The effects of burrow nesting seabirds on soils and vegetation on Broughton Island, New South Wales

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Note to examiners

This thesis has been written in self-contained journal article format. The works included as chapters in this thesis have been significantly contributed by me from field sampling, data collection, statistical analysis and writing. Each chapter may contain minor formatting adjustments required by the individual journal to which separate papers were submitted to a journal at the time of thesis submission. Chapters which have not been submitted follow a consistent format to one another. By nature of manuscript format, repetition is unavoidable in places, specifically within the site descriptions. I have attempted to minimise repetition wherever possible.

Abstract

The offshore islands of New South Wales host millions of migratory seabirds that gather in dense colonies on islands to breed. Seabirds have the capacity to drive ecosystem function through dual roles of marine-derived nutrient subsidies via guano deposition and bioengineering through burrow-nesting. Broughton Island is managed as part of the Myall Lakes National Park estate and has experienced a range of environmental disturbances in the past decade including the introduction of invasive plants and mammals, which led to significant changes to seabird populations and native vegetation communities. In response to the threats imposed by grazing rabbits and predatory rats on seabird habitat and breeding success, these invasive animals were successfully eradicated from the island in 2009 with the goal of restoring seabird populations and plant communities. The trajectory of ecological change, however, remained largely unknown. The aims of the research presented in this thesis were to first gain scope on the effect of seabird nutrient subsidies and nesting activities on island soils and plants in colonies of the most abundant seabird species on the island, *Ardenna pacifica* (wedge-tailed shearwaters).

The results revealed novel evidence of seabird colony soils more depleted in soil C, N and P compared to both adjacent and sloping areas of hydrological accumulation. It was also found that vegetation was distinctly different within seabird colonies and was defined by the presence of an invasive cactus, *Opuntia stricta*. This result will be the first to describe in detail how burrowing seabirds on islands with deep and sandy soils in a subtropical climate, affect their environment, thereby giving new insights onto the mechanisms driving ecosystem function and the management implications for such islands.

Another key research aim was to elucidate the effectiveness of eradication of rats and rabbits was effective in restoring native vegetation cover and richness on Broughton Island by analysing data collected from 7 years of vegetation surveys. Overall positive effects were seen in vegetation height, species richness, and ground cover, but it may take successional plant communities longer time to recover and require additional interventions for optimal outcomes. It was concluded that positive outcomes of vegetation recovery may be confounded by areas with disturbance by burrowing seabirds, and was supported by the evidence supplied by the research comparing vegetation and soil characteristics inside and outside of seabird colonies.

Two experimental habitat suitability models were created taking different but complementary approaches to predict preferred and projected colony habitat on Broughton Island. Both models had high accuracy at detecting suitable habitat on the island, and both models identified unoccupied areas of high habitat suitability which were used in conjunction with other results to make robust conclusions.

Identifying the fundamental effects of seabirds on soils and plants in nesting areas provided evidence to predict how expanding seabird colonies may change the soil and vegetation environment on this distinctive island ecosystem. The spatial results, combined with the knowledge of biophysical effects on soils and vegetation from seabird colonies, identified precise areas which are predicted to experience change in vegetation and guano subsidies if seabird colonies should expand to these highly suitable areas. Since expansion of seabird colonies into suitable habitat is likely now Broughton Island is predator-free, the opportunity for effective biocontrol of weeds, and protection of habitat now exists.

This work demonstrates how multifaceted approach using field surveys, laboratory and geospatial analyses strengthen ecological conclusions and can be applied to effective and real-world conservation plans on islands experiencing ecological changes. The results will be utilised by the New South Wales National Parks and Wildlife Service to inform future island management.

Certification

I certify that the ideas, experimental work, results, analyses, software and conclusions reported in this thesis are entirely my own effort, except where otherwise acknowledged. I also certify that the work is original and has not been previously submitted for any other award, except where otherwise acknowledged.

[redacted]	15 February, 2023
Candidate Name	Date

Dedication

To the women who told me I could.

Acknowledgements

This candidature was made possible by funding through the University of New England International Post Graduate Research Award, and in collaboration with the New South Wales Department of Planning and Environment and New South Wales National Parks and Wildlife Service. This candidature was also made possible by my principal supervisor, Brian Wilson, who trusted me with this endeavour and gave me an opportunity that changed my life. From the bottom of my heart I thank Brian for this experience. Throughout my candidature he was the Bernie Taupin to my Elton John, and I couldn’t have asked for a better experience with an advisor. It will be hard to top the experiences I’ve had with him and some sampling gear, on an island with tiny fairy penguins, makeshift intertidal trails and quirky local stories.

I’m deeply grateful for my co-supervisor Priyakant Sinha, who took the time to teach me the foundations of remote sensing and GIS, and positively assisted me throughout conducting the spatial analyses for this thesis. He opened up many new interests and opportunities for me both during my graduate studies and in the future. Associate Professor Matt Tighe assisted me with statistical analyses with mixed effect linear modelling and taught me how to write better coding scripts in R (a skill I will force myself to use the rest of my career simply because of the disturbing amount of time I spent learning it). My co-supervisor Professor Brian Sindel was always available to me as an addition to my supervisory team and provided insightful comments and for that I extend sincere appreciation for him. I am grateful for the assistance from University staff Craig Johnson in the research laboratory, particularly for his assistance with the mass spectrometer, and for believing me when I said the laboratory was cursed when experiments I conducted had failed. Dr. Melanie Robertson-Dean supported statistical analyses for two chapters within this thesis and she was a delight to work with. Susan Callaghan is a park ranger who manages Broughton Island, and assisted with trips we took to the island and kindly offered accommodation and advice.

The dedication to ‘the women who told me I could’ is one which has existed as a personal mantra since before I began my doctoral work. I remember being terribly nervous to tell my mom I was accepted into graduate school in Australia. I think I was afraid to say the words because it would mean they were real and I was capable of doing something so monumental. We were sitting in a restaurant in Orlando, Florida when I told her. Without hesitation she beamed with joy for me, and immediately I knew it was on from there. With that moment in mind, the first and foremost of these women to acknowledge are my grandmother, Kate Pringle, and my mother, Amy Garrard. I am grateful to them for continually believing in me and supporting me during this time. My grandmother worked hard every day and achieved many milestones on her own without seeking any reward other than selflessly taking care of the people she loves. She inspires me with her tenacity, independence and rationality. My mom teaches me by her seemingly magical example of life and career: she follows her heart and dreams no matter what anyone says or thinks. Tapping into the creative energy she emits has helped me be a better person and surprisingly a better scientist. Being far from home during graduate school and a global pandemic was tough at times, but they were always there for me and gave me the support I needed to keep going with confidence. I am really lucky to have these two in my life.

There are many other women who supported me and kept me inspired to work hard and helped me remain living a safe and joyful life during my candidature. My Aunt Pam, my sisters, Jessica and Holly. Cindy Sigler, Meg Tickle, Ellie McDonald, Momena Khandaker, Callie Sonter and many more. Through knowing them, I have living proof that women can change the world when we lift each other up. Many difficult moments during my candidature were turned into comforting, hilarious, inspiring and enjoyable memories because they were present.

I thank my father Doug Garrard for selflessly supporting my early and undergraduate education. My academic successes are because of his relentless hard work and commitment to family.

They obviously can’t read this, but I’d like to acknowledge two little cats, Poco and Savannah, for making me smile every single day during my candidature.

Finally, living, working and learning on Aboriginal land has been a great privilege. What an honour it was to be among the sacred plants and animals on this land and hopefully make a small contribution to their protection. I acknowledge that my work was done on the country of the Anaiwan and Worimi peoples, and I pay my respect to their Elders past, present and emerging. It always was, and always will be Aboriginal land.

