and nests both on the ground and in trees – Brown Noddies (*Anous stolidus*; ‘ōio;

Richter-Gravier, 2019). We made several predictions about the habitat associations of these four seabird species. We predicted that Red-footed Boobies would be positively associated with areas dominated by native shrubs and near coastlines. We predicted that Black Noddies and White Terns would be positively associated with stands of *Pisonia grandis*, and other native forest trees, and negatively associated with *Cocos nucifera*. Finally, we predicted that Brown Noddies would show the weakest habitat associations because of their generalist nature. Our results can inform vegetation restoration across Pacific atolls for the purpose of conserving seabird populations (Carr et al., 2021), along with the important ecosystem services that they provide (Benkwitt et al., 2021).

3.3 Methods

3.3.1 Study System

Atoll ecosystems have distinct terrestrial habitats which are delimited by soil development, salinity, and groundwater levels (Mueller-Dombois & Fosberg, 1998; Steibl et al., 2024b). Tetiaroa Atoll is one of five coral atolls in the Society Island chain of French Polynesia (17°00′S, 149°34′W), consisting of 12 motu (islets) of varying sizes, habitats, and histories. One of the motu, Onetahi, is human-inhabited and was not included in our data collection efforts. Residual *Cocos nucifera* monocultures, regenerating and old-growth native forests, belts of coastal herbaceous vegetation, inland brackish ponds with sedges, and more than a dozen mixed microhabitats (Mueller-Dombois & Fosberg, 1998; Stoll et al., 2023) cover the other motu. Two main forest types are found on the atoll: native forest dominated by either *Pisonia grandis* or *Pandanus tectorius* with secondary species such as *Guettarda speciosa* and *Cordia subcordata,* and former interior plantations dominated by invasive *Cocos nucifera* (Figure 1; Stoll et al., 2023). Coastal vegetation typically lines the motu perimeters, and primarily includes *Heliotropium arboreteum, Pemphis acidula, Suriana maritima,* and *Scaevola taccada*. *Casuarina equisetifolia* and *Calophyllum inophyllum*, tree species introduced by early voyagers, are also scattered throughout (Sachet & Fosberg, 1983).

During our study period (2022-2024), eleven seabird species were found breeding on Tetiaroa. We focus here on four of them. The most abundant species in the family Sulidae on Tetiaroa is the pantropical tree-nesting Red-footed Booby. They are plunge-divers that feed on squid, flying fish, and other forage fish (Nelson, 1978). Brown Noddies are a tropical member of the family Laridae that forage in large fixed flocks for small squid and fish (Mlodinow et al., 2025). They are the most abundant seabird species on Tetiaroa and are generalists that can nest both on the ground and in trees. Black Noddies are one of the only true tree-nesting members of Laridae, along with Lesser Noddies (*Anous tenuirostris*) and White Terns (Thibault & Cibois, 2017). White Terns are notable in their nesting habits as they balance their egg on a tree branch instead of building a nest structure. They are found throughout tropical and subtropical oceans (Thibault & Cibois, 2017) , and are present across all motu on Tetiaroa (Vansse et al., 2023).

3.3.2 Avian Point Counts

From January 2022 – November 2024, we conducted *n* = 824 repeated point counts at 110 fixed locations (Figure 3.1). We conducted between 5 and 11 counts per site, with this variation due to scheduling amidst other data collection activities. The 110 sites were spread across the 11 motu that are uninhabited by humans. An initial set of 41 sites were selected along the coastlines of each of the 11 motu, with the number of sites proportional to motu size and sites randomly placed either ~10m or ~100m inland from the shoreline. On four motu of particular interest for seabird study, we placed a grid over the motu and selected additional sites, again with the number of sites proportional to the size of the motu, resulting in 110 sites.

We conducted instantaneous point counts in a 15-m radius circle around the center of each site. The sampling radius was delineated using a range-finder or a measuring tape. We conducted the instantaneous count after an initial 5-minute settling period, during which observers remained stationary at the center of the site. Observers recorded all species within the 15-m radius, and provided a breakdown of the count by age (adult or juvenile) and whether the individual was sitting or flying. However, we only included sitting birds and we used the sum of adults and juveniles in our analysis. A subset of the point counts included multiple independent observers, which allowed us to estimate detection probability. When multiple observers participated in a point count, they worked to remain independent of each other during the count. Of the 824 point counts, 572 involved one observer, 238 involved two observers, and 14 involved three observers. A total of 12 different observers participated in point counts over the >3-year period of data collection. Black Noddies were only observed on a single motu, Reiono, during all counts. Therefore, we decided to limit our analysis for Black Noddies to this motu only. For Black Noddies, we modeled data from 156 point counts at 22 sites, with between 6 and 9 counts per site. Of those counts, 96 involved one observer, 58 involved two observers, and 3 involved three observers.

3.3.3 Vegetation Surveys

We sampled vegetation at the 110 sampling sites in April and May 2023 (Figure 3.1). We identified four habitat strata of interest: ground cover, herbaceous layer, juvenile trees, and large mature trees (>10m high for *Cocos nucifera*, >5m for all other species). Ground cover and herbaceous layer data were collected at two locations 10 m from the center of the site, in two cardinal directions that were selected randomly at each site. Sampling for ground cover and herbaceous layer was conducted inside a 1-m diameter circular hoop. Percentages were estimated visually with the sum equal to 100%. For ground cover, categories were bare sand, leaf litter, coral rubble, *Cocos* debris, *Pandanus* debris, cyanobacteria, grasses and sedges, and other ground plants. The herbaceous layer was categorized by percentages of each plant species present, as well as the percentage of empty ground (Table 3.1). For trees, we counted all juvenile and adult trees by species within 5 m of the center of each site (Table 3.1).

3.3.5 N-Mixture Modeling

We built *N*-mixture models (Royle & Nichols, 2003; Royle & Nichols, 2004) to analyze the avian point count data. These models exploit repeat counts (i.e., by two observers at the same time) to address imperfect detection in abundance estimation. For each species individually, we modeled observed counts, $y_{s,k,o}$, for each site s, visit k, and observer o as a random sample from a binomial distribution with probability of detection p_o and abundance $N_{s,k}$:

$$y_{s,k,o} \sim Binomial(p_o, N_{s,k}).$$

We modeled the detection probability using a logit link function with an intercept, $\overline{\alpha}$, and a random effect of observer with variance $\sigma^2_{(p-observer)}$, for 12 individual observers who participated in counts during the study period:

$$logit(p_o) = \overline{\alpha} + \alpha_o$$

$$\alpha_o \sim Normal(0, \sigma^2_{(p-observer)}).$$

We modeled abundance using a Poisson-Bernoulli mixture distribution to account for zero-inflation. We modeled abundance, $N_{s,k}$, at site s on visit k, as:

$$N_{s,k} \sim Poisson(z_{s,k} * \lambda_{s,k})$$

$$z_{s,k} \sim Bernoulli(\gamma_{s,k})$$

where $z_{s,k}$ is a Bernoulli outcome with expectation $\gamma_{s,k}$ that controls the zero-inflation component of the model while $\lambda_{s,k}$ is the expected mean of the Poisson component of the model conditional on $z_{s,k}$.

We then modeled $\gamma_{s,k}$ with a logit link, a set of species-specific fixed effects $X\beta_{(\gamma)}$ and random effects of site (ε_s) with variance $\sigma^2_{(\gamma-site)}$. We modeled $\lambda_{s,k}$ with a log link, a set of species-specific fixed effects $X\beta_{(\lambda)}$, random effects of site (ξ_s) with variance $\sigma^2_{(\gamma-site)}$, and random effects of the month in which k survey occurred ($\xi_{month[k]}$) with variance $\sigma^2_{(\gamma-month)}$, as follows:

$$logit(\gamma_{s,k}) = X\beta_{(\gamma)} + \varepsilon_s$$

$$\varepsilon_s \sim Normal(0, \sigma^2_{(\gamma-site)})$$

and

$$log(\lambda_{s,k}) = X\beta_{(\lambda)} + \xi_s + \xi_{month[k]}$$

$$\xi_s \sim Normal(0, \sigma^2_{(\lambda-site)})$$

$$\xi_{month} \sim Normal(0, \sigma^2_{(\lambda-month)}).$$

We used this general model structure for all species, but analyzed a unique model for each species. For three species – Red-footed Booby, Brown Noddy, and Black Noddy – we primarily modeled fixed effects on the Poisson component of the model, $\lambda_{s,k}$, because the counts were relatively large (ranging up to 24 for Red-footed Booby, 55 for Brown Noddy, and 68 for Black Noddy). However, for White Tern, the largest count ever observed was 9, so we focused on modeling fixed effects on the Bernoulli component of the model, $\gamma_{s,k}$, for this species. Covariates that appeared in one or more models included: mature *Cocos nucifera* counts over >10m in height, mature *Pandanus tectorius* counts >5m in height, mature native forest tree (summed counts of *Pisonia grandis*, *Guettarda speciosa*, and *Cordia subcordata* >5m in height) counts, *Heliotropium arboretum* counts of all heights, *Pemphis acidula* counts of all heights, estimated percentage cover that was free of herbaceous plants (open space), and the distance of plot centers from the nearest shoreline in meters. We determined what to include as fixed effects based on observations and life-history considerations for each species. See Table 3.2 for covariates included in the models for each species.

In a secondary analysis, we used a multivariate clustering method to classify all sampling points into one of three habitat classes, and we modeled habitat associations between seabird presence and abundance as a function of habitat class. Detailed methods and results for this analysis are reported in Appendix 3A.1.

3.3.5 Model Implementation

All analyses were conducted in R, version 4.4.2 (R Core Team 2024) using the NIMBLE package, version 1.3.0 (NIMBLE Development Team). We standardized all continuous covariates. We specified relatively uninformative priors for all parameters. Intercepts and fixed covariate effects in the zero-inflation portion of the model were assigned Normal priors with mean = 0 and either SD = 1 or SD = 2; intercepts and fixed covariate effects in the Poisson portion of the model were assigned Normal priors with mean = 0 and SD = 2. The parameter representing the mean detection probability was assigned a Normal prior with mean = 0 and SD = 1. The variances of random effects (observer-, point-, and month-level) were assigned Gamma(5, 5) priors. We quantified the probability of direction (pd) as the proportion of posterior samples with the same sign as the posterior mean. The pd represents the certainty that an effect is either positive or negative, with values near 1 indicate strong support for an effect, and lower values reflecting higher uncertainty in the direction of an effect. We ran the model for 200,000 iterations for Red-footed Boobies, Brown Noddies, and White Terns, and 400,000 iterations for Black Noddies across each of three Markov chains and discarded the first 50,000 iterations from each chain as burn-in. We visually checked chains for convergence and mixing and we ensured that the Gelman-Rubin $\hat{R}$ statistic (Gelman & Rubin, 1992) for all parameters was < 1.1. Code and data are available at https://github.com/EveMHallock/TetiaroaPointCounts.

3.4 Results

3.4.1 Red-footed Boobies

We identified several useful predictors of abundance for Red-footed Boobies (Table 3.3). Abundance of Red-footed Boobies was positively associated with *Heliotropium arboreum* counts (mean estimate = 0.77; 95% credible interval (CRI) = (0.39, 1.18); pd = 1.00; Figure 3.2), positively associated with mature native forest trees (0.58; (0.10, 1.08); pd = 0.99; Figure 3.3), positively associated with an open herbaceous layer (0.49; (–0.12, 1.12); pd =0.94; Figure 3.4), and negatively associated with *Cocos nucifera* counts (–1.46; (–2.50, –0.53); pd = 1.00; Figure 3.5). Presence of Red-Footed Boobies was negatively associated with distance to shoreline (–2.56; (–3.74, –1.40); pd = 1.00; Figure 3.6). We did not detect an association between Red-footed Booby abundance and counts of *Pemphis acidula*. Predicted abundance of Red-footed Boobies, though credible intervals were wide in some months, which may be masking some season variation that was not detected likely due to sparse observations (Figure 3.7).

3.4.2 Brown Noddies

We found fewer useful predictors for Brown Noddies (Table 3.4). We found support for a negative effect of *Pandanus tectorius* counts on Brown Noddy abundance (–0.43; 95% CRI = (–0.82, –0.04); pd = 0.98; Figure 3.8) and a positive effect of an open herbaceous layer (0.28; (–0.08, 0.64); pd = 0.94; Figure 3.9). We found no effects of *Cocos nucifera* counts or counts of native forest trees on abundance, and no effect of distance from shoreline on presence (Table 3.4). Brown Noddies exhibited relatively stable abundance across most months, with a peak in abundance in August (Figure 3.10).

3.4.3 Black Noddies

We detected a positive effect of mature native forest trees (0.74, 95% CRI: 0.04, 1.43; pd = 0.98; Figure 3.11) on Black Noddy abundance. We found no discernible effects of *Cocos nucifera* counts or *Pandanus tectorius* counts on abundance (Table 3.5). No point counts were conducted in January, August, or December on Reiono, however some variation was observed across months, with a peak in abundance in June (Figure 3.12).

3.4.4 White Terns

For White Terns, which had the lowest observed counts, we modeled effects of habitat variables only on the zero-inflation (presence) component of the model. Mature native forest trees had a positive effect on presence (1.97, 95% CRI: (0.97, 3.08); pd = 1.00; Figure 3.13). Similarly, mature *Pandanus tectorius* trees had a positive effect on presence (0.57; (–0.31, 1.32); pd = 0.97). Mature *Cocos nucifera* trees had a negative effect on presence (–0.33, (–1.00, 0.34); pd = 0.84; Table 3.6). We did not detect an effect of distance to shoreline on White Tern presence (Table 3.6). Some variation was observed across months, with a peak in abundance in February (Figure 3.14).