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Chapter 1: Introduction

Seabirds connect ecosystems globally by exchanging energy from marine to terrestrial environments (Ellis et al. 2006). Nutrient subsidies of seabird guano are so substantial they contribute to global cycles of nitrogen and phosphorus at magnitudes analogous to atmospheric deposition (Mulder et al. 2011; Otero et al. 2018). Colloquially, seabird guano is often referred to as ‘white gold’ for its historical effectiveness in fertilizing crops (Szpak et al. 2012; Santana-Sagredo et al. 2021). Ecologically, seabird guano influences all trophic levels, from soils to insects, primary producers, land mammals, and nearshore marine systems (Savage 2019; Pascoe et al. 2021; Gaiotto et al. 2022). Seabirds occur on every continent of the globe and primarily nest on islands, and the ecosystems of many of these have evolved with seabird enrichment (Leblans et al. 2014). Seabirds are recognized as integral components of island ecosystems, but their effects on a range of terrain and habitat types has yet to be fully explored (De la Peña-Lastra 2021). Elucidating the impact of seabirds on island ecosystems is therefore globally important in order to effectively conserve natural landscapes and seabird populations.

Island communities are under threat and particularly vulnerable to ecosystem degradation because of their geographic isolation and high rates of endemism. Native species on islands have generally evolved in the absence of disturbance and predation, have lower genetic diversity, smaller population sizes and habitat range (MacArthur & Wilson 1967; Kier et al. 2009; Tershy et al. 2015). Exotic predatory mammals and invasive weeds are recognized as one of the greatest threats to seabird habitat, breeding success and island biodiversity through predation, competition and disease (Towns et al. 2011; Szabo et al. 2012; Stuart et al. 2017). Invasive mammals prey on eggs, chicks, and adults which can result in significant decreases in population size, breeding success and nutrient pathways via guano deposition (Towns et al. 2006; Jones et al. 2008; Ruffino et al. 2009; Benkwitt et al. 2022). Grazing also disrupts normal cycles of seed dispersal and viability, decreasing the likelihood of seeds reaching maturity and has significant impacts on native vegetation communities and habitat (Calvino-Cancela 2011; Grant-Hoffman et al. 2010; Shaw et al. 2005). Restoration programs on islands, such as pest eradications, can restore historic seabird population sizes and show promising results on vegetation (Courchamp et al. 2003; Brooke et al. 2017). Invasive pest management however has only been utilised extensively over the past 60 years, and there is an urgent need to assess the dynamics of ecological change following removal to determine effective methods of conservation and control (Courchamp et al. 2003; Segal et al. 2021). Because of their biogeographical features, islands are ideal sites for ecological observation because they can provide novel insights into mechanisms of ecological function and change (Vitousek 2002). The results of this research are intended to inform stakeholders in similar island systems in the region and beyond.

The themes and ecosystem components within this research are reviewed in detail within a literature review and discussed throughout the various chapters within this thesis (see Figure 1-1 for a depiction of each theme). The intentions of this research are to help fill knowledge gaps within the scientific community and to produce meaningful results which can support conservation and restoration initiatives on vulnerable ecosystems.

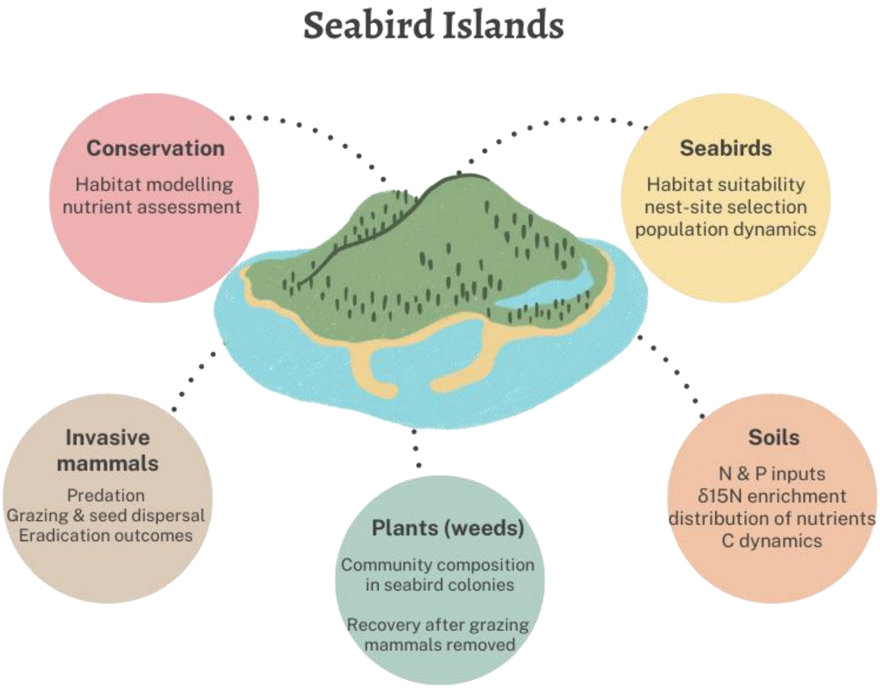

Figure 1-1 Themes of the research within the thesis as they relate to seabird islands

1.1 Broughton Island

Broughton Island (32.616° S, 152.314° E) is part of the Myall Lakes National Park and is the largest offshore island in New South Wales (NSW), with an area of 132 hectares. The island is located 170 km north of Sydney, 16 km northeast of Port Stephens, and 2.4 km east of the closest point to the mainland. Though it is of relatively limited size, Broughton Island contains a distinctive assemblage of soil and vegetation types. The geology of the island formed in association with the Carboniferous Nerong Volcanics, and is comprised of felsic rhyolitic rocks with basalt intrusions, conglomerates, and sandstones (Rose et al. 1966; Roberts et al. 1990). Landscapes on Broughton Island are however, dominated by two central aeolian sand dunes and extensive sandsheets with mosaics of shrubs and ferns, sandy beaches and foredunes, and endangered *Themeda triandra* (kangaroo grass) grasslands on coastal headlands (Somerville et al. 2018; Tulau & Wilson 2018). Broughton Island experiences a subtropical climate with temperatures ranging from an average minimum of 9.1 ℃ in winter to an average maximum of 27.3 ℃ in summer, and a mean of 1,339 mm of annual rainfall (Data based on Nelson Bay, BOM, 2021). Since its establishment of a National Park Reserve in 1972, the only human structures on the island include a small cluster of fisher huts and a camping platform and it is otherwise protected from external development.

Broughton Island hosts thousands of migratory seabirds from the Pacific and Indian Oceans who use the island for breeding from August to May (Marchant & Higgins 2006; Carlile et al. 2012). The most common seabirds which presently nest on Broughton Island include *Ardenna pacifica*, wedge-tailed shearwater and *Ardenna tenuirostris* short-tailed shearwater. Historic reports have documented the keystone species *Pelagodroma marina*, white-faced storm-petrel, though its local extirpation is attributed to the introduction of rats in the 1930's (Carlile et al. 2012). The island presently hosts dense colonies of *Ardenna pacifica* (wedge-tailed shearwaters) on the order of 64,500 breeding pairs, and they are regarded as key contributors of marine nutrient subsidies (Carlile et al. 2012).

The introduction of invasive mammals on Broughton Island has caused limitations to seabird populations, with the ultimate suppression of colony density and removal of some keystone species (e.g. white-faced storm petrel) (Carlile et al. 2012). These disturbances presented subsequent opportunity for a number of weed taxa to dominate, particularly prickly pear (*Opuntia stricta*) and bitou bush (*Chrysanthemoides monilifera*), and management efforts are still required to maintain optimum environmental outcomes (NPWS 2002; Priddel et al. 2012; Hunter 2015). Motivated by the disruption to plant and seabird communities, an invasive mammal eradication program was initiated by the NSW Government and National Parks and Wildlife Service (NPWS) in 2009 to target *Rattus rattus* (black rats) and *Oryctolagus cuniculus*

(European rabbits) using aerially dispersed cereal pellets with brodifacoum (20 ppm), bait stations with pellets and carrots sprayed with rabbit haemorrhagic disease. The operation was undertaken in an effort to restore seabird habitat and breeding success, and to promote growth of native plant communities (Priddel et al. 2011). The island was declared free of rats and rabbits in 2011 and as of this date there are no rats or rabbits present on Broughton Island. Expansion of shearwater colonies has been documented following eradication, but the broader trajectory of ecological change on the island however remained largely unknown (Carlile et al. 2022).