3.5 Discussion

We predicted that *Cocos nucifera* stands would provide little habitat for seabirds, that Black Noddies and White Terns would select native forest stands such as *Pisonia grandis* and *Pandanus tectorius* trees for breeding and roosting, and Red-footed Boobies would select native coastal shrubs, while Brown Noddies would be less selective by using a variety of habitats, including open areas. We anticipated finding lower seabird abundances in areas with higher densities of invasive vegetation compared to sites with more intact native forests or native flora. As expected, we found that the presence of *Cocos nucifera*, a widespread invasive tree on tropical atolls, was generally associated with reduced seabird abundance or probability of presence. In contrast, native plant species such as *Heliotropium arboreum*, *Pandanus tectorius*, and mixed native forest trees tended to show more positive associations for some species. These results are consistent with previous studies on other ecologically similar atolls, including Palmyra Atoll and in the Chagos Archipelago, where seabirds have also been found avoiding dense coconut monocultures in favor of subtropical island native broadleaf forests (Carr et al., 2021; Young et al., 2010).

Consistent with our results, Red-footed Boobies have been observed nesting and roosting on most coastlines of Tetiaroa's motu, in areas with mature *Pisonia grandis and Heliotropium arboreum.* However, we did not detect an effect of *Pemphis acidula* on abundance, despite it being a commonly used tree species for Red-footed Booby nests on Tetiaroa. Our selection of point count locations resulted in relatively few sites containing *Pemphis acidula* trees; this plant usually grows on rock or coral aggregate substrate directly on the shoreline (Sachet & Fosberg, 1983; Mueller-Dombois & Fosberg, 1998). Few studies have examined microhabitat or nesting site selection for Red-footed Boobies, however *Cordia, Pandanus, Ficus, Suariana*, and *Scaevola* species have been noted as nesting trees, particularly *Cordia sebestena* in Belize (Verner, 1961). We found that abundance decreased in areas with more *Cocos nucifera*, while on Clipperton Island, Red-footed Boobies were observed using introduced and expanding groves of

Cocos nucifera and *Casuarina equisetifolia* trees for roosting and nesting, with a noted lack of available native trees or shrub species (Dodson & Fitzgerald, 1980).

Brown Noddies may exhibit more flexibility in their habitat selection, using a variety of flora species as well as open ground. We did not detect a relationship between Brown Noddy abundance and *Cocos nucifera*, consistent with previous findings of their behavioral flexibility (Mlodinow et al., 2025). While individual effects of flora were generally weak or uncertain, mature *Pandanus* had a negative association with abundance (Table 3.4; Figure 3.8). However, Brown Noddies do nest in *Pandanus tectorius* on motu such as Aie, which had yellow crazy ants depredating small chicks on the ground (DeVore & Ducatez, personal communication). Percentage of open space showed a slight positive effect on Brown Noddy abundance (Table 3.4), although we expected a stronger effect, as they do nest on the ground on some motu, particularly those that are free of invasive rats. Rats have been documented depredating Brown Noddy eggs on Tetiaroa (DeVore & Ducatez, personal communication). On other islands, it has been noted that Brown Noddy nests tend to be near the perimeters of islands, avoiding areas dominated by Sooty Terns (*Onychoprion fuscatus*) (Saliva, 2009). We did not detect an effect of distance on Brown Noddy presence (Table 3.4), though they only overlap with Sooty Terns in four of our point count sites. Brown Noddies display a high degree of behavioral flexibility and less colonial behavior than the ground-nesting Larids. Across their range, many colonies are near cliffs, and frequently used substrates include bare rock, coral, sand, gravel, soil, tree branches, palm fronds, grass, and other plant matter (Mlodinow et al., 2025). Nests can be placed in a variety of heat-tolerant trees and shrubs. On the Dry Tortugas, the primary plant species used is *Suriana maritima* (Stevenson & Anderson, 1994), a tree that is also used in Puerto Rico (Saliva, 2009). In the Indian Ocean, *Cocos nucifera*, *Pandana* spp., *Heliotropium arboretum*, and *Scaevola ssp.* provide nest sites (Mlodinow et al., 2025). On Ile du Coin, Banhos Atoll, researchers found similar probabilities of breeding habitat use across non-native forest, native forest, and savanna habitats, and use of beaches (Carr et al., 2021). On Tetiaroa, Brown Noddies are observed nesting in almost any tree species, including living *Cocos nucifera*, or on the ground.

Few comprehensive microhabitat or nest site selection studies have been conducted on Black Noddies, but they are thought to usually nest in *Pisonia grandis* and *Guettarda speciosa* across their range (Thibault & Cibois, 2017). We had expected a strong preference for native forest dominated by *Pisonia grandis* and other mixed broadleaf trees, and we did find a 0.98 probability of a positive effect of mature native forest trees on abundance (Table 3.5; see also Figure 3.11). Black Noddies tend to form dense colonies in a limited number of trees, which led to unexpectedly high counts in some of our sites. Our results for Black Noddies likely reflect a combination of spatial clustering at colony sites and relative lack of floristic diversity on Reiono, which is the only motu they nested on Tetiaroa during this study. They construct cup-shaped arboreal nests out of large dead *Pisonia grandis* on Reiono, but in other locations, such as Tern Island, Hawaii, they have been known to use guano, seaweed, sticks, feathers, fur, and grass (Amerson, 1971). We did not find strong evidence of a negative effect of *Cocos nucifera,* which contrasts with findings from other tropical atolls where this palm species is considered poor habitat for seabird nesting due to its structure and lack of branches (Young et al., 2010). Black Noddy nesting may be influenced by sociality and historical nest-site fidelity rather than specific tree species alone.

We found positive associations between the probability of White Tern presence and counts of mature *Pandanus tectorius* and other mature native forest trees (*Pisonia grandis*, *Guettarda speciosa*, and *Cordia subcordata*; Table 3.6; Figure 3.13), which was expected. Vansse (2023) reported that both *Pisonia grandis* and *Pandanus tectorius* were commonly used for nesting trees, but that nests were more numerous in *Pandanus*-dominant forest. They did not document any nests in *Cocos nucifera* stands (Vansse et al., 2023), and while we found less certain but negative effects of *Cocos nucifera* counts on probability of White Tern presence (Table 3.6), we did record two nests in dead palm trunks at our sites. On Ile du Coin, Peros Banhos Atoll, White Terns used both non-native (classified as 92% *Cocos nucifera* monoculture stands in their study) and native forest (Carr et al., 2021). While we did not find an effect of distance to shoreline on probability of presence, Vansse (2023) found that White Terns on Tetiaroa preferred to nest closer to shorelines. On Onetahi, the motu without avian point count sites, introduced *Causarina equisetifolia* is used by White Terns (Hallock, personal observation), and this tree was reported to be the most common choice on Midway Atoll (Howell, 1978). On Christmas Island, they were found using old Black Noddy nests and *Heliotropium arboreum* branches (Gallagher, 1960), while in the Seychelles they use *Pisonia grandis* and other native trees (Skerrett et al., 2001) and on Sapwuahfik Atoll, White Terns were reported as common in *Pandanus spp*. and *Cocos nucifera* trees, although it is unclear if nesting sites were determined (Buden, 1999). Targeted investigation into tree species availability versus probability of usage given availability would improve our understanding of this species' habitat selection, and potential behavioral flexibility.

We also expected temporal variation in the avian count data, with fluctuations in abundance and presence corresponding with relatively subtle tropical seasonal changes in environmental conditions. For example, preference for specific habitat types during the breeding season could shift during non-breeding periods. All four seabird species displayed slightly different seasonal patterns, with peaks in abundance occurring in different months (Figures 3.7, 3.10, 3.12-3.14). Longer-term phenology studies are underway on Tetiaroa for all seabird species and will provide insight into these remaining questions (DeVore & Ducatez, personal communication).

Native forests on islands like those remaining on Tetiaroa are of great conservation importance. Globally, 63% of islands with highly threated breeding vertebrate species are located in the central Indo-Pacific biogeographic region (over 800), 42% of which support tropical and subtropical moist broadleaf forest habitats (Spatz et al., 2017). Vegetation in tropical environments can grow and shift quickly, and is vulnerable to invasive species and climate change (Stoll et al., 2023.; Wolf et al., 2018). Less than 25% of Tetiaroa's land area is comprised of broadleaf canopy today, a lasting impact of plantation development (Burnett et al., 2024). It would be useful to repeat our vegetation surveys to detect habitat changes over time, especially as rat eradication efforts continue, which will likely impact native seedling recruitment, as observed on Palmyra Atoll (Wolf et al., 2018). Information from the habitat assessments could also be used to ground-truth existing lidar surveys (Stoll et al., 2023), and in predicting which areas may experience vegetation changes or new seabird activity. As seen on other atolls, when rat densities diminish and vegetation management begins to be implemented, habitats shift as native plants expand into new areas (Wolf et al., 2018). The eradication of invasive predators, paired with targeted *Cocos nucifera* control and removal may lead to habitat recovery and increased seabird occupancy in previously disturbed areas (Carr et al., 2021). While similar ecological restoration efforts are underway, results from our models will be important in establishing baseline seabird species distributions and terrestrial habitat use patterns on Tetiaroa Atoll.

3.6 Acknowledgements

Funding was provided by the USDA Bridging the Gap Fellowship through the University of Washington School of Environmental and Forest Sciences. Funding was also provided by the Tetiaroa Society, and the Seeley, Bailey, and Alexander families. Additional support was provided by the Washington Cooperative Fish and Wildlife Research Unit. We thank Dee Boersma and Julia Parrish, and numerous volunteers who participated in fieldwork and data processing. Avian point counts were conducted under University of Washington Institution Animal Care Protocol #4448-01 and under French Polynesian research permits.

3.7 Literature Cited

Amerson, A. B. (1971). The natural history of French Frigate Shoals, Northwestern Hawaiian Islands. *Atoll Research Bulletin*, 150. Benkwitt, C. E., Gunn, R. L., Le Corre, M., Carr, P., & Graham, N. A. J. (2021). Rat eradication restores nutrient subsidies from seabirds across terrestrial and marine ecosystems. *Current Biology*, *31*(12), 2704-2711.e4. https://doi.org/10.1016/j.cub.2021.03.104

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

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

Block, W. M., & Brennan, L. A. (1993). The Habitat Concept in Ornithology. In D. M. Power (Ed.), *Current Ornithology: Volume 11* (pp. 35–91). Springer US. https://doi.org/10.1007/978-1-4757-9912-5_2

Budden, D., W. (1999). The birds of Sapwuahfik Atoll, with first record of the Grey Wagtail, *Motacilla cinerea*, from the Federation States of Micronesia. *Bulletin of the British Ornithologists' Club.* 119(4), p. 266. https://www.biodiversitylibrary.org/page/40025531

Burnett, M. W., French, R., Jones, B., Fischer, A., Holland, A., Roybal, I., White, T., Steibl, S., Anderegg, L. D. L., Young, H., Holmes, N. D., & Wegmann, A. (2024). Satellite imagery reveals widespread coconut plantations on Pacific atolls. *Environmental Research Letters*, *19*(12), 124095. https://doi.org/10.1088/1748-9326/ad8c66

Carr, P., Trevail, A., Bárrios, S., Clubbe, C., Freeman, R., Koldewey, H. J., Votier, S. C., Wilkinson, T., & Nicoll, M. A. C. (2021). Potential benefits to breeding seabirds of converting abandoned coconut plantations to native habitats after invasive predator eradication. *Restoration Ecology*, *29*(5), e13386. https://doi.org/10.1111/rec.13386

Dodson, J. J. and G. J. Fitzgerald. (1980). Observations on the breeding biology of the boobies (Sulidae) at Clipperton Islands, eastern Pacific. Nat. Can. 107:259-267.

Duda, M. P., Glew, J. R., Michelutti, N., Robertson, G. J., Montevecchi, W. A., Kissinger, J. A., Eickmeyer, D. C., Blais, J. M., & Smol, J. P. (2020). Long-Term Changes in Terrestrial Vegetation Linked to Shifts in a Colonial Seabird Population. *Ecosystems, 23*(8), 1643–1656. https://doi.org/10.1007/s10021-020-00494-8

Fosberg, F.R. (1949). Atoll vegetation and salinity. *Pac Sci 3*(1): 89-92.

Gallagher, M. D. (1960). Bird notes from Christmas Island, Pacific Ocean. *Ibis.* 102 (4):489-502.

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

Howell, T. R. (1978). Ecology and reproductive behavior of the White, or Fairy, Tern. In Ecology and reproductive behaviour of the Gray Gull and of the Red-tailed Tropicbird and the White Tern on Midway Island, 274-284. *Natl. Geogr. Soc. Res. Rep.* 10.

Meyer, J.-Y., & Butaud, J.-F. (2009). The impacts of rats on the endangered native flora of French Polynesia (Pacific Islands): Drivers of plant extinction or coup de grâce species? *Biological Invasions*, *11*(7), 1569–1585. https://doi.org/10.1007/s10530-008-9407-y

Miller-ter Kuile, A., Orr, D., Bui, A., Dirzo, R., Klope, M., McCauley, D., Motta, C., & Young, H. (2021). Impacts of rodent eradication on seed predation and plant community biomass on a tropical atoll. *Biotropica*, *53*(1), 232–242. https://doi.org/10.1111/btp.12864

Mlodinow, S. G., J. W. Chardine, R. D. Morris, M. Gochfeld, J. Burger, G. M. Kirwan, and E. Garcia (2025). Brown Noddy (*Anous stolidus*), version 2.0. In *Birds of the World* (S. M. Billerman and M. G. Smith, Editors). *Cornell Lab of Ornithology*, Ithaca, NY, USA. https://doi.org/10.2173/bow.brnnod.02

Molle, G., Hermann, A., Lagarde, L., & Stoll, B. (2019). The Long-Term History of Teti'aroa (Society Islands, French Polynesia): New archaeological and ethnohistorical investigations. *Research Report*, *10*(2).

Mueller-Dombois, D. & Fosberg, F.R. (1998). Vegetation of the Tropical Pacific Islands. Springer, New York.

Nelson, J. B. (1978). *The Sulidae: Gannets and Boobies* (1st ed.). University of Aberdeen.

Nigro, K. M., Hathaway, S. A., Wegmann, A. S., Miller-ter Kuile, A., Fisher, R. N., & Young, H. S. (2017). Stable isotope analysis as an early monitoring tool for community-scale effects of rat eradication. *Restoration Ecology*, *25*(6), 1015–1025. https://doi.org/10.1111/rec.12511

NIMBLE Development Team. (2024). NIMBLE: MCMC, Particle Filtering, and Programmable Hierarchical Modeling. doi:0.5281/zenodo.1211190. R package version 1.3.0, https://cran.r-project.org/package=nimble.

R Core Team (2024). _R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.

Richter-Gravier, Raphael. (2019). Manu Narratives of Polynesia: A Comparative Study of Birds in 300 Traditional Polynesian Stories. PhD Thesis. *University of Otago, L'Université de la Polynésie Française*.

Royle, J.A. and Nichols, J.D. (2003), Estimating Abundance from Repeated Presence–Absence Data or Point Counts. Ecology, 84: 777-790. https://doi.org/10.1890/0012-9658(2003)084[0777:EAFRPA]2.0.CO;2

Royle, J. A. (2004). N-Mixture Models for Estimating Population Size from Spatially Replicated Counts. *Biometrics*, *60*(1), 108–115. https://doi.org/10.1111/j.0006-341X.2004.00142.x

Sachet, M.-H., & Fosberg, F. R. (1983). An ecological reconnaissance of Tetiaroa Atoll, Society Islands. *Atoll Research Bulletin*, *275*, 1–67. https://doi.org/10.5479/si.00775630.275.1

Sandin, S. A., Becker, P. A., Becker, C., Brown, K., Erazo, N. G., Figuerola, C., Fisher, R. N., Friedlander, A. M., Fukami, T., Graham, N. A. J., Gruner, D. S., Holmes, N. D., Holthuijzen, W. A., Jones, H. P., Rios, M., Samaniego, A., Sechrest, W., Semmens, B. X., Thornton, H. E., Zgliczynski, B. J. (2022). Harnessing island–ocean connections to maximize marine benefits of island conservation. *Proceedings of the National Academy of Sciences*, *119*(51), e2122354119. https://doi.org/10.1073/pnas.2122354119

Skerrett, A., Bullock, I., & Disley, T. (2001). *Birds of Seychelles*. Christopher Helm.

Spatz, D. R., Zilliacus, K. M., Holmes, N. D., Butchart, S. H. M., Genovesi, P., Ceballos, G., Tershy, B. R., & Croll, D. A. (2017). Globally threatened vertebrates on islands with invasive species. *Science Advances*, *3*(10), e1603080. https://doi.org/10.1126/sciadv.1603080

Steibl, S., Steiger, S., Wegmann, A. S., Holmes, N. D., Young, H. S., Carr, P., & Russell, J. C. (2024a). Atolls are globally important sites for tropical seabirds. *Nature Ecology & Evolution*, *8*(10), 1907–1915. https://doi.org/10.1038/s41559-024-02496-4

Steibl, S., Bunbury, N., Young, H. S., & Russell, J. C. (2024b). A Renaissance of Atoll Ecology. *Annual Review of Ecology, Evolution, and Systematics*, *55*(Volume 55, 2024), 301–322. https://doi.org/10.1146/annurev-ecolsys-102722-013447

Steibl, S., Kench, P. S., Young, H. S., Wegmann, A. S., Holmes, N. D., Bunbury, N., Teavai-Murphy, T. H., Davies, N., Murphy, F., & Russell, J. C. (2024c). Rethinking atoll futures: Local resilience to global challenges. *Trends in Ecology & Evolution*, *0*(0). https://doi.org/10.1016/j.tree.2023.11.004

Stoll, B., Tuheiava, P., Badie, M., & Oliveira, L. D. (2023). *Cartographie lidar des biotopes terrestres, marins et intertidaux de l'atoll de Tetiaroa*.

Thibault, J.-C., & Cibois, A. (2017). *Birds of eastern Polynesia: A biogeographic atlas* (First edition). Lynx Edicions.

Verner, J. (1961). Nesting Activities of the Red-Footed Booby in British Honduras. *The Auk*, *78*(4), 573–594. https://doi.org/10.2307/4082191

von Brandis, R. G. (2012). Rehabilitation of abandoned coconut plantations at D'Arros Island, Republic of Seychelles. *Ocean & Coastal Management*, *69*, 340–346. https://doi.org/10.1016/j.ocecoaman.2012.09.003

Wegmann, A. (2009). *Limitations to tree seedling recruitment at Palmyra Atoll*. Honolulu: University of Hawaii at Manoa.

Wolf, C. A., Young, H. S., Zilliacus, K. M., Wegmann, A. S., McKown, M., Holmes, N. D., Tershy, B. R., Dirzo, R., Kropidlowski, S., & Croll, D. A. (2018). Invasive rat eradication strongly impacts plant recruitment on a tropical atoll. *PLOS ONE*, *13*(7), e0200743. https://doi.org/10.1371/journal.pone.0200743

Young, H. S., McCauley, D. J., Dunbar, R. B., & Dirzo, R. (2010). Plants cause ecosystem nutrient depletion via the interruption of bird-derived spatial subsidies. *Proceedings of the National Academy of Sciences*, *107*(5), 2072–2077. https://doi.org/10.1073/pnas.0914169107

Young, H. S., McCauley, D. J., Pollock, A., & Dirzo, R. (2014). Differential plant damage due to litterfall in palm-dominated forest stands in a Central Pacific atoll. *Journal of Tropical Ecology, 30*(3), 231–236. doi:10.1017/S026646741400008X

Young, H. S., Miller-ter Kuile, A., McCauley, D. J., & Dirzo, R. (2017). Cascading community and ecosystem consequences of introduced coconut palms (*Cocos nucifera*) in tropical islands. *Canadian Journal of Zoology*, *95*(3), 139–148. https://doi.org/10.1139/cjz-2016-0107

Table 3.1 Ground cover, herbaceous layer cover, and plant stem count groupings used for flora-specific covariate models. Rarely counted species were excluded or grouped based on ecological similarity, structure, and observed height.

Response Category	Response	Included Species or Cover Types
Cover	**Bare ground**	Percent bare sand, cyanobacteria, and coral rubble
Cover	**Native plant debris**	Percent leaf litter, *Pandanus* debris, sticks, and logs
Cover	**Grasses**	Percent grasses (*Fimbristylis cymosa*, and others) and sedges (*Cladium mariscus*, and others)
Cover	***Cocos* debris**	Percent *Cocos* debris
Cover	**Native ground plants**	Percent *Laportea ruderlis*, *Portulaca lutea, Boerhavia tetrandra, Triumfetta procumbens*, and *Psilotum nudum*
Cover	**Tree seedlings**	Percent *Pandanus tectorius, Pisonia grandis, Morinda citrifolia, Calophyllum, Hibiscus (Hibiscus tiliaceus or Talipariti tiliaceum), Suriana maritima, Heliotropium arboreum, Guettarda speciosa, Pemphis acidula,* and *Cordia subcordata*
Cover	**Other native plants**	Percent *Timonius uniflorus, Scaevola taccada*, *Tacca leontopetaloides*, *Davallia solida*, *Asplenium nidus,* and *Microsorum grossum*
Cover	**Sprouted coconut**	Percent juvenile palm/sprouted coconut
Cover	**Open space**	Percent empty (no growing plants)
Stem Count	**Mature native forest trees**	*Pisonia grandis*, *Guettarda speciosa*, *Cordia subcordata*
Stem Count	**Mature introduced trees**	*Calophyllum inophyllum*, *Morinda citrifolia*, *Hibiscus (Hibiscus tiliaceus or Talipariti tiliaceum)*
Stem Count	**Mature *Pandanus***	*Pandanus tectorius* (individuals > 5m tall)
Stem Count	**Mature *Cocos***	*Cocos nucifera* (individuals > 10m tall)
Stem Count	**Juvenile *Cocos***	*Cocos nucifera* (<10m, including sprouted coconuts and saplings)
Stem Count	**Juv. native forest trees**	*Pandanus tectorius*, *Pisonia grandis*, *Guettarda speciosa*, *Cordia subcordata* (<5m)
Stem Count	**Juv. introduced trees**	*Casuarina equisetifolia*, *Calophyllum inophyllum*, *Morinda citrifolia*, *Hibiscus tiliaceus* (<5m)
Stem Count	**Native hedges**	*Scaevola taccada*, *Timonius uniflorus*
Stem Count	***Heliotropium***	*Heliotropium arboreum* (all sizes)
Stem Count	***Pemphis***	*Pemphis acidula* (all sizes)
Stem Count	***Suriana***	*Suriana maritima* (all sizes)

Table 3.2 Fixed effects included in N-mixture models for abundance of four seabird species on Tetiaroa Atoll, French Polynesia. The covariates included mature (>10m in height) *Cocos nucifera* counts, mature (>5m in height) *Pandanus tectorius* counts, mature (>5m in height) native forest tree (summed *Pisonia grandis*, *Guettarda speciosa*, and *Cordia subcordata*) counts, *Heliotropium arboretum* counts of all heights, *Pemphis acidula* counts of all heights, estimated percentage cover that was free of herbaceous plants (open space), and the distance of plot centers from the nearest shoreline in meters. All covariates were *Z*-scored before inclusion in models. Listed in the table for each species is information on whether a given covariate was included in the model for the Bernoulli component of the abundance model (thereby controlling the zero-inflation component of the model) or the Poisson component of the abundance model (thereby controlling the non-zero counts).

Covariates	**Red-footed Booby**	**Brown Noddy**	**Black Noddy**	**White Tern**
Cocos nucifera	Poisson	Poisson	Poisson	Bernoulli
Pandanus tectorius		Poisson	Poisson	Bernoulli
native forest trees	Poisson	Poisson	Poisson	Bernoulli
Heliotropium arboreum	Poisson			
Pemphis acidula	Poisson			
open space	Poisson	Poisson		
distance	Bernoulli	Bernoulli		Bernoulli

Table 3.3 Posterior summary statistics for parameters from the N-mixture model for Red-footed Booby (*Sula sula*). The model includes detection, abundance, and presence components. Parameters include an intercept and variance of the random effect of observer on the detection probability (p); an intercept and effects of the counts of mature *Cocos nucifera*, mature native forest trees, all sizes of *Heliotropium arboreum*, all sizes of *Pemphis acidula*, the percentage of the herbaceous layer free of plants (open space), variance of the random effect of site, and variance of the random effect of month on abundance (λ); and an intercept, effect of distance to shore, and variance of the random effect of site on presence (γ). Reported are the mean, standard deviation (SD), 95% credible interval (CRI), and the posterior probability that the parameter has the same sign as its mean.

Parameter	**Mean**	**SD**	**95% CRI**	**Probability of direction (pd)**
$p - intercept$	0.19	0.42	–0.64, 0.98	–
$\sigma_{(p-observer)}$	0.69	0.32	0.23 1.47	–
$\lambda - intercept$	–2.96	0.56	–4.07, –1.84	–
$\lambda - Cocos$	–1.46	0.51	–2.50, –0.53	1.00
$\lambda - native\ forest\ trees$	0.58	0.25	0.10, 1.08	0.99
$\lambda - Heliotropium$	0.77	0.20	0.39, 1,18	1.00
$\lambda - Pemphis$	0.13	0.30	–0.38, 0.94	0.67
$\lambda - open\ space$	0.49	0.32	–0.12, 1.12	0.94
$\sigma_{(\lambda-site)}$	2.72	0.56	1.77, 3.95	–
$\sigma_{(\lambda-month)}$	0.67	0.29	0.26, 1.38	–
$\gamma - intercept$	–0.01	0.64	–1.19, 1.34	–
$\gamma - distance$	–2.56	0.59	–3.74, –1.40	1.00
$\sigma_{(\gamma-site)}$	1.24	0.52	0.44, 2.45	–

Table 3.4 Posterior summary statistics for parameters from the N-mixture model for Brown Noddy (*Anous stolidus*). The model includes detection, abundance, and presence components. Parameters include an intercept and variance of the random effect of observer on the detection probability (p); an intercept and effects of the counts of mature *Cocos nucifera*, *Pandanus tectorius*, and native forest trees (*Pisonia grandis*, *Guettarda speciosa*, *Cordia subcordata*), the percentage of the herbaceous layer free of plants (open space), variance of the random effect of site, and variance of the random effect of month on abundance (λ); and an intercept, effect of distance to shore, and variance of the random effect of site on presence (γ). Reported are the mean, standard deviation (SD), 95% credible interval (CRI), and the posterior probability that the parameter has the same sign as its mean.

Parameter	**Mean**	**SD**	**95% CRI**	**Probability of direction (pd)**
$p - intercept$	0.70	0.37	–0.03, 1.44	–
$\sigma_{(p-observer)}$	0.81	0.34	0.31, 1.62	–
$\lambda - intercept$	–0.93	0.42	–1.73, –0.08	–
$\lambda - Cocos$	0.01	0.18	–0.34, 0.38	0.53
$\lambda - Pandanus$	–0.43	0.20	–0.82, –0.04	0.98
$\lambda - native\ forest\ trees$	–0.13	0.20	–0.52, 0.26	0.75
$\lambda - open\ space$	0.28	0.18	–0.08, 0.64	0.94
$\sigma_{(\lambda-site)}$	1.72	0.48	0.86, 2.72	–
$\sigma_{(\lambda-month)}$	0.71	0.29	0.29, 1.42	–
$\gamma - intercept$	0.50	0.51	–0.48, 1.49	–
$\gamma - distance$	–0.14	0.27	–0.66, 0.42	0.71
$\sigma_{(\gamma-site)}$	1.65	0.67	0.58, 3.14	–

Table 3.5 Posterior summary statistics for parameters from the N-mixture model for Black Noddy (*Anous minutus*). The model includes detection, abundance, and presence components. Parameters include an intercept and variance of the random effect of observer on the detection probability (p); an intercept and effects of the counts of mature *Cocos nucifera*, *Pandanus tectorius*, and native forest trees (*Pisonia grandis*, *Guettarda speciosa*, *Cordia subcordata*), variance of the random effect of site, and variance of the random effect of month on abundance (λ); and an intercept and variance of the random effect of site on presence (γ). Reported are the mean, standard deviation (SD), 95% credible interval (CRI), and the posterior probability that the parameter has the same sign as its mean.