Broughton Island was an ideal study site as it is a National Park with minimal external disturbances experienced on mainland locations (e.g. human disturbance, development etc.) and it represents numerous islands with similar conservation threats and abatement goals (Holmes et al. 2019). Logistically the island was largely accessible with the generous assistance from the New South Wales National Parks and Wildlife Service.

1.2 Research gap and justification

Studies of seabird soil nutrient subsidies have identified a general trend of seabird point-source soils being enriched in N and P but the descriptions or role of soil type are rarely mentioned in this work (Grant et al. 2022). Soils are incredibly diverse and affect the behaviours of nutrients in terms of cycling, runoff and retention. Elucidating the role of soil and topography in the distribution and movement of seabird nutrient subsidies will improve our understanding how seabirds affect terrestrial ecosystems.

The effect of invasive mammal eradications on the restoration of seabird population sizes and breeding success has been well documented, however the ecosystem components that encourage recovery remain vague. Research on vegetation change post-eradication is limited and rarely reported leaving land managers unable to predict ecological change in native vegetation communities (Segal et al. 2021). Elucidating the changes in vegetation after a top predator(s) is(are) removed can be used to improve the efficacy of restoration projects and prediction of ecological outcomes.

Seabird populations face a suite of threats to their habitat structure and breeding success on islands, and their conservation is a priority on New South Wales islands. Despite their prevalence and importance on these islands, knowledge on the mechanisms of seabird nest site-selection is limited (Lewison et al. 2012). Effective conservation efforts require an understanding of behavioural and habitat preferences of seabirds. (Rodriguez et al. 2019; Pagenaud et al. 2022). With a deeper understanding of seabird behaviour on land, better management strategies can be employed for optimal conservation achievements.

1.3 Research aims

The overarching objective of this research was to elucidate the ecological relationships between nesting seabirds, soils, and plants on particular island ecosystems. Including the post-invasive mammal eradications in this theme was necessary and meaningful as they are the most prevalent threat to biodiversity on islands globally. Much of the field research planned was postponed or cancelled due to the COVID-19 pandemic during the candidature, but the limitations of study took an unexpectedly positive turn while also achieving the main research questions. Using GIS and spatial modelling in seabird island studies allowed the combination of a number of existing spatial datasets and provide meaningful results by discovering the connection between topographical and seabird habitat, and nest-site selection. Each of these chapters cohesively explain how different ecosystem components (seabird colony activity, pest eradication, soils, and plants), and can be used to inform land managers to make informed decisions related to conservation and biocontrol.

The primary research questions for this thesis are listed below:

1. What do we know about the effect of seabirds on offshore islands and what are the key research gaps in the area?
2. What is the spatial distribution of soil nutrients in seabird colonies with deep, sandy soils?
3. What is the effect of seabird colonies on soil chemistry and plant community composition?
4. How has Broughton Island vegetation changed since the removal of invasive rats and rabbits?
5. What is the habitat suitability of Wedge-tailed Shearwaters on Broughton Island and therefore predicted colony expansion?
6. Is there suitable habitat for Wedge-tailed Shearwaters that is uninhabited and how might this knowledge be used to optimise recovery of seabird colonies on Broughton Island?

1.4 Thesis structure

This thesis is structured by a general introduction (Chapter 1), and a literature review (Chapter 2), five (5) experimental research manuscripts (Chapters 3-7) and a general conclusion (Chapter 8). Each experimental research chapter includes an abstract, introduction, methods, results and discussion section. To reduce repetition of citations, a single list of references is compiled at the end of the thesis which includes all citations from chapters 1-8. A brief description of the chapter contents is below:

Chapter 2 is a review of literature which extensively explores the main themes of the thesis, including seabirds and their impacts on island ecosystem components, threats to seabirds and seabird islands, and current status of seabird islands in New South Wales.

C**hapters 3 and 4** describe the experimental research exploring the direct effect of burrowing seabird (Wedge-tailed Shearwater) colonies on soil nutrient distribution, concentration, and forms, as well as organic carbon, pH. Stable isotope analysis of $\delta^{15}N$ and $\delta^{13}C$ are included to provide a more robust dataset which gave some insights on nutrient pathways and sources on a sophisticated scale. The purpose was to understand the spatial distribution (Chapter 3) and effect of seabirds on nutrients in deeper, less documented soils, using appropriate non-colony systems for comparison (Chapter 4).

Chapter 5 describes the results from the analysis of data collected by the NPWS on vegetation characteristics following the removal of eradication of invasive rats and rabbits on Broughton Island.

Chapters 6 and 7 use spatial information to map the habitat suitability of Wedge-tailed Shearwaters on Broughton Island using two different, yet uniquely instructive, modelling approaches. Chapter 6 presents a GIS-based weighted overlay analysis, which is a multi-criterion analysis of environmental raster layers which are assigned user-defined values of importance. Chapter 7 describes maximum entropy modelling (MaxEnt), a machine learning approach which uses presence/absence data to algorithmically correlate species occurrences with their environmental features. Both models use the same base input layers which are important factors in seabird nest-site selection (Digital elevation model (DEM), slope, aspect, soil type, vegetation type) and seabird occurrence locations on Broughton Island. The aim of building these models was to identify the features of suitable habitat and therefore nest-site selection from the species, and to potentially identify uninhabited areas of suitable habitat and considered as useful information from a management perspective. Different approaches are used to compare the practicability, strengths and weaknesses of each approach, and determine their applications in future seabird conservation efforts.

Chapter 8 includes general conclusions describing how the results of each research chapter contribute to the general aim and scope of the thesis. It also describes how the findings of the work contribute to the knowledge of the effect of seabirds on offshore island ecosystems. Limitations of the work as well as recommendations for future directions in research are discussed.

Chapter 2: Seabird Islands of New South Wales, Australia: Effects of seabirds on the terrestrial environment

2.1 Introduction to seabirds and seabird islands in New South Wales, Australia

There are 8,222 islands in the territory of Australia, 102 of which are in New South Wales (Geoscience Australia 2021). Millions of migratory seabirds visit many of these islands each year as they migrate south to breed in the spring and summer months (Marchant et al. 2006). Seabirds migrate thousands of kilometres around the globe from Asia and Antarctica for breeding and head to Australia to provision themselves with abundant marine prey for energy and to reproduce on islands (Kerry et al. 1983; Pauly et al. 1998; Klomp & Schultz 2000). Migratory seabirds spend most of their time at sea and use islands principally for breeding. Offshore islands are ideal habitat for nesting seabirds because of their isolation and proximity to pelagic zones for food sources. Once they arrive on land, disturbance regimes and nutrient loading begin as they deposit excreta (guano) and some species begin to construct burrows which significantly alters plant-soil systems through the stimulation of primary productivity and bioturbation (Bancroft et al. 2005; De la Peña Lastra 2021). Seabirds are direct conduits for trans-boundary nutrient transfer which is substantial enough to drive ecosystem properties, such as soil fertility, vegetation community dynamics and trophic structures of islands (e.g. Mulder et al. 2011; Duda et al. 2020; Turner-Meservy et al. 2022).

Islands are particularly vulnerable to disruption of natural cycles and population decline due to high endemism of plants and animals (Kier et al. 2009). Islands lend themselves as examples of fragile ecosystems as they are typically small, geographically defined and enclosed lands which mimic other broad-scale ecological processes in a simplified manner (Bancroft et al. 2004; Wardle 2002). Because of these attributes of isolation, islands are places with high conservation value and a source of refuge for a variety of rare or endemic species (Towns & Broome 2003; Kier et al. 2009). Furthermore, island-dwelling seabirds are particularly vulnerable to disturbance as they have evolved in the absence of humans or introduced predators and have ill adapted defence mechanisms (Burger & Gochfeld 1994; Blackburn et al. 2004). This is especially true for threats from human influence and invasive animals and weeds which have caused massive declines in seabird populations and are considered to be significant threats to biodiversity in these island systems (Franklin & Steadman, 1991; Towns et al. 2006).

New South Wales National Parks have employed major conservation projects on numerous islands in order to restore seabird habitat and seabird breeding success (Priddel et al. 2011). The offshore islands of New South Wales have each experienced differing levels of disturbance from human activities such as cultivation, fire, and perhaps most notably, the introduction of invasive mammals and plants. These efforts include extensive operations to eradicate exotic plant and animal species, minimizing damaging fire regimes, and monitoring seabird populations in order to reduce threats and build resilience in the face of climate change.