Parameter	**Mean**	**SD**	**95% CRI**	**Probability of direction (pd)**
$p - intercept$	–0.28	0.39	–1.07, 0.48	–
$\sigma_{(p-observer)}$	0.82	0.33	0.33, 1.60	–
$\lambda - intercept$	1.11	0.54	0.03, 2.15	–
$\lambda - Cocos$	0.23	0.37	–0.50, 0.97	0.73
$\lambda - Pandanus$	–0.24	0.41	–1.04, 0.55	0.72
$\lambda - native\ forest\ trees$	0.74	0.36	0.04, 1.43	0.98
$\sigma_{(\lambda-site)}$	2.42	0.58	1.33, 3.64	–
$\sigma_{(\lambda-month)}$	1.14	0.39	0.55, 2.04	–
$\gamma - intercept$	3.20	0.78	1.66, 4.82	–
$\sigma_{(\gamma-site)}$	1.07	0.54	1.33, 3.64	–

Table 3.6 Posterior summary statistics for parameters from the N-mixture model for White Tern (*Gygis alba*). The model includes detection, abundance, and presence components. Parameters include an intercept and variance of the random effect of observer on detection probability (p); an intercept and variances of the random effects of site and month on abundance (λ); an intercept and effects of counts of mature *Cocos nucifera*, *Pandanus tectorius*, and native forest trees (*Pisonia grandis*, *Guettarda speciosa*, *Cordia subcordata*) and distance to shore on presence (γ). Reported are the mean, standard deviation (SD), 95% credible interval (CRI), and posterior probability that the parameter has the same sign as its mean.

Parameter	**Mean**	**SD**	**95% CRI**	**Probability of direction (pd)**
$p - intercept$	0.52	0.40	–0.28, 1.30	–
$\sigma_{(p-observer)}$	0.81	0.36	0.27, 1.66	–
$\lambda - intercept$	–1.12	0.45	–2.0, –0.24	–
$\sigma_{(\lambda-site)}$	1.79	0.47	0.99, 2.83	–
$\sigma_{(\lambda-month)}$	0.65	0.29	0.23, 1.34	–
$\gamma - intercept$	–0.52	0.51	–1.49, 0.56	–
$\gamma - Cocos$	–0.33	0.34	–1.00, 0.34	0.84
$\gamma - Pandanus$	0.57	0.34	–0.31, 1.32	0.97
$\gamma - native\ forest\ trees$	1.97	0.54	0.97, 3.08	1.00
$\gamma - distance$	–0.27	0.36	–0.99, 0.42	0.79
$\sigma_{(\gamma-site)}$	1.41	0.54	0.54, 2.64	–

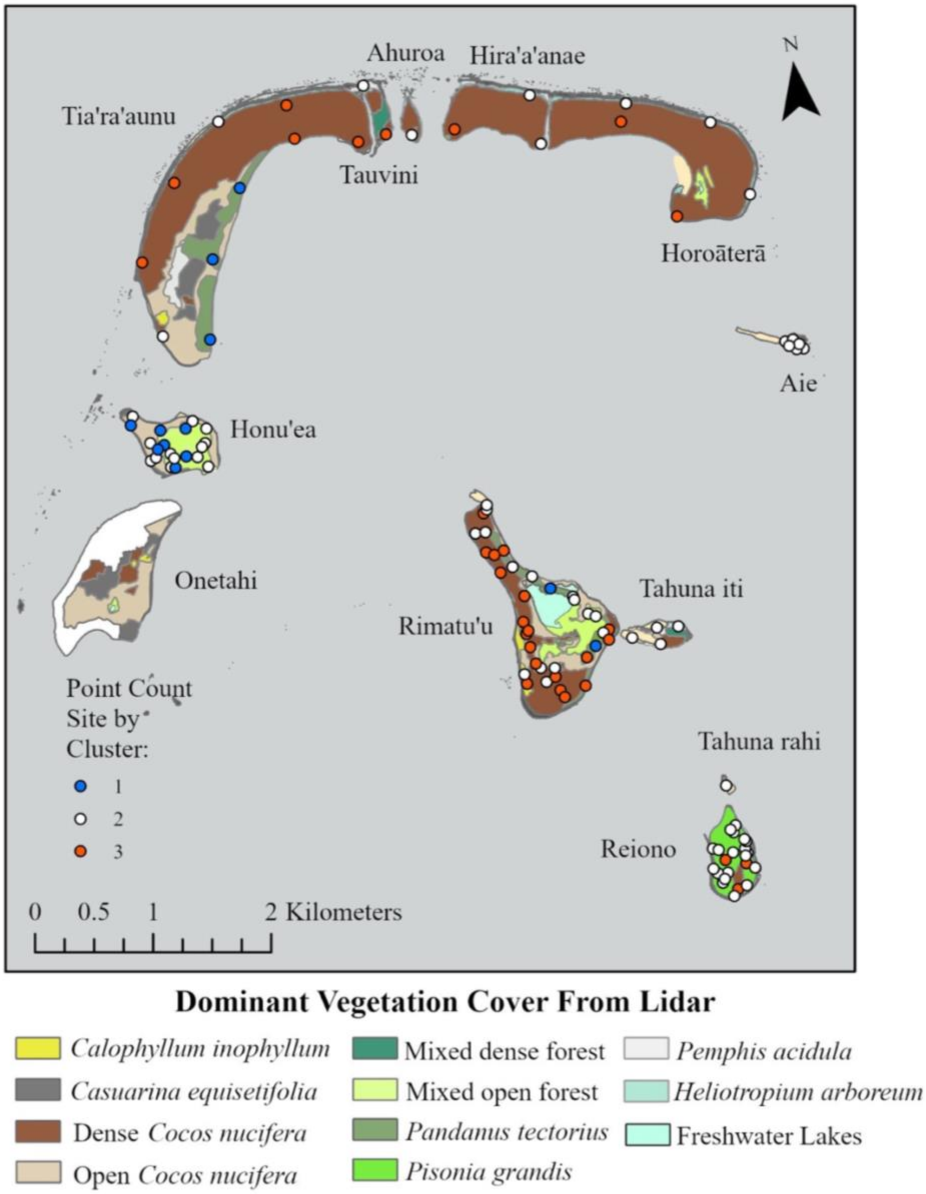

Figure 3.1 Map of dominant vegetative cover categories using lidar (light detection and ranging) data collected on Tetiaroa Atoll, French Polynesia in 2017 by Stoll et al. (2023). Many categories and layers were excluded, however all classified forest types were included, as well as two of the most distinct shrub layers, *Pemphis acidula* and *Heliotropium arboretum*. Others were condensed into the mixed open forest category. Our 110 avian point count site locations are overlain.

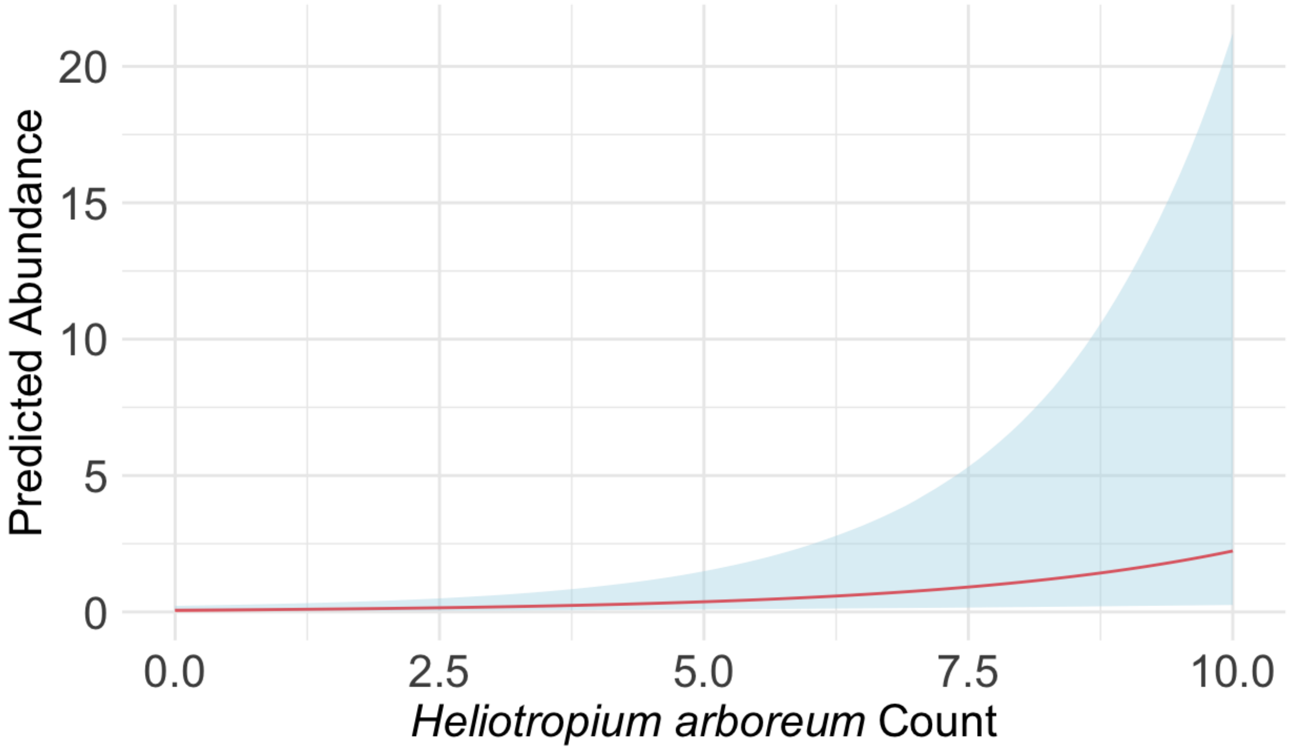

Figure 3.2 Posterior predictions of Red-footed Booby (*Sula sula*) abundance across a range of observed *Heliotropium arboreum* counts. The red line represents the posterior mean, and the shaded ribbon indicates the 95% credible interval, based on back-transformed estimates from the *N*-mixture model.

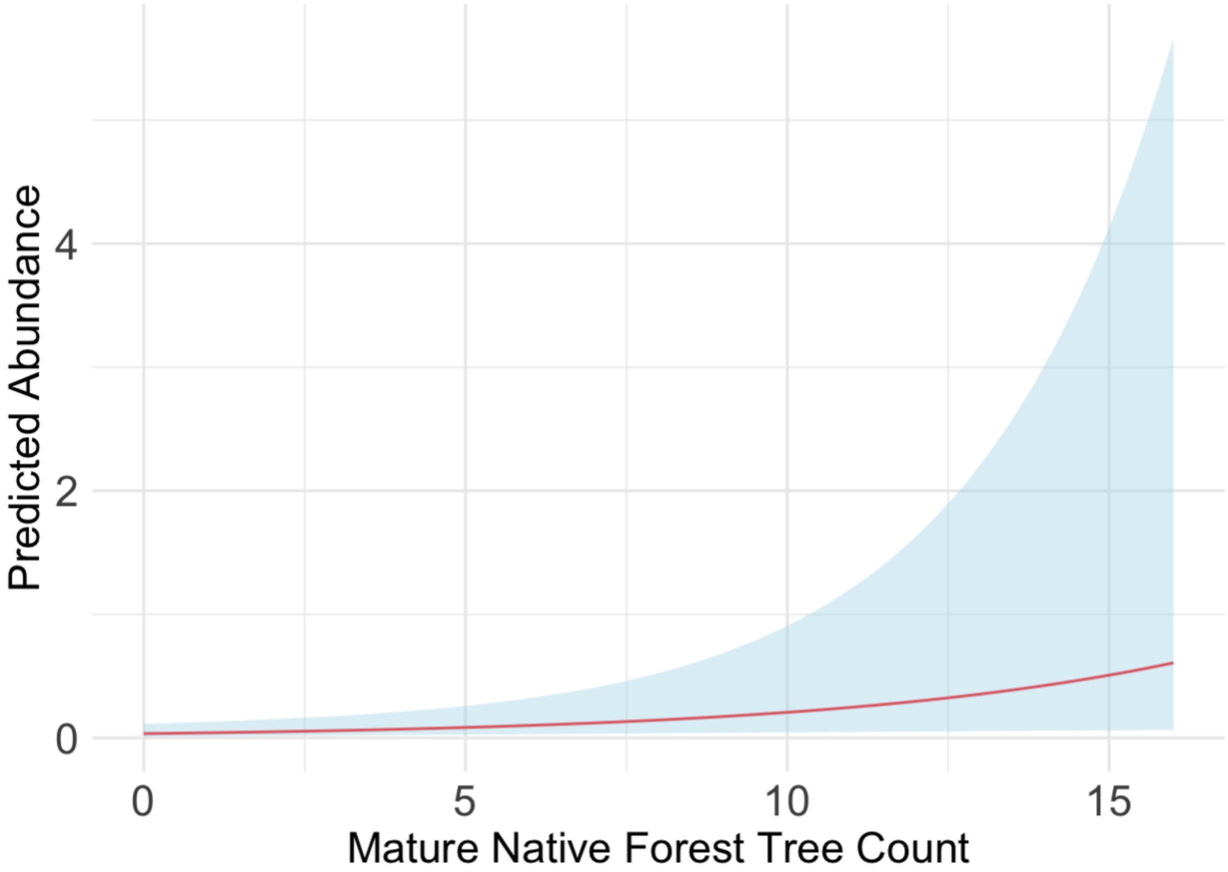

Figure 3.3 Predicted Red-footed Booby (*Sula sula*) abundance across a range of observed counts of mature native forest trees (*Pisonia grandis*, *Guettarda speciosa*, and *Cordia subcordata*). The red line represents the posterior mean from the *N*-mixture model, and the shaded area shows the 95% credible interval.