2.1.1 Trans-boundary nutrient transfer: Energy flux from sea to land

Seabirds link marine and terrestrial ecosystems and are recognized as one of the greatest contributors to global nutrient cycling of nitrogen (N) and phosphorus (P) in the order of 591 and 99 Gg y^{-1} respectively (Burger et al. 1978; Wainwright et al. 1998; Otero et al. 2018). This impact is so substantial that some seabird islands or ‘guano islands’ in Peru and Chile have sedimentary layers where guano has accumulated, and was historically mined as a source of organic fertilizer prior to the 20th century due to its success in enhancing crop production (Duffy 1994; Dyer, Hill & Barnes1995; Szpak et al. 2012; Cushman 2013).

Seabirds forage in near-shore and pelagic environments, feeding on fish, krill, squid and crustaceans (Smith, Mulder & Ellis 2011; Hamer 2018). Seabird prey is often high on marine trophic levels and are enriched in macronutrients such as N and P (Anderson & Mulder 2011). Elemental isotopes of such materials bioaccumulate and become incorporated into seabird tissue, feathers, and most notably their excrement, through the process of trophic enrichment which is the phenomenon by which 'heavier' isotopic fractions of an element, such as ^{15}N are enriched as trophic level increases (Fry 1988; Hobson, Piatt & Pitocchelli 1994; Bird et al. 2008; Mulder & Ellis 2011). Nutrient dense flesh or carrion, eggs, fish scraps, vomit, and guano are often deposited on nesting sites and incorporated into the terrestrial ecosystem (Sanchez-Pinero & Polis 2000). The flux pathways of marine C originate from seabirds ingesting marine carbon and is deposited through seabirds as well as algae and marine detritus brought onshore from oceanic shore drift, seabird carrion and dropped fish scraps (Anderson & Polis 1999; Hawke & Condron 2014). These element concentrations and isotopic signatures are then incorporated into soils, plants, and animals in the vicinity of seabird colonies through several flux pathways, with guano deposition being the primary conduit (Smith, Mulder & Ellis 2011).

The transport of seabird nutrients has direct and indirect, bottom-up influences on primary production and trophic dynamics (Polis & Hurd 1996; Rose & Polis 1998; Kazama 2019). Nitrogen and phosphorus are bioelements and are often the limiting nutrients for both marine and terrestrial ecosystems (Chapin 1980). High concentrations of N and P are ubiquitous in seabird island soils, and often plants reflect this enrichment in biomass, thus altering nutrient availability and elemental isotopic signatures of N and C in terrestrial ecosystems (Anderson & Polis 1998; Wait et al. 2005; Young et al. 2011). This flux of nutrients by seabirds exerts both bottom-up influences on the recipient system by stimulating primary productivity and enriching trophic levels with nutrients both on land and sea (Sanchez-Pinero & Polis 2000, Elser et al. 2007; Mulder et al. 2011). This biotic exchange supports community and ecosystem structure and function that would not be possible on enclosed systems alone when nutrients would otherwise be internally sourced (Wardle 2002; Stapp et al. 2003; Polis et al. 2004; Ellis et al. 2006). Terrestrial guano may run off into nearshore ecosystems and even stimulate phytoplankton and coral reef ecosystems (Elser et al. 2007; Shatova et al. 2016; Lorrain et al. 2017; Kazama 2019; Benkwitt et al. 2021). Seabirds therefore are trans-boundary sources of nutrients which support terrestrial and marine biospheres.

2.1.2 Dual roles of burrow-nesting seabirds

The dual impact from nesting activities drives plant species composition, spatial heterogeneity nutrients, and distribution of plants on islands from two primary conduits: nutrient deposition and bioturbation (Bancroft et al. 2005b; Durrett et al. 2014). Nesting seabirds affect terrestrial systems in a variety of ways through biophysical soil engineering. Nutrient transport via seabirds from marine to terrestrial systems has been extensively described (Otero et al. 2018; Grant et al. 2022). Allochthonous inputs of guano, feathers, carcasses and eggs influences all aspects of trophic systems (De la Peña-Lastra 2021; Gaiotto 2022), including soil biota (Fukami et al. 2006), terrestrial producers and consumers (Stapp & Polis, 2003), and surrounding marine environments (Kazama 2019; Finne et al. 2022). These nutrient subsidies are exacerbated by the colonial nature of seabirds which in turn deposit great quantities within dense colony areas (Otero et al. 2018). Spatial subsidies of seabird nutrients alone make seabirds integral components of nutrient cycling and trophic function in the spaces they inhabit.

Many burrowing seabird species are gregariously colonial, nest in dense colonies and construct conical shaped burrows to 2 m deep with the nest located at the base (Warham 1990). Continual soil excavation throughout the breeding season can remove 10.51 t ha^{-1} of soil per year^{-} comparable in magnitude and scale with many other geomorphic mammals such as tortoises and rabbits (Bancroft, Hill & Roberts 2004). The physical act of burrowing, trampling and burying creates bare soil, increases hydrological and aeolian erosion, and suppresses adult and seedling growth (Bancroft et al. 2005b). Burrowing alters soil bulk densities, water-holding capacities and may increase soil surface temperature (Ellis 2005). Burrowing seabirds are considered to be ecosystem engineers for their direct physical impacts on the soil and plant environment.

It is not a simple matter to elucidate the isolated effects of chemical and physical disturbance seabirds have on ecological parameters, such as soil food webs and development, vegetation patterns, and trophic relationships (Bancroft et al. 2005a). There are physical and chemical disturbances and additions at a range of spatial and temporal scales on seabird-dominated islands, making the ecological responses complex and challenging to delineate (Durrett et al. 2014). The result of seabirds on soils and plants largely depends on the soil type, topographical and climate feature, and species of seabird, colony density, and nesting type. The dual perturbations exerted by seabirds significantly modulate the physical and chemical properties of soils, therefore making them important drivers of ecosystem function.

2.3 Impacts of seabirds on soil nutrient concentrations

The greatest form of nutrient subsidy on land from seabirds is from guano, which contains up to 28.6 % N and 10 % P in primary forms of uric acid, insoluble phosphate and proteins, and can increase input of N on land by 100 and 400 times respectively (Furness 1991; Smith & Johnson 1995; Bird et al. 2008; Otero et al. 2019). N and P supplied by seabirds therefore plays a significant role in soil biogeochemical cycles (Riddick et al. 2012; Otero et al. 2018). The soils within seabird colonies have been shown to have elevated soil nutrient concentrations in most regions of the world, particularly in ammonium (NH_4^+), nitrate (NO_3^-), phosphate (PO_4^-), potassium (K), and magnesium (Mg_2^+) (Burger et al. 1978; Anderson & Polis

1999; Ellis 2005). These elements experience many organic and inorganic transformations as they are cycled through ecosystems. Nutrient cycling is principally governed by, and largely dependent on, biological activity from microbial communities to convert nutrients to bioavailable forms (Wardle 2002; Wright et al. 2010). Seabirds, through guano inputs have been shown to increase microbial biomass and respiration, thus increasing mineralisation of detritus (Fukami 2006). Under high nutrient loading from seabirds, net retention and enrichment of nutrients in soils may vary, depending on the physiological mechanisms and/or inorganic factors driving productivity in ecosystems (Erskine et al. 1998; Markwell & Dougherty 2003; Hawke & Newman 2004; Hawke 2005).

N and P have contrasting biogeochemical properties and behaviours in terrestrial systems and the fractionation, mobility and transformation of these elements on differing landscape types has not yet been synthesised. Nitrogen can be fixed from the atmosphere but phosphorus lacks a gaseous stage, is relatively stable, and may stay in the soil for thousands of years, and its elevated concentration is often referred to as a legacy effect (Hutchinson 1950). This property of phosphorus is why soil P is typically better correlated with seabird colony nest density and guano cover than N (Anderson & Polis 1999; Hawke et al. 1999; Mulder et al. 2011). Guano-N on the other hand is rapidly mineralized into inorganic forms where it may stay in the soil, be leached through percolating water or runoff to nearshore waters, or transformed to atmospheric gas (Lorrain et al. 2017; Kazama 2019). The lasting significance of seabird nutrient inputs onto island ecosystems is such that it may even remain as N (0·41–1·4%) and P (1780–5285 mg/kg) in soils even after breeding seabirds cease to maintain activity (Hawke et al. 1999; Otero et al. 2015). The input of nutrient subsidies from seabird colonies therefore has long-lasting effects on soil fertility.

2.3.1 Nitrogen

Nitrogen (N) is a primary macronutrient necessary for plant growth, and is often found to be limiting to primary production in terrestrial ecosystems (Chapin 1980; Vitousek 1981). Seabirds enrich primary and secondary consumers with nitrogen and enhance terrestrial productivity through N availability and these external inputs have great importance in terrestrial ecosystems (Hutchinson 1950; Ellis 2005; Caut et al. 2012; Wilson et al. 2019). Seabird guano contains from 1-25 % N as crystalline uric acid, where uric acid itself contains as much as 40-90 % N (Mizutani et al. 1985; Otero et al. 2018). Other guano-N is in the form of ammonia (NH_3) and urea, which generally account for < 25 % total N (Sabat et al. 2004; Bird et al. 2008). The nitrogenous waste in guano becomes available after it is mineralized through ammonification and nitrification, producing labile nitrate (NO_2^-), nitrite (NO_3^-) and ammonium (NH_4^+) (Mizutani, Kabaya and Wada 1985). Only after N is transformed in the soil solution can plants readily use it. Concentrations of $NH_4^+$and NO_2^- in soil as well as plant productivity and nutrient concentration have been consistently correlated with seabird colony densities on a range of landscape types (Mizutani et al. 1985; Ellis, Farina & Whitman 2006; Schmidt et al. 2010).

Ornithogenic-N may also be lost through several processes. A study conducted in Australia found up to 48 % of seabird-N was lost within 4 days on a seabird island, the N being lost as it is cycled through NH_3 volatilization, immobilization from microbes and leaching of nitrates (Smith & Johnson 1995; Mulder & Keall 2001; Riddick et al. 2012). These nitrates may end up in coastal systems by transfer of groundwater or surface runoff, denitrified into nitrous oxide (N_2O) or nitrogen gas (N_2) (Kazama 2019). The volatilization of ammonium often occurs under anaerobic conditions in the soil, where bacteria reduce nitrate to nitrite through denitrification then to elemental N_2 gas, at which point is lost to the atmosphere (Hillel 2008).

Climatic and biogeochemical factors may accelerate rates of N loss through pathways pressured by temperature, humidity and even latitude. For example, NH_3^- can also be lost through high soil surface temperature and alkaline soil conditions. Atmospheric ammonia concentrations are found to be higher in seabird colonies and it has been reported that more than 30 % of seabird N is volatilised as NH_3^-N (Mizutani, Kabaya and Wada 1985; Blackall 2008). Studies of soil in sub-arctic seabird soils have linked ^{15}N enriched ammonium soils and water to ammonia volatilization, this especially true in soils which have longer time for decomposition of uric acid and volatilization (Mizutani et al. 1985; Erskine et al. 1998). The amount of volatilised ammonia is so great, 2-5 % ammonia in polar region-colonies and up to 31-65 % in tropical climate colonies have been reported, which are some of the highest emissions from animals on the globe (Riddick et al. 2012; Blackall et al. 2008; Otero et al. 2018).

2.3.2. Phosphorus

Phosphorus (P) is a macronutrient essential for plant growth and stability. While P is an essential component of geochemical cycles for plants, is one of the least plant-available soil macronutrients despite its relative abundance (Schlesinger 1997). Phosphorus therefore is often limiting in terrestrial ecosystems, and of all the total phosphorus stored in plant biomass and soil, <1 % labile for plant use at any time (Stewart et al. 2005). As soils age, P becomes more limiting as it is lost through leaching, organic and inorganic immobilization and offshore erosion, thus making seabird-P more influential in terrestrial productivity (Vitousek 2004; Wardle et al. 2004; Condron & Tiessen 2005). Without the influence of seabirds, the most abundant internal source of P is derived from the weathering of primary minerals, specifically the dissolution of apatite minerals (Polis et al. 2004). Apatite is sparingly soluble and the availability of terrestrial P is restricted by the rate of release, which is dependent to a large degree on climatic conditions (Newman 1995; Filipelli 2016). Phosphates are converted into soluble forms in acidic soils or through solubilisation of inorganic phosphate or mineralization of organic phosphate by bacteria into dihydrogen phosphate ($H_2PO_4^{2-}$) and hydrogen phosphate

(HPO_4^-) (Hillel 2008; Nguyen, Zapata & Adu-Gyamfi 2016). Organic forms of P (P_o) are largely derived from microbes, plant and animal residues (Nguyen, Zapata & Adu-Gyamfi 2016) but is largely unavailable to plants. These processes illustrate the deficiencies of P in most biogeochemical systems, and conversely how guano deposition is a source of bioavailable P.

Phosphorus in seabird guano is largely made up phosphates and insoluble forms of P, ranging from 0.12 to 16 % total P (Vitousek & Howarth 1991; Mulder et al. 2011; Otero et al. 2015). The range in chemical composition of guano-P can depend on the diet and physiology of specific bird species but overall mobilize impressive amounts of P to soil systems (Zhong et al. 2017). Seabirds subsidise substantial amounts of soluble and insoluble P through guano deposition. Containing as much as 2% P, guano can increase P supply on land by as much as 400 times (Furness 1991; Smith & Johnson 1995; Bird et al. 2008). Phosphorus in soil has been found to be more strongly correlated with guano than N, because phosphate is more stable in the soil compared to N, which can be lost through volatilisation and decomposition of uric acid, particularly in areas of high temperature and/or humidity (Anderson & Polis 1999). Phosphorus may remain in soil for thousands of years, even after seabirds depart leaving a legacy effect on islands even in the event of an extinct colony, leaving plants with a P saturation (Hutchinson 1950; Otero et al. 2015). Soil P inputs via seabirds therefore are irreversible and is a rare biogeochemical process experienced in terrestrial biogeochemical systems.

2.3.3. Carbon

Soil organic carbon is a key constituent in soil organic matter, and can be modulated by burrowing animals (Platt et al. 2016). Seabirds alter C storage indirectly through burrowing activities and directly through C input (Wardle et al. 2007; Leblans et al. 2014). With regard to C stock and storage, there are two possible, conflicting outcomes as a result of seabird activity. Due to nutrient enrichment in seabird colonies, plant biomass may increase, which leads to an increase in SOC, which improves soil structure (Kögel-Knabner et al. 2013; Long et al. 2013). Seabirds transfer significant C resources from the ocean to land which can directly increase C storage in the soil, through the movement of marine biomass to land and incorporating surface litter into burrows, thus increasing C stocks (Polis & Hurd 1996; Mulder & Keall 2001). Deposition of N and P alters stoichiometric values in soil, driving microbial biomass and mineralisation, thus potentially priming litter decomposition (Fukami et al 2006; Hawke & Vallance 2015). In contrast, the displacement of soil via burrowing alters below-ground decomposition of biomass (Warham 1996; Mulder & Keall 2001; Bancroft 2004). Root disruption by burrowing can damage trees and shrubs stability, thereby reducing biomass and C storage in tissue (Maesako 1999; Wardle et al. 2007). Nesting activities additionally creating bare soil, increased soil erosion and a range of other edaphic alterations affecting plant biomass, which ultimately may have negative effects on carbon sequestration (Mulder & Keall 2001; Bancroft et al. 2005). Despite its importance in terrestrial ecosystems, the literature is arguably under-represented in the effects of organic C in terrestrial seabird environments, and therefore more information is needed to fully understand mechanisms of C in seabird systems.