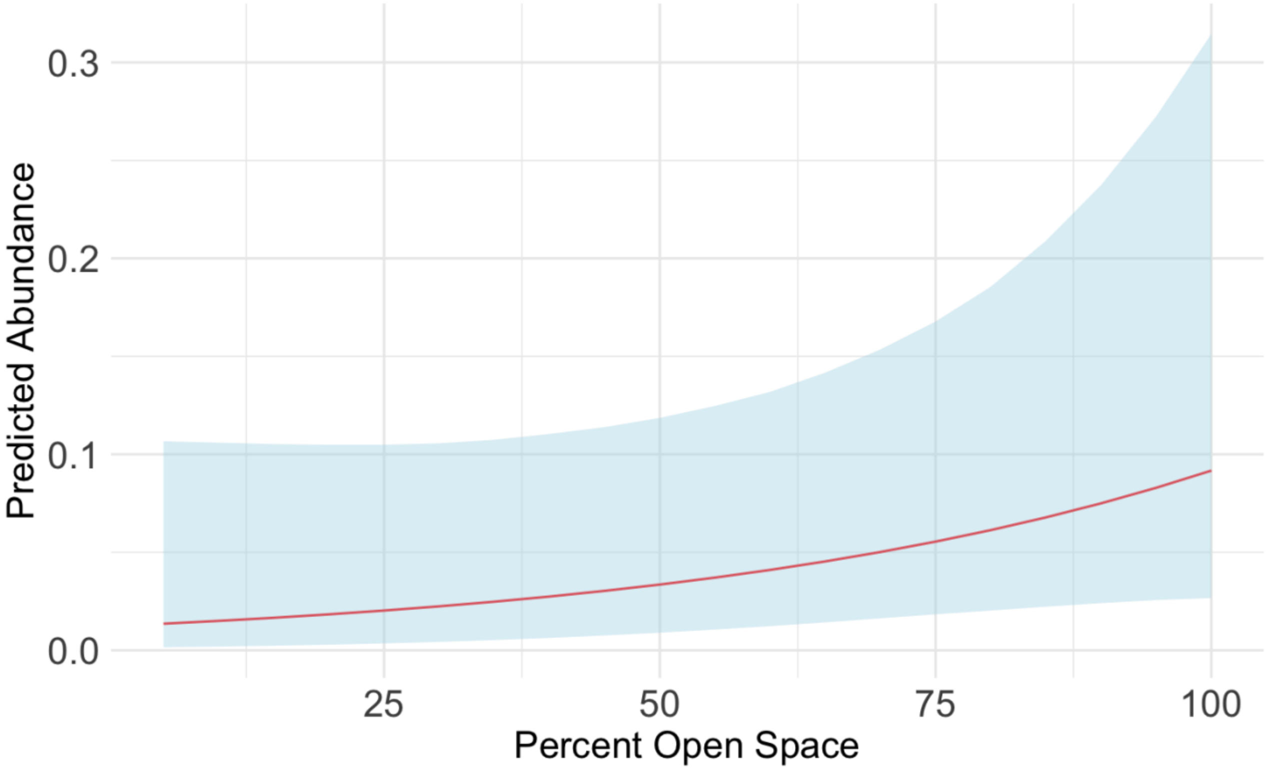

Figure 3.4 Posterior predictions of Red-footed Booby (*Sula sula*) abundance in relation to the percentage of open space in the herbaceous layer. The red line represents the posterior mean, and the shaded ribbon indicates the 95% credible interval, based on back-transformed estimates from the *N*-mixture model.

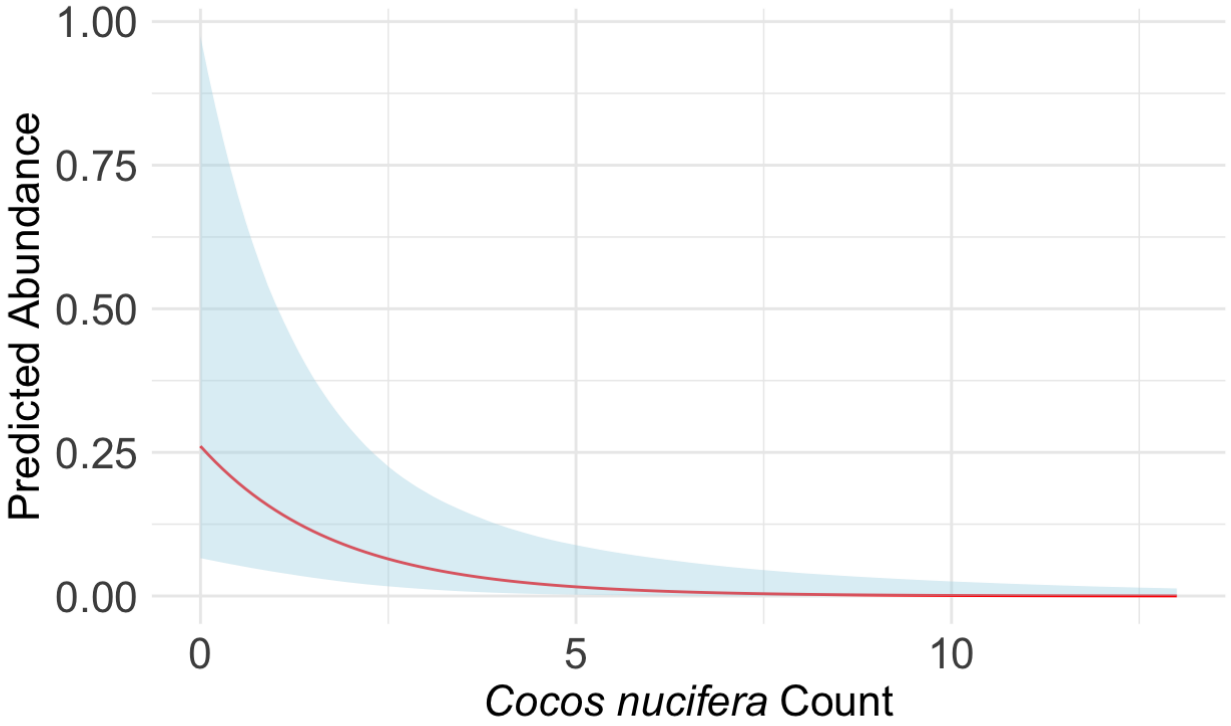

Figure 3.5 Predicted abundance of Red-footed Booby (*Sula sula*) as a function of mature *Cocos nucifera* tree count. The red line represents the posterior mean, and the shaded ribbon indicates the 95% credible interval, based on back-transformed estimates from the *N*-mixture model.

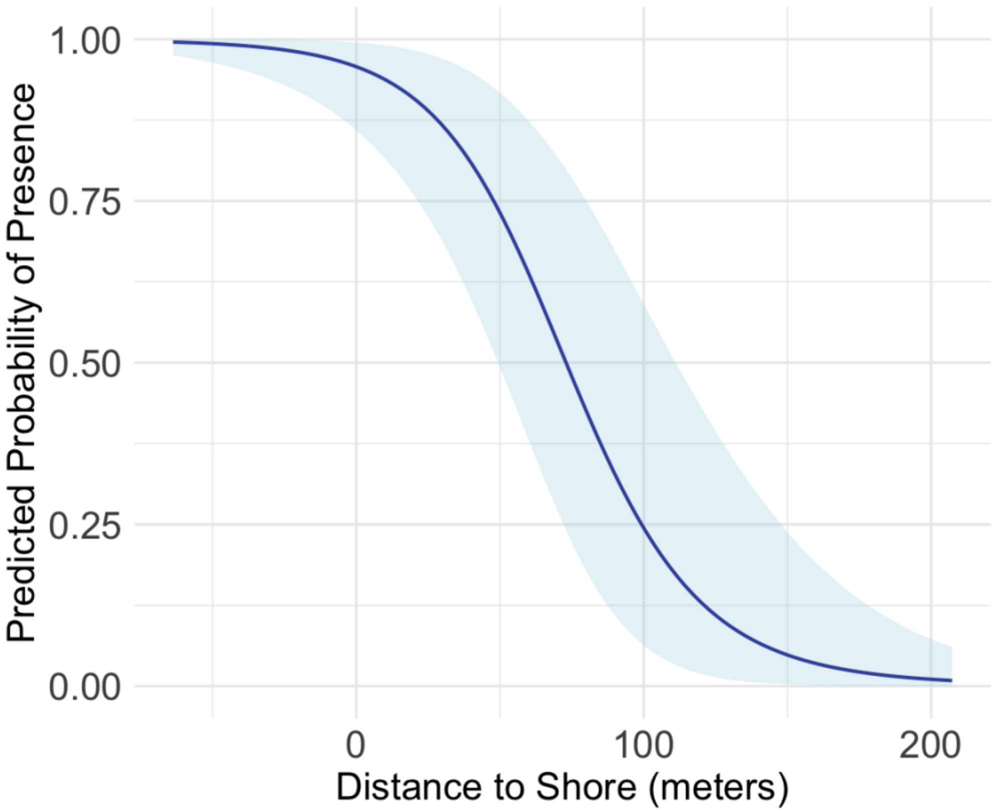

Figure 3.6 Predicted probability of Red-footed Booby (*Sula sula*) presence as a function of distance from the shoreline based on the zero-inflated component of the N-mixture model. The blue line represents the posterior mean prediction, and the shaded area shows the 95% credible interval.

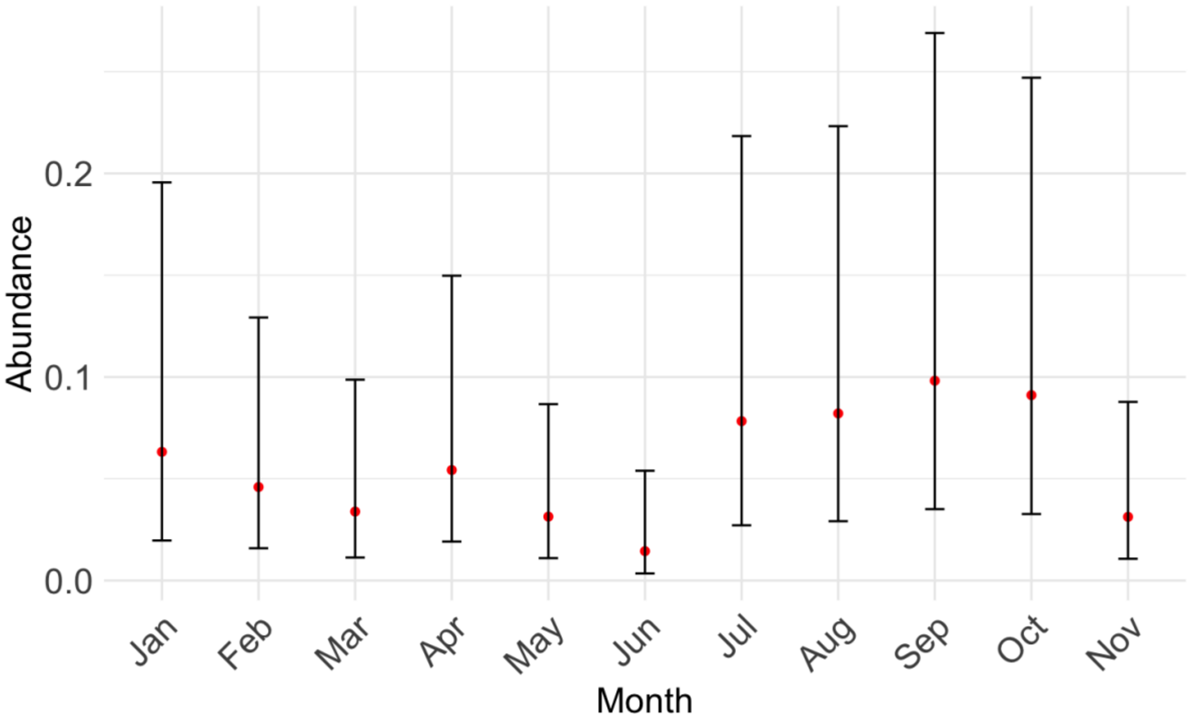

Figure 3.7 Monthly variation in Red-footed Booby (*Sula sula*) abundance across Tetiaroa Atoll. Posterior mean abundance estimates (points) with 95% credible intervals (bars) are shown for each month, based on a zero-inflated *N* -mixture model. Abundance estimates are based on back-transformed estimates, with monthly random effects incorporated to reflect temporal variation in detection-adjusted counts. Counts were not conducted in December, so no December estimate is displayed.

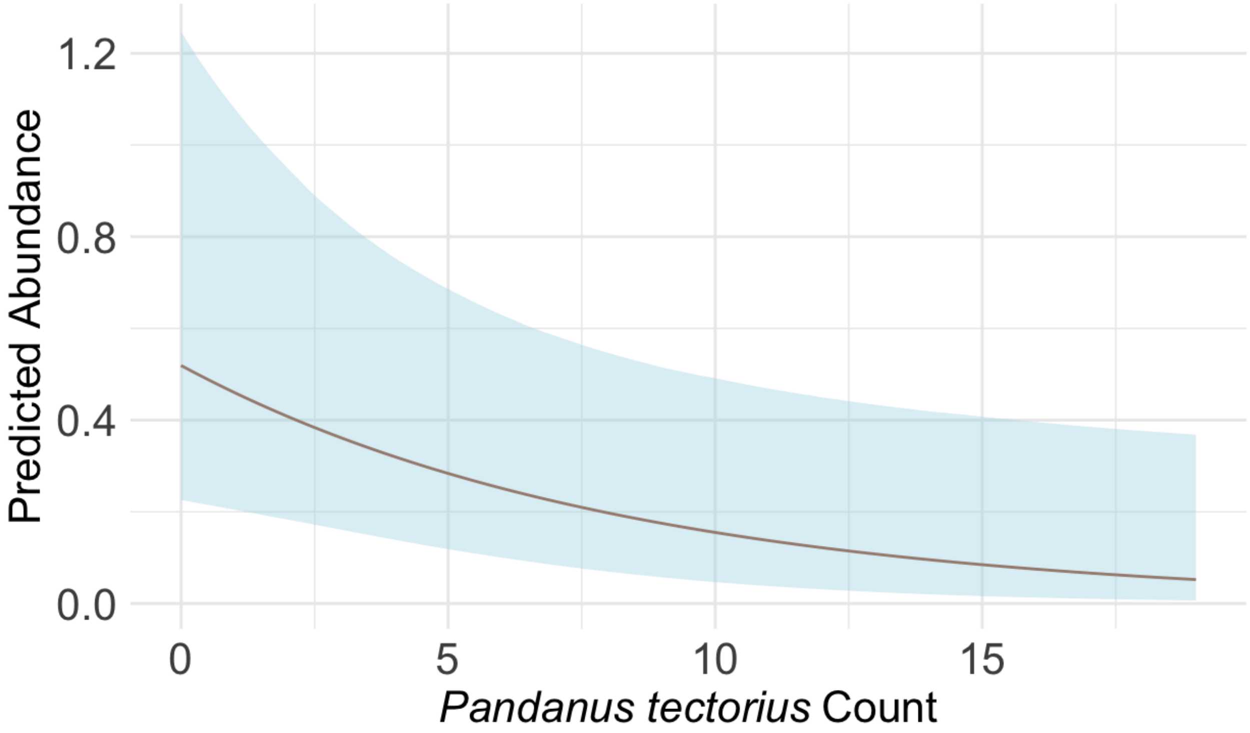

Figure 3.8 Predicted abundance of Brown Noddies (*Anous stolidus*) as a function of mature *Pandanus tectorius* tree count. The brown line represents the posterior mean, and the shaded ribbon indicates the 95% credible interval, based on back-transformed estimates from the *N*-mixture model.