2.4 The role of stable isotopes in tracing marine-derived seabird nutrients in plant-soil systems

Isotopic signatures of nitrogen and carbon have been widely used in ecological studies to trace flows and fractionation of nutrients as they are cycled from the ocean, into seabirds, deposited on land and cycled through soils, plants, and animals (Kelly 2000; Tiunov 2007; Wilson et al. 2019). The analysis of stable isotopes has been a revolutionary tool in linking ecological patterns which would otherwise be unknown. As the name suggests, stable isotopes are the stable form of the same element, (as opposed to radioactive forms), which contain the same number of protons and electrons, but contain a different number of neutrons, resulting in differing atomic mass numbers, dependent on the weight of the nucleus (Fry 2006). For example, nitrogen (N) has an atomic number 7 which remains constant. If N has 7 neutrons, 7 electrons and 7 protons this is ^{14}N as 14 is the atomic mass, which is the sum of the number of protons and neutrons. However, ^{15}N contains 7 neutrons, 7 electrons and 8 protons. Thus, the species of stable isotopes in nitrogen are ^{14}N and ^{15}N (Peterson & Fry 1987). Each of these isotopes of N exist in nature and are transferred, mixed, and fractionated as they cycle through trophic systems in plants, soils, and animals.

Isotope fractionation occurs as elemental species are partitioned through reactions which separate the 'heavy' to 'light' isotopes, i.e. changing nitrogen and carbon ratios (Peterson & Fry 1987). Common reactions like precipitation, evaporation, and animal digestion are factors which change isotopic ratios of an element. Calculating isotope ratio values is an analytical approach which considers changes in the ratio (δ) of the relative abundance of 'heavy' to 'light' isotopes within a sample of solids, liquids or gases. The measurement of elemental isotopes is conducted by isotope ratio mass spectrometry (IRMS) using ratios of a standard ($R_{standard}$) compared to a sample (R_{sample}) expressed as the deviation (δ) of the ratio in parts per thousand (‰) (Lajtha & Marshall 1999; Fry 2006):

$$\delta X = [(R_{sample}/R_{standard})-1] \times 1{,}000$$

Stable isotope analysis has been utilised in seabird studies for tracing diet, and is most applied to the analysis of ^{15}N and ^{13}C; as both of these signatures are compared to seabird tissue and excrement and compared using isotope ratios to that entity, in plants, soils, and living organisms they encounter (Conroy et al. 2015; Kazama 2019). Isotope ratios of $^{13}C/^{12}C$ ($\delta^{13}C$) and $^{15}N/^{14}N$ ($\delta^{15}N$) are interpreted to detect the contrast between marine and terrestrial sources of C and N. For example, closed systems relying on terrestrial sources of nitrogen (e.g. N fixation or precipitation of NO_3^- and NH_4^+) typically reflect an isotope ratio $\delta^{15}N$ of 0‰

(Högberg 1997). However, when transfers among trophic levels occur (such as marine animals > seabirds > land plants), enrichment of ^{15}N takes place and the $\delta^{15}N$ increases values by about 3-5 ‰ for each trophic transfer, a process referred to as trophic enrichment (Hobson et al. 1994; Mulder et al. 2011). These values may range from 5-40 ‰ $\delta^{15}N$ in plants, soils and animals (Szpak 2012). Stable carbon isotopes of $\delta^{13}C$ are discriminated due to fractionation, diffusion, and dissolution (Ehlringer et al. 1993; Lajtha & Marshall 1994; Hull et al. 2019). Less negative carbon stable isotope ratios have been used as indicators of samples with marine origin (Mizutani and Wada, 1988). Therefore, stable isotopes can reveal much about not only the concentration, but the source of N and C in soil systems. Furthermore, stable isotope signatures of N and C are reliable sources of information to compare ecosystem components (soil) to nutrient sources (seabirds).

There are two general processes of isotopic fractionation and enrichment of N from seabird guano on terrestrial ecosystems: one is through trophic enrichment of isotopic N (^{15}N). Seabirds are higher on food chains as are their prey (e.g. squid and krill) which contain higher concentrations of nutrients and a heavier isotope ratio compared to lower trophic levels (Mulder et al. 2011). Thus, the approach of stable isotope analysis relies on the theory that isotopic signatures in tissue of the consumer are reflected through prey (Peterson & Fry 1987; Hobson 1999; Kelly 1999; Forero & Hobson 2003). The nutrients in seabird colony areas typically show similar values to a high trophic level marine source, and similar to that of guano (Irick et al. 2015; Pascoe et al. 2022). Another source for enrichment in ^{15}N occurs from the fractionation of N as it is volatilised as NH_3^-. Through its release to the atmosphere, it carries with it the lighter isotope, leaving behind a greater abundance of ^{15}N (Mizutani et al. 1985). Enrichment of ornithogenic ^{15}N in terrestrial plants and soils can occur from the volatilisation of ammonia and trophic enrichment (Wainright et al. 1998). The process of ammonification occurs when gasses from the lighter isotope are favoured to volatilise, leaving the heavier isotope behind. Legacy isotopic signatures of $\delta^{15}N$ from seabird nutrients are retained in island ecosystems even long after seabirds are gone, thereby shaping trophic ecology (Hawke et al. 1999).

Foundational studies of seabird nutrient loading and cycling on seabird islands have been based on broad, descriptive studies of nutrient concentrations and pools in colony vs. non-colony landscapes (Mizutani et al. 1986; Mizutani & Wada 1988; Pascoe et al. 2021). The use of stable isotope analysis allows the investigation of ecosystem dynamics to occur on a much more detailed and sophisticated level (Forero & Hobson 2003). Stable isotopes therefore facilitate ecological studies by elucidating the sources and transformation of nutrients (Wainwright et al. 1988; Hawke 2004).

2.5 Impacts of seabirds on vegetation communities

Plant communities are largely dependent on edaphic factors, which are the chemical, physical, and biological aspects of soil, thus seabirds have profound impacts on vegetation communities on the islands where they nest by altering soil characteristics. Much of guano N and P is readily soluble or rapidly mineralized and bioavailable for plant uptake, stimulating primary and secondary production (Schmidt et al. 2004; Vitousek 2004; Otero et al. 2018). Despite the importance of ornithogenic-N enhancing terrestrial plant and animal communities, the relationship between seabird nutrient subsidy and plant biomass and productivity is not always a linear trend. For example, although seabird guano itself tends to be alkaline or neutral, high concentrations of NH_4^+ in guano tends to decrease soil pH in due to microbial nitrification, thereby decreasing survival for intolerant plants (Smith & Johnson 1995; Blake 2005; Mulder & Keall 2001). Various physiochemical alterations in the soil, such as acidity, temperature, compaction, or salt additions may cause nutrients to become less bioavailable as they may be locked in other insoluble forms, therefore stress for plants shifting vegetative communities

(Hillel 2008). Seabird colony landscapes often exhibit distinct vegetation best adapted to pulses of high nutrient loads and frequent disturbance, thereby resulting in both positive and negative consequences for native vegetation communities which may remain for centuries (Mizutani et al. 1991; Bancroft et al. 2005b).

The physical mechanisms by which seabirds affect their local colony environment show distinct differences in vegetative patterns when compared to non-bird islands and seabird island areas with no colonies (Lameris et al. 2016). At the individual level, the trampling and pulling of plant roots increases plant leaf water stress and decreased understory (Mulder et al. 2011). Large numbers of seabirds can cause physical damage to seeds, seedlings and fully developed plants through burrowing, making it difficult for regeneration to occur (Masaeko 1999; Mulder & Keall 201). Seabird burrowing activities can cause root damage and aerate soil, resulting in alterations in plant nutrient and water uptake (Mulder et al. 2011). The impacts and adaptations of individual plant species affected by seabird disturbance often drives the community patterns by favouring plant species with certain attributes (McKenchie et al. 2006).

As a result of the covariate factors of nutrient subsidy and soil disturbance burrowing seabirds have on landscapes, ecosystem parameters respond at different spatial scales as resource availability, soil disturbance, and colony size increases (Durrett et al. 2014). While plant nutrient levels and productivity may be higher in seabird colony areas, vegetation patterns also often include decreased species diversity and structural complexity compared to non-colony landscapes (Anderson & Polis 1999; Bancroft et al. 2005b). Distinct vegetation community characteristics in seabird colonies are defined by plants which can withstand heavy nutrient loads and disturbance regimes, often ruderal species (Ellis 2005; Mckenchie et al. 2006; Lameris et al. 2016). Seabird colony vegetation tends to be shorter lived, shorter in vertical structure, denser and defined by annual plants and succulents (Abbot et al. 2000; Bancroft et al. 2005b).