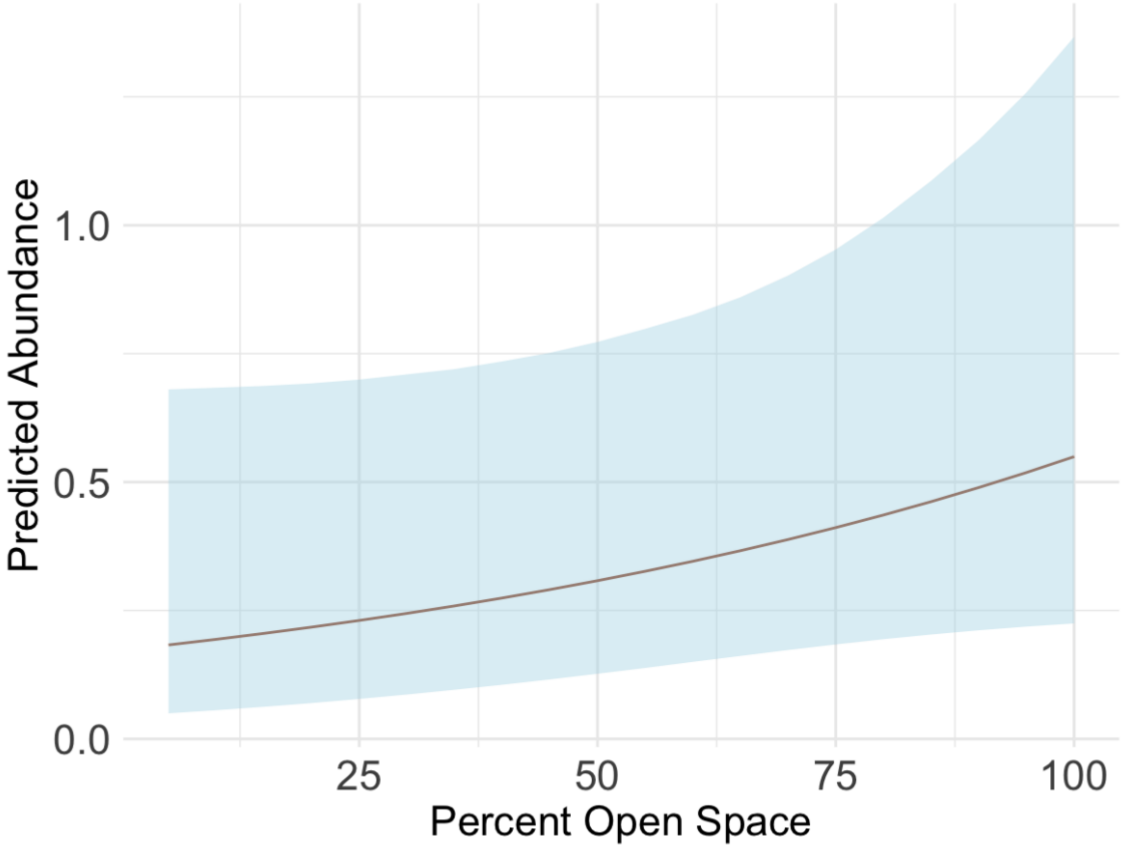

Figure 3.9 Posterior predictions of Brown Noddy (*Anous stolidus*) abundance in relation to the percentage of open space in the herbaceous layer. The brown line represents the posterior mean, and the shaded ribbon indicates the 95% credible interval, based on back-transformed estimates from the *N*-mixture model.

.

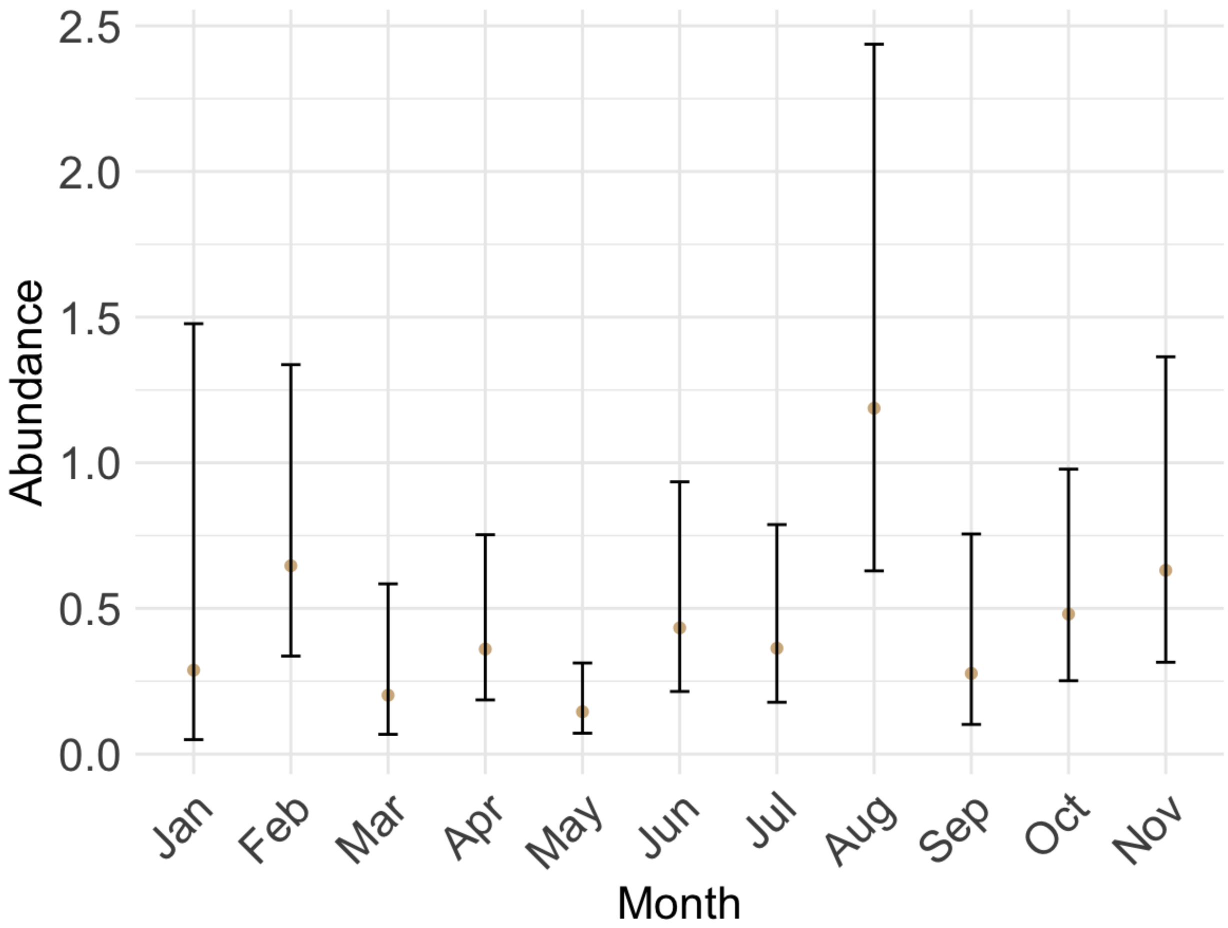

Figure 3.10 Monthly variation in Brown Noddy (*Anous stolidus*) abundance across Tetiaroa Atoll. Posterior mean abundance estimates (points) with 95% credible intervals (bars) are shown for each month, based on a zero-inflated N-mixture model. Abundance estimates are based on back-transformed estimates, with monthly random effects incorporated to reflect temporal variation in detection-adjusted counts. Counts were not conducted in December, so no December estimate is displayed.

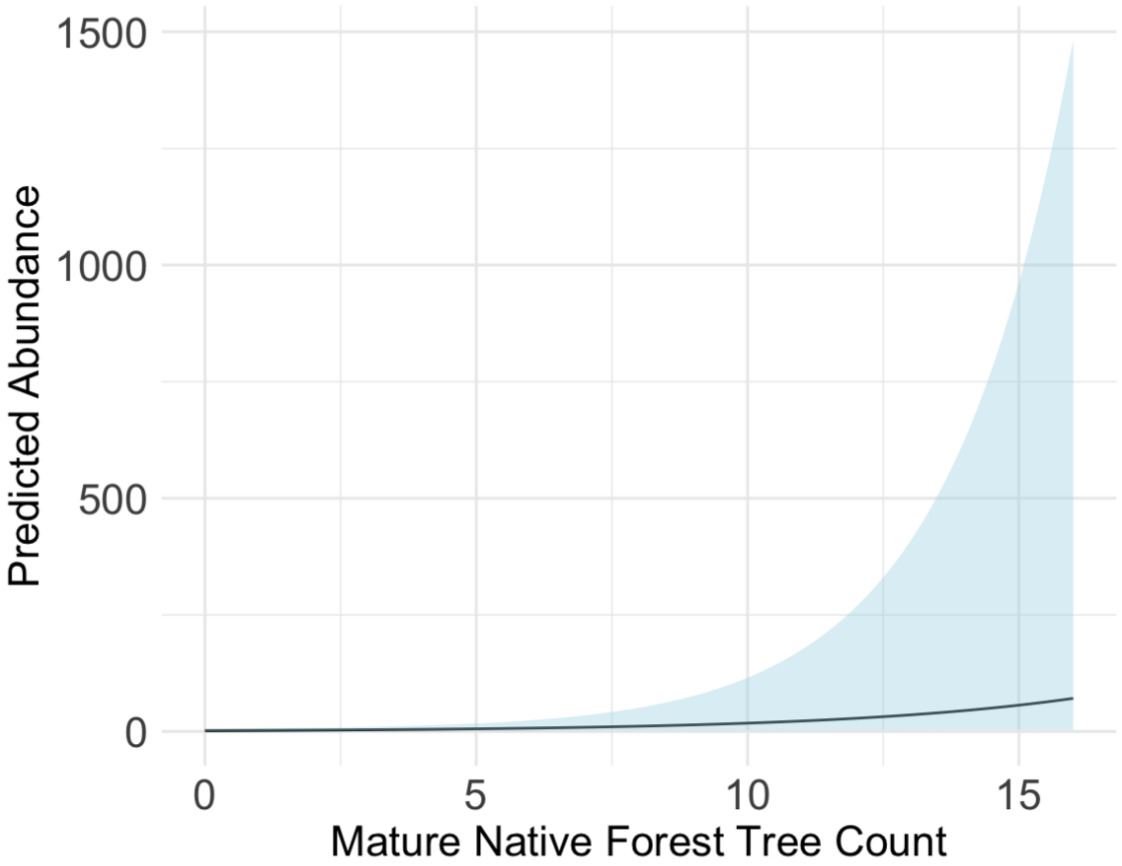

Figure 3.11 Predicted Black Noddy (*Anous minutus*) abundance across a range of observed counts of mature native forest trees (*Pisonia grandis*, *Guettarda speciosa*, and *Cordia subcordata*). The black line represents the posterior mean from the *N*-mixture model, and the shaded area shows the 95% credible interval.

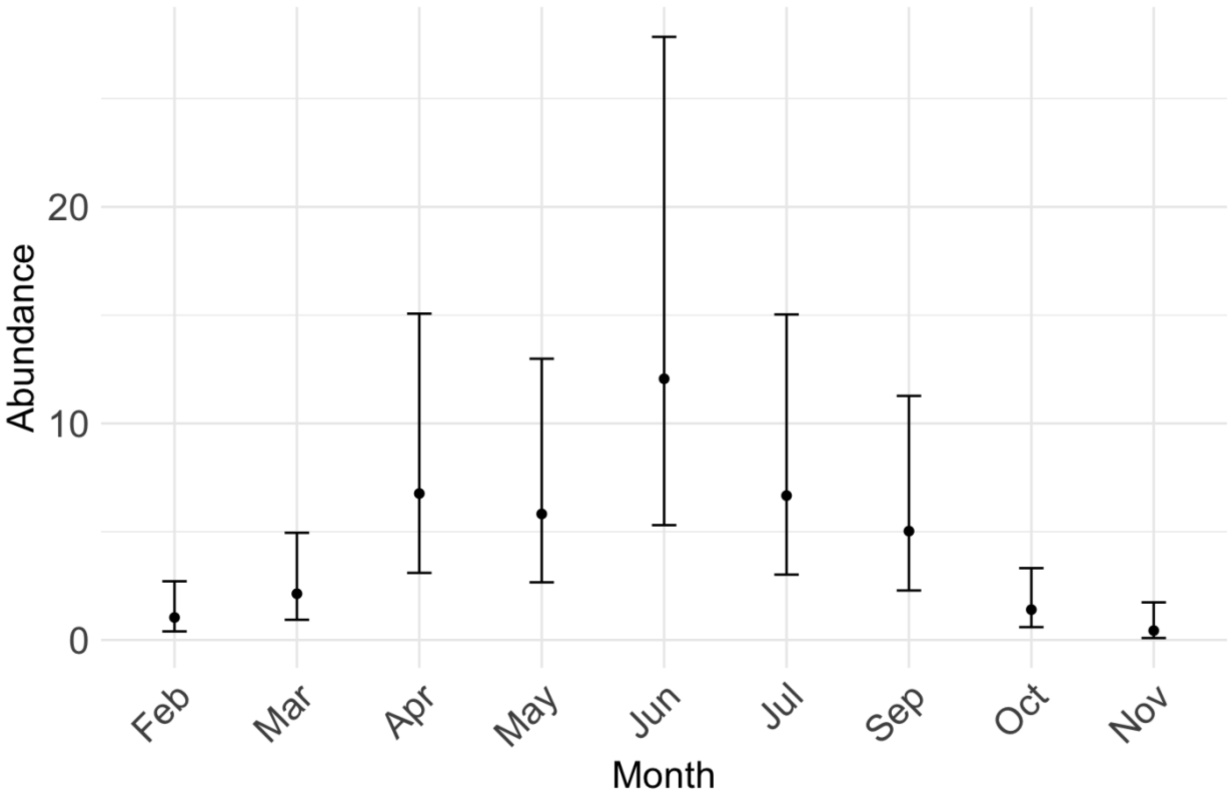

Figure 3.12 Monthly variation in Black Noddy (*Anous minutus*) abundance across Tetiaroa Atoll. Posterior mean abundance estimates (points) with 95% credible intervals (bars) are shown for each month, based on a zero-inflated *N*-mixture model. Abundance estimates are based on back-transformed estimates, with monthly random effects incorporated to reflect temporal variation in detection-adjusted counts. Counts were not conducted in January, December, or August, so those estimates are not displayed.