Many native island plants are not evolved to withstand such disturbance and nutrient concentrations compared to weed species, which typically grow faster and compete for nutrients and water, and have a greater threshold for environmental pressure (Bancroft et al. 2005; Mulder & Keall 2001). Native island vegetation can be sensitive to changes in nutrient availability, water availability, and physical disturbance and have a threshold at which they can survive. For example, native species have been observed to withstand minor disruption from burrows, but die off at high densities (Gillham 1963). Seabirds therefore drive vegetation patterns on the islands they inhabit, and the prevalence of invasive plants may be exacerbated by seabird activities. The soil and physical environment seabirds create therefore is an important factor in the management plans of biological control.

2.6 Major threats to seabirds and seabird islands

Seabirds face a suite of threats at sea and on land which affects their distribution and breeding patterns. Numerous anthropogenic pressures have resulted in declining seabird populations through marine bycatch, poaching, commercial development, and plastic and light pollution (Anderson et al. 2011; Žydelis et al. 2013; Dias et al. 2019). Persistent pesticide use of chlorinated pesticides, polychlorinated biphenyls (PCBs) and polycyclic aromatic hydrocarbons (PAHs), as heavy metals and microplastics are being found carried by seabirds (Taniguchi et al. 2009; Lopes et al. 2022). The biggest threat to seabird survival and breeding success on land is due to invasive mammals (Paleczny et al. 2015; Spatz et al. 2017; Dias et al. 2019). These threats are responsible for declining trends in 70% of global seabird populations (Paleczny et al. 2015). (Croxall et al. 2012). Management of invasive mammals therefore is a critical component in global conservation issues.

2.6.1 Invasive mammals

Invasive mammals have been introduced to over 80% of the major islands of the world, causing enormous threats to native species, especially seabirds (Atkinson 1985; Towns et al. 2006; Jones et al. 2008). Invasive mammals pose major threats to seabirds and the effects cascade directly and indirectly, altering native population sizes, trophic structure, soil fertility, seed banks, and plant communities (Fukami et al. 2006; Grant-Hoffman et al. 2010). Rats, cats, foxes, goats, dogs and mice are historically introduced to islands either intentionally or accidentally; they arrive on cargo ships, as pets, and as food sources (Kolar & Lodge 2006; Harper & Bunbury 2015). Rats (*Rattus*) are a ubiquitous genus adapted to living in most island habitats and can even swim distances up to hundreds of meters to colonise islands (Harper & Bunbury 2015; Bagasra et al. 2016). When invasive mammalian populations are left unmanaged, these animals engage in competition and often become dominant predators and drive seabird species to local or total extinction (Priddel et al. 2011). After the arrival of exotic rodents more than 20 subspecies of endemic species have become extinct on Australian islands, most of which are birds, and many of which were native to the remote Lord Howe Island, an offshore island of NSW (Australian Government 2009). Invasive animals are therefore a key issue with regard to seabird colonisation success and persistence.

Invasive predatory mammals directly affect seabird colonies by the consumption of birds and their eggs as prey (Mulder & Keall 2011; Priddel et al. 2011). As the seabird population decreases, so do the trickle-down effects of their ecosystem services. For instance, fewer seabirds equate to less soil disruption and fewer marine nutrients transported by seabirds foraging at sea and depositing guano and fish scraps on islands (Mulder & Keall 2001; Fukami et al. 2006). In the presence of predators and decreasing seabird populations, soil fertility and vegetation patterns are altered as a result of decreasing soil nutrients and plant biomass (Fukami et al. 2006). For example, introduced foxes in the Aleutian Islands reduced seabird populations, thus cutting off nutrient flows and, as a result, vegetation patterns shifted from nutrient tolerant grasses to shrubby tundra species (Croll et al. 2005). Introduced mammals also consume plants and seeds, decreasing success of seedling dispersion (Grant-Hoffman et al. 2010). Conversely, the eradication of exotic mammals on seabird islands has been shown to restore seabird population and ecosystem function (Jones et al. 2016; Brooke et al. 2018).

The interactions of biological invaders and native taxa are complex, and impacts of exotic mammals on ecosystem structure can vary (Russell 2011). For example, soil carbon stock has been observed to be higher in the presence of exotic mammals, as with plant biodiversity because they abate some of the negative effects seabirds have on plant systems, such as trampling roots and decreasing plant water-holding capacity (Bancroft et al. 2005; Wardle et al. 2007). Similarly, the decline of invasive mammals has been linked to the increase of fruiting invasive weeds, as was observed on Pacific island as cats and rats foraged on fruiting parts of weeds before they were eradicated (West 2011).

Introduced pests most prevalent in NSW islands include ship rats (*Rattus rattus*), house mice (*Mus musculus*), and the European rabbit (*Oryctolagus cuniculus*), each of which are targeted species for eradication programs due to the burden they place on native biota seen around the world (Atkinson 1985; Priddel et al. 2011). Even despite effective invasive mammal eradications, established relationships between biological invaders and the ecosystem are complex and eradication may have unintended consequences on population size, vegetation shift, and overall ecosystem structure and function (Russell 2011). The knowledge of consequences after removal at the ecosystem level is crucial for effective island habitat recovery (Drake & Hunt 2009; Anderson et al. 2016).

2.6.2 Invasive plants

Invasive plants threaten native plant communities as they compete for soil nutrients, water, and space. Invasive plants not only threaten native plant communities, they have also been documented to be detrimental to seabirds. For example, entanglement from the sticky fruits of the birdlime tree (*Pisonia umbellifera*) have been observed, impairing flight and causing death by starvation (Priddel & Carlile 1997). Invasive weeds like lantana (*Lantana camara*) or prickly pear (*Opuntia stricta*) have also been observed to encroach on seabird colonies and threaten nesting success on Mudjimba Island in Queensland (Dyer 2000). Overgrowth of ground-level vegetation can also weaken habitat suitability and breeding success for surface nesting seabirds (Weerheim 2003; Lamb 2015). The suppression of weed species therefore is a priority for native landscapes and seabird habitat.

2.6.3 Climate change & weather anomalies

Seabirds are already threatened on many islands in New South Wales, but population stress is likely to be exacerbated by threats of climate change (Chambers et al. 2011). Components of climate change such as rising temperature, fluctuating weather patterns, and decreased rainfall alter seabird distributions, migratory patterns, and breeding success (United Nations 2016). In Australia, the temperature is predicted to increase by 1.8 and 5.5 degrees Celsius by 2070 (Suppiah et al. 2007). Increasing atmospheric temperatures will expose birds to direct and indirect effects, including heat waves causing mortality of birds and eggs through water loss or hyperthermia (McKechnie & Wolf 2010). Temperature increases in birds may also alter change in breeding time, migration times, foraging efficiency and loss in body mass (Garnett & Franklin 2014). For example, a study on the Great Barrier Reef correlated elevated sea surface temperature with decreased chick provisioning by adult wedge-tailed shearwaters (Smithers et al. 2003). Many migratory seabirds have high sensitivity to sea surface temperature and climatic events (e.g. ENSO cycle) for their breeding and foraging success (Dunlop et al. 2002). Seabird abundance is closely associated with sea surface temperature where upwelling and productive areas are ideal foraging ranges and islands near these areas tend to be hotspots for seabird presence and nesting distribution (Hunt et al. 1999; Byrd et al. 2005; Vilchis et al. 2006; Grecian et al. 2016). Many impacts of climate change ultimately result in threatening and decreasing seabird populations, which will cascade unto the island ecosystems, many of which are heavily reliant on ecosystem services provided by seabird nutrient subsidies (Durrett 2014).

2.7 Implications for conservation management and biocontrol

Studies of the impact of invasive mammal eradications have demonstrated success in restoring seabird populations and breeding success and restoring nutrient flows (Towns & Broome 2003; Jones et al. 2016; Brooke et al. 2018; Benkwitt et al. 2021). Many invasive mammals have existed in island systems for such long periods of time they have taken over functional roles of the ecosystem, and permanent removal may present unexpected or even adverse effects to restoration goals (Courchamp et al. 2003). A need for research has been established to elucidate trends of change and restoration after invasive mammal eradications (Segal et al. 2021).