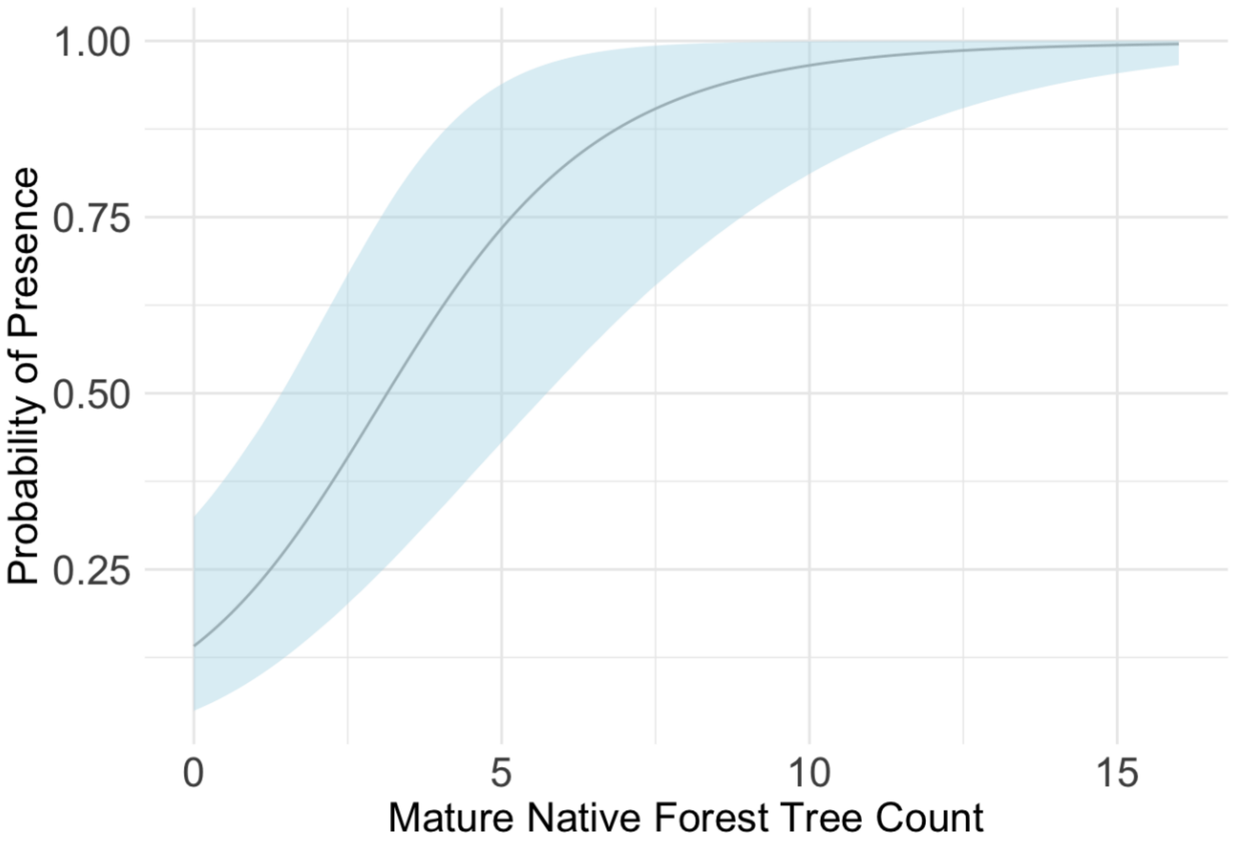

Figure 3.13 Predicted probability of White Tern (*Gygis alba*) presence in relation to the count of mature native forest trees (summed *Pisonia grandis*, *Guettarda speciosa*, and *Cordia subcordata*). The gray line shows the posterior mean prediction from the Bernoulli component of the *N*-mixture model, and the shaded ribbon represents the 95% credible interval.

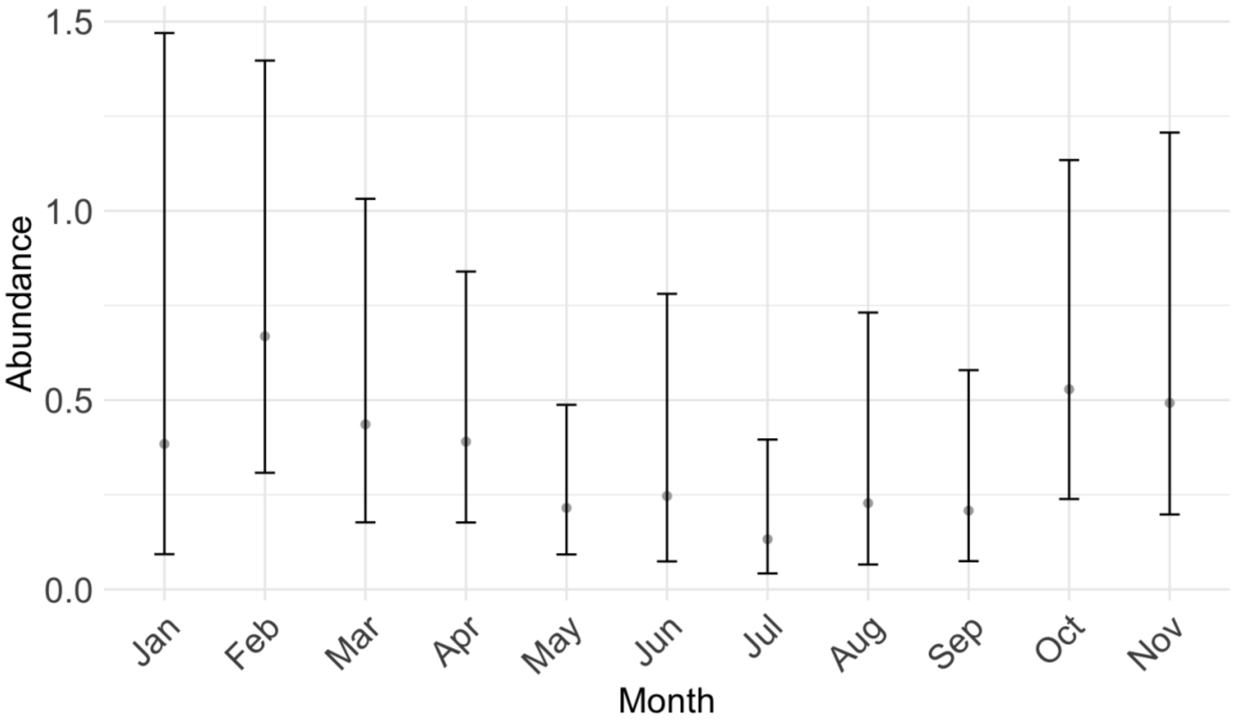

Figure 3.14 Monthly variation in White Tern (*Gygis alba*) abundance across Tetiaroa Atoll. Posterior mean abundance estimates (points) with 95% credible intervals (bars) are shown for each month, based on a zero-inflated *N* -mixture model. Abundance estimates are based on back-transformed estimates, with monthly random effects incorporated to reflect temporal variation in detection-adjusted counts. Counts were not conducted in December, so no December estimate is displayed.

Appendix 3A. Modeling Seabird Habitat Associations as a Function of Habitat Class

As an alternative approach for modeling seabird habitat associations, we classified broad habitats on Tetiaroa Atoll and then modeled seabird presence and abundance as a function of habitat classes.

3A.1 Methods

3A.1.1 Classification of Habitat Groups

We used the habitat data described in the main text and in Table 3.1 for developing habitat classes. We applied a combined Principal Component Analysis (PCA) and Hierarchical Clustering on Principal Component (HCPC) analysis to each site's percentage of ground substrate herbaceous layer coverage, and stem counts of juvenile and mature trees (Table 3.1). This allowed us to reduce the number of vegetation and substrate variables to a set of uncorrelated components (Pagenaud et al., 2022). We conducted the classification analysis in R (v.4.4.2; R Core Team 2024) using the FactoMiner package (v.2.3; Lê et al., 2008) and the Factoextra package (v.1.0.7; Kassambara, 2020). The optimal number of clusters was determined based on the recommendation provided by the FactoMiner package. The HCPC algorithm grouped variables based on their proximity (i.e., inherent similarity) aiming to minimize total within-cluster variance with Ward's minimum variance clustering method (Kassambara, 2020). Our vegetation and substrate cover variables were merged into three habitat clusters depending on their position along the two dimensions of a Principal Component Analysis (PCA). The PCA function scaled each variable with a zero mean and a unit standard deviation. For each resulting cluster, three values quantified variable contributions: the overall mean of the variable (OM), the mean within the cluster (MIC), and a test statistic that assessed the direction and statistical significance of the MIC–OM difference (Pagenaud et al., 2022). A value-test (*v.test*) exceeding 1.96 indicated that the variable significantly contributed to the corresponding cluster at a 95% confidence level. Based on the resulting cluster, each of our 110 sites were then assigned to habitat class 1, 2, or 3. These broadly corresponded to dense mixed native forest, open areas with scattered native flora, and *Cocos nucifera*-dominated areas, respectively.

3A.1.2 N-Mixture Modeling

We only undertook modeling by habitat class for Red-footed Boobies and Brown Noddies, because Black Noddies were restricted to one motu with limited botanical diversity, and due to limited White Tern counts. For these two species, we used the *N*-mixture model described in the main text, including the same random effects, but the fixed effects included habitat classes rather than habitat variables. Specifically, we modeled effects of habitat class on abundance for each species and distance to shoreline on presence for each species. Habitat class 3, *Cocos nucifera*-stand dominated areas, was used as the reference class in the model.

3A.2 Results

For Red-footed Boobies, class 2 (open native vegetation) had a strong positive effect on abundance ($\beta = 1.83$, 95% CRI: 0.73, 2.97; Table 3A.3), while class 1 (dense native forest) showed a negative but uncertain effect ($\beta = -0.89$, 95% CRI: −2.55, 0.72; Table 3A.3), relative to the *Cocos nucifera* stand-dominated reference class. Red-footed Boobies showed the highest estimated abundance at sites classified as class 2 (open native vegetation), with much lower abundance at sites classified as class 3 (*Cocos nucifera* stand-dominated) or class 1 (dense native forest; Figure 3A.1). However, credible intervals for the class 2 effect were wide, reflecting considerable uncertainty. Presence was strongly negatively associated with distance to shore (β = −2.72, 95% CRI: −3.87, −1.63), indicating a preference for coastal sites.

For Brown Noddies, class 1 (dense native forest) had a negative effect on abundance (β = −1.25, 95% CRI: −2.40, −0.12; Table 3A.4), while the effect of class 2 (open native vegetation) was uncertain (β = 0.06, 95% CRI: −0.61, 0.70; Table 3A.4), both relative to the *Cocos*-dominated reference. Brown Noddies showed similar estimated abundance in class 3 (*Cocos*-dominated) and class 2 (open native vegetation), and lower estimated abundance in class 1 (dense native forest) (Figure 3A.2). However, credible intervals overlapped broadly across all habitat clusters, indicating uncertainty in habitat associations. Distance to shore had an uncertain effect (β = −0.16, 95% CRI: −0.66, 0.40).

3A.3 Discussion

Our habitat classification via PCA (Table 3A.1) and HCPC (Table 3A.2) followed the approach used by Pagenaud et al. (2022) in their study of Tahiti Petrel (*Pseudobulweria rostrata*) nest-site selection. They used HCPC analysis to classify vegetation and substrate variables associated with nesting burrows into three habitat clusters: “open” habitats with shrubs, soil, and grass; “closed” habitats with mature forest, and rocky substrate habitats with large trees, which are partially comparable to our three resulting habitat classes (Pagenaud et al., 2022), although we have the habitat class of *Cocos nucifera* monodominant stands. Mature native forest trees (*Pisonia grandis, Guettarda speciosa,* and *Cordia subcordata*) were placed in class 1, however had a *v.test* score of -2.04 and were not included. Juvenile trees and seedlings from these species were still included in class 1. *Pemphis acidula*, which was used in our flora-specific covariate models, did not appear in any of the habitat classes, suggesting this species was not a major component of our sampled habitats. *Suriana maritima*, a different native coastal shrub, was placed in class 2, and could potentially be an important flora species to consider in future analyses, although may not be sturdy enough to host larger seabird nesting structures. We selected the first four components of the PCA, which explained 47.9% of the total variance in our vegetation data (Table 3A.1). Although our first two PCs explained a smaller portion of total variance (PC1 = 16.6%, PC2 = 12.7%; Table 3A.1) compared to theirs (PC1 = 28.9%, PC2 = 20.0%; Pagenaud et al., 2022), this method still proved suitable in reducing covariate dimensions without removing potentially interesting habitat strata, and avoiding issues with correlation.

Our clustering analysis revealed similar patterns as models with flora-specific covariates. Habitat class 2 was characterized by *Heliotropium*, and *Suriana*, both coastal shrub species, native grasses and ground plants, and more open habitat. We expected Red-footed Boobies to prefer open habitat and coastal shrubs, which was supported by the positive association between this species and habitat class 2. Class 1 was characterized by mature *Pandanus*, thick hedges, and denser native forest seedlings. Brown Noddies had a negative association with this habitat class, which is also similar to effects reported in our model using flora-specific covariates.