With an improved understanding of burrowing seabird behaviour and impacts on weeds and invasive species and their effects on island ecosystem dynamics, we might expect more effective management plans (Rodríguez et al. 2019). While nesting seabirds, particularly endemic and native species, have a high conservation value, population patterns and effects should be considered when constructing management plans. For example, large populations of seabirds may have negative effects on seedling survival and seed germination (Mulder & Keall 2001). Careful consideration should be made for island managers in terms of invasive mammal eradication and the effects of though few studies have described the effects of island ecosystem properties post-eradication, probably because these interactions are so complex and dynamic (Russell 2011). For example, there have been interesting findings on the impacts of invasive mammals on ecosystem structure. Soil carbon stocks have been observed to be higher in the presence of invasive mammals, as with plant biodiversity because they abate some of the negative effects seabirds have on plant systems, such as trampling roots and decreasing plant water-holding capacity while burrow-nesting (Bancroft et al. 2005; Wardle et al. 2007). Similarly, the decline of invasive mammals has been linked to the increase of fruiting invasive weeds, as was observed on Pacific island as cats and rats foraged on fruiting parts of weeds before they were eradicated (West 2011). This information supports the importance of proper planning and preparedness of ecosystem responses to eradication programs.

Eradication efforts of exotic mammals can be tremendously costly, and often require considerable government and stakeholder support (Aguirre-Munoz et al. 2011; Carrion et al. 2011; Holmes et al. 2015). In fact, The Australian Department of Environment, Water, Heritage and Arts estimated $200 AUD/ hectare to eradicate rodents, which would equate to $68 million dollars for each island under 10,000 ha (2009). This causes significant stresses on governmental budgeting, many institutions of which are limited by budgets and must allocate funds according to priorities (Pimental 2014). Moreover, a recent estimate for the cost of monitoring seabird population ranges around $74.6K per year over fifty years' time as a result of the impacts of climate change (Garnett & Franklin 2014).

There are implications for collecting isotopic data from seabirds, as it may disturb colonies, euthanize birds for sampling (Bird et al. 2008). However, research invested in the interactions, effects and ecology of exotic species and seabirds is necessary, and effective management is dependent upon it (Towns & Broome 2003; Caut et al. 2007).

2.7.1 Benefit of geospatial analysis in seabird conservation

GIS is a powerful tool used to extract and observe environmental information which would not as easily be observed on land. GIS and spatial modelling have been increasingly utilised in the field of seabird conservation (Mackin 2000; McGowan et al. 2013; Borelle et al.

2015; Troy et al. 2017; Massaro et al. 2018). Migratory seabirds can be difficult to monitor on the ground as they spend most their time at sea and visit islands only during part of the year (often on remote islands with terrain that is difficult to access). Because they also are characterised by high survival rates, long lives, and low reproductive rates, long-term population monitoring can be difficult to measure and expensive to carry out (Nisbet 1989; Oro 2003). Geospatial analysis allows for the integration of multiple data sources which can provide robust results to solve complex location-oriented problems such as seabird population monitoring (Wilhelm et al. 2015; Edney & Wood 2021), conservation priorities for habitat (Borelle et al. 2015) and assess threats to seabird habitat (Bradbury et al. 2014; Matthiopoulos et al. 2021). The benefits of utilising GIS for ecological applications allows for more land coverage, can consider multiple criteria, and can be a cost effective, easily reproduced and adjusted to specific project requirements (Pacifici et al. 2017; Matthiopoulos et al. 2021).

2.8 Conclusion

Seabird islands are complex ecosystems which are principally driven by seabird nutrient subsidies. With over 100 million birds in the Australasian region, islands are critical places to conserve as seabird habitat for the continuation of ecosystem function (Riddick et al. 2012; Otero et al. 2018). This review has detailed many of the most important aspects of seabird dominated island ecosystems, and their importance in the environment.

Chapter 3: Novel insights into the spatial distribution of soil nutrient subsidies from nesting seabirds on dune landscapes

3.1 Abstract

Marine nutrient influx on terrestrial islands with seabirds is a recognised phenomenon, but the distributions of nutrients within a range of soil landscapes are not well described. To assess the spatial and depth distribution of soil properties in high density seabird colonies, surface and subsurface (0-50 cm) soil samples were taken from sample transects on two dune systems with wedge-tailed shearwater (*Ardenna pacifica*) colonies on Broughton Island, New South Wales. Total organic carbon (TOC), total nitrogen (TN), extractable phosphorus (ext. P) and Electrical Conductivity (EC) were significantly higher in lower slope and swale regions compared to colony areas located on the top of dunes indicating swales acting as nutrient sinks. Subsurface accumulation of P increased below 10 cm depth on inland dune systems. Isotopic signatures of $\delta^{15}N$ and $\delta^{13}C$ in soil were analysed to determine the source of carbon and nitrogen (e.g. marine or terrestrial), and were enriched in ^{15}N in all areas except for foredunes, indicating seabirds as the source of soil enrichment. This study highlights the role of soil landscape on the distribution of bio-available seabird nutrient inputs in soil, and its potential to accumulate in locations indirectly affected by seabirds. This study found novel evidence of patterns of nutrient distribution in deep sandy soils of seabird colonies where soil and landscape type play a role in mobility of nutrients.

3.2 Introduction

Seabirds drive primary productivity and botanical structure on islands they inhabit as they transport materials from pelagic foraging areas to breeding sites on land and deposit guano, egg shells, marine scraps, and carcasses (Anderson and Polis 1999; Mulder et al. 2011). Seabirds are one of the most important bio-resources for nutrient cycling and contribute to global budget of nutrient cycling of nitrogen (N) and phosphorus (P), up to 591 and 99 million kg P year $^{-1}$ respectively (Otero et al. 2018). Guano is rich in nitrogenous compounds, soluble and insoluble phosphorus, much of which is rapidly available for plant uptake and would otherwise be recalcitrant without digestion and redistribution from seabirds (Hobbs 1996). N and P availability often limit plant growth and biodiversity in terrestrial ecosystems, and seabird islands are unique in that they have evolved with allochthonous nutrient input (Vitousek et al. 1997; Thomas et al. 2013). Thus, seabird nutrient subsidy in soil has the capacity to support terrestrial communities both above- and below-ground and in marine communities like coral reefs as nutrients runoff to surrounding waters (Fukami et al. 2006; Wright et al. 2010; Graham et al. 2019; Kazama 2019). The role of seabirds as vectors for recycling nutrients becomes increasingly important as key bio-resources for nutrients decline through habitat loss, invasive predators, and seabird population decline (Abraham et al. 2022).

Wedge-tailed shearwaters (*Ardenna pacifica*) belong to the order *Procellariiformes* which includes petrels, albatross and shearwaters. Wedge-tailed shearwaters dig to 2 m to construct burrows for nesting, and excavate often during nesting periods (Warham 1990; Hamer 2019). Burrow nesting displaces significant amounts of soil by nesting in dense colonies (Bancroft et al. 2004). Through burrowing, seabirds become agents of seed dispersal, leaf litter cycling, and altered carbon stock processes, essential components for soil and plant productivity (Grant-Hoffman et al. 2010). Physical and chemical disturbance due to seabirds and their isolated effects on ecosystem properties are often hard to elucidate and are rarely quantified (Bancroft et al. 2005). However, it has been consistently shown that physiochemical engineering by seabirds affects vegetation composition, biodiversity, spatial heterogeneity and productivity of primary producers and consumers in terrestrial ecosystems (Ellis 2005; Wait et al. 2005; Yoshihara et al. 2010; Mulder et al. 2011). Soil properties (such as N) are impacted at varying scales by seabird burrow density (Durret et al. 2014). As a consequence, the community structure of plants in seabird colonies is often distinct due to this physical disturbance and nutrient input (Grime 1973; White & Harrod 1997; Abbot et al. 2000; Bancroft et al. 2005).

The various mechanisms by which nutrients and soil organic matter (SOM) are cycled through an ecosystem