Terrestrial habitats are not comprised of independent tree species, but a combination of vegetation layers in different successional states. While models using flora-specific covariates offer insight into seabird use of individual plant taxa (e.g., *Pandanus tectorius*, *Cocos nucifera*, *Heliotropium arboreum*), models using habitat classes provide a more holistic perspective. By reducing complex vegetation data into ecologically meaningful habitat types, a clustering approach might better reflect how birds perceive their environment. This might also align with potential management efforts in habitat zones (e.g., dense native tree stands, coastal shrub perimeters, *Cocos nucifera* monoculture), making results more relevant for conservation planning.

3A.4 Literature Cited

Kassambara, A. and Mundt, F. (2020) Factoextra: Extract and Visualize the Results of Multivariate Data Analyses. R Package Version 1.0.7. https://CRAN.R-project.org/package=factoextra

Lê, S., Josse, J., & Husson, F. (2008). FactoMineR: An R Package for Multivariate Analysis. *Journal of Statistical Software*, *25*(1), 1–18. https://doi.org/10.18637/jss.v025.i01

Pagenaud, A., Ravache, A., Bourgeois, K., Mathivet, M., Bourguet, É., Vidal, É., & Thibault, M. (2022). Nest-site selection and its influence on breeding success in a poorly-known and declining seabird: The Tahiti petrel *Pseudobulweria rostrata*. *PLOS ONE*, *17*(4), e0267408. https://doi.org/10.1371/journal.pone.0267408

R Core Team (2024). _R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.

Table 3A.1 Results of a principal component analysis (PCA) for identification of habitat classes on Tetiaroa Atoll, including the eigenvalues, percentage of variance explained, and cumulative variance for the first eight principal components (PCs). Together, these eight components account for 72.41% of the total variance in the dataset. The first four were used in making the habitat clusters.

Component	Eigenvalue	% Variance Explained	Cumulative % Variance
PC1	3.31	16.56%	16.56%
PC2	2.54	12.72%	29.28%
PC3	2.04	10.21%	39.48%
PC4	1.69	8.45%	47.93%
PC5	1.48	7.39%	55.31%
PC6	1.21	6.07%	61.39%
PC7	1.18	5.90%	67.29%
PC8	1.02	5.12%	72.41%

Table 3A.2 Indicator variables (with *v.test* >1.96) associated with each of the three habitat clusters identified via hierarchical clustering on principal components (HCPC) for habitats on Tetiaroa Atoll. For each variable, the table reports the *v.test* statistic, mean value within the cluster, overall mean across all plots, and associated *p*-value.

Class	**Variable**	***v.test***	**Mean in Cluster**	**Overall Mean**	***p*-value**
Dense native forest (1)	Juv. native forest trees	5.25	1.430	-2.12e-17	1.52e-07
	Native plant debris	5.08	1.384	3.19e-16	3.77e-07
	Tree seedlings	5.05	1.375	8.98e-17	4.50e-07
	Native hedges	4.99	1.359	-1.67e-16	6.13e-07
	Mature *Pandanus*	3.96	1.079	6.46e-17	7.51e-05
	Other native plants	3.71	1.012	3.23e-17	2.03e-04
Open native plants (2)	Bare ground	4.89	0.373	8.33e-18	1.02e-06
	Open space	4.41	0.337	-3.01e-16	1.02e-05
	Heliotropium	2.60	0.199	1.30e-16	9.21e-03
	Native ground plants	2.55	0.195	5.95e-17	1.09e-02
	Suriana	2.28	0.174	-8.58e-17	2.28e-02
	Grasses	2.18	0.167	8.88e-17	2.91e-02
Cocos nucifera stands (3)	*Cocos* debris	8.01	1.220	-6.96e-17	1.12e-15
	Mature *Cocos*	7.11	1.082	-1.03e-16	1.16e-12
	Juv. *Cocos*	5.46	0.831	-1.69e-16	4.77e-08
	Sprouted coconut	4.56	0.694	7.44e-18	5.05e-06
	Juv. introduced trees	3.81	0.580	-2.32e-16	1.38e-04
	Mature introduced trees	3.24	0.493	-8.43e-17	1.21e-03
	Native plants	2.16	0.329	3.23e-17	3.08e-02

Table 3A.3 Posterior summary statistics for parameters from the N-mixture habitat clustering model for Red-footed Boobies (*Sula sula*). The model includes detection, abundance, and presence components. Parameters include an intercept and variance of the random effect of observer on the detection probability (p); an intercept, effects of habitat cluster, variance of the random effect of site, and variance of the random effect of month on abundance (λ); and an intercept, effect of distance to shore, and variance of the random effect of site on presence (γ). Reported are the mean, standard deviation (SD), 95% credible interval (CRI).

Parameter	**Mean**	**SD**	**95% CRI**
$p - intercept$	0.20	0.42	-0.63, 1.00
$\sigma_{(p-observer)}$	0.70	0.32	0.23, 1.48
$\lambda - intercept$	-3.08	0.70	-4.38, -1.62
$\lambda - Cluster\ 1$	-0.89	0.83	-2.55, 0.72
$\lambda - Cluster\ 2$	1.83	0.57	0.73, 2.97
$\sigma_{(\lambda-site)}$	2.95	0.63	1.80, 4.27
$\sigma_{(\lambda-month)}$	0.67	0.29	0.25, 1.37
$\gamma - intercept$	-0.61	0.65	-2.04, 0.61
$\gamma - distance$	-2.72	0.57	-3.87, -1.63
$\sigma_{(\gamma-site)}$	1.39	0.62	0.47, 2.90

Table 3A.4 Posterior summary statistics for parameters from the *N*-mixture model for Brown Noddies (*Anous stolidus*). The model includes detection, abundance, and presence components. Parameters include an intercept and variance of the random effect of observer on the detection probability (p); an intercept, effects of habitat cluster, variance of the random effect of site, and variance of the random effect of month on abundance (λ); and an intercept, effect of distance to shore, and variance of the random effect of site on presence (γ). Reported are the mean, standard deviation (SD), 95% credible interval (CRI).

Parameter	**Mean**	**SD**	**95% CRI**
$p - intercept$	0.69	0.38	-0.06, 1.42
$\sigma_{(p-observer)}$	0.82	0.34	0.31, 1.62
$\lambda - intercept$	-0.86	0.43	-1.73, -0.02
$\lambda - Cluster\ 1$	-1.25	0.58	-2.40, -0.12
$\lambda - Cluster\ 2$	0.06	0.34	-0.61, 0.70
$\sigma_{(\lambda-site)}$	1.78	0.43	1.01, 2.71
$\sigma_{(\lambda-month)}$	0.71	0.29	0.29, 1.42
$\gamma - intercept$	0.57	0.48	-0.34, 1.52
$\gamma - distance$	-0.16	0.27	-0.66, 0.40
$\sigma_{(\gamma-site)}$	1.54	0.61	0.55, 2.92

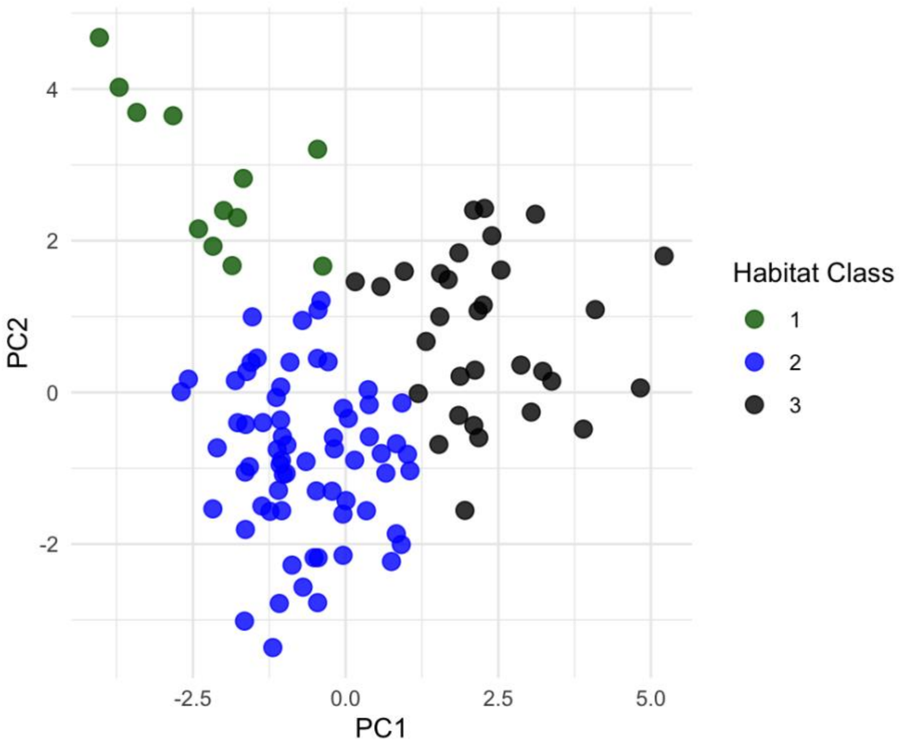

Figure 3A.1 Principal Component Analysis (PCA) of vegetation structure variables across survey sites on Tetiaroa Atoll, colored by habitat class identified via Hierarchical Clustering on Principal Components (HCPC). The *x*- and *y*-axes represent the first two principal components (PC1 and PC2), which together capture major gradients in vegetation composition. Class 1 (green) represents dense mixed native forest, class 2 (blue) represents open native plant-dominated habitat, and class 3 (black) represents *Cocos nucifera stand*-dominated habitat.

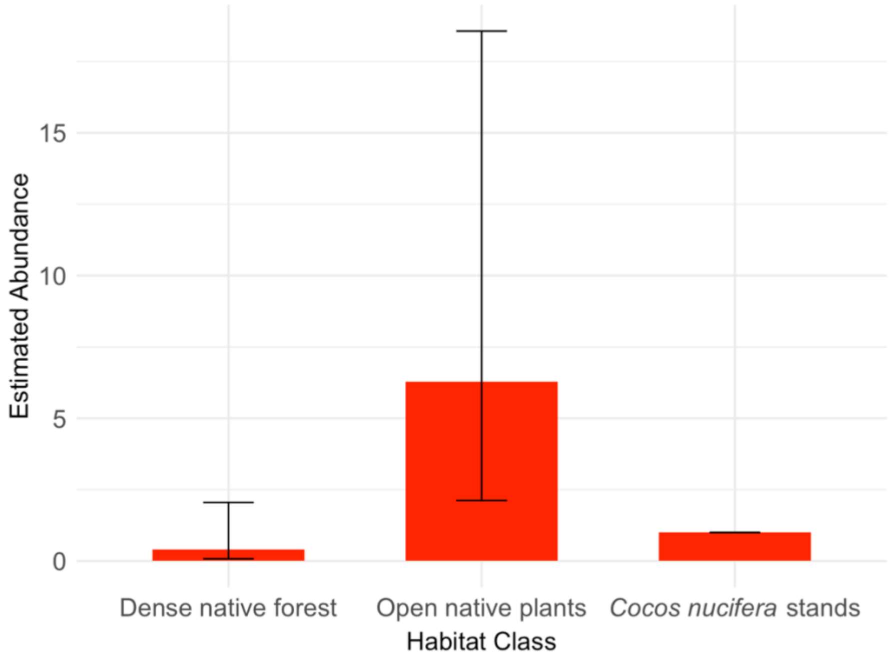

Figure 3A.2 Predicted abundance of Red-footed Boobies (*Sula sula*) across three habitat clusters on Tetiaroa Atoll. These classes represent dense mixed native forest, open native plant-dominated habitat, and *Cocos nucifera* stand-dominated habitat. Bars represent the posterior mean abundance for each cluster, and error bars indicate the 95% credible intervals. *Cocos nucifera* stands were the reference category and was fixed at the intercept level (log-scale = 0).

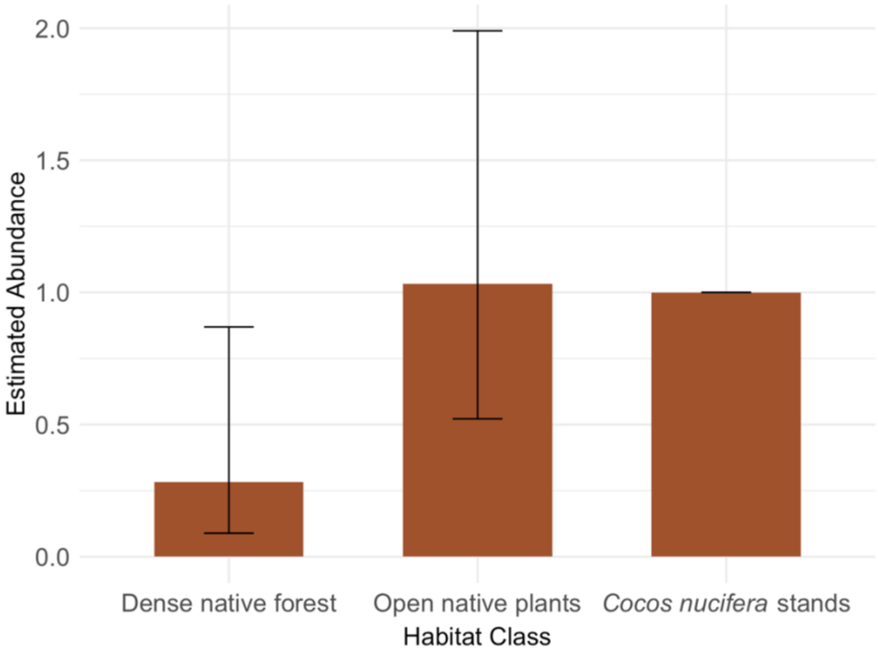

Figure 3A.3 Predicted abundance of Brown Noddies (*Anous stolidus*) across three habitat clusters on Tetiaroa Atoll. These classes represent dense mixed native forest, open native plant-dominated habitat, and *Cocos nucifera* stand-dominated habitat. Bars represent the posterior mean abundance for each cluster, and error bars indicate the 95% credible intervals. *Cocos nucifera* stands were the reference category and was fixed at the intercept level (log-scale = 0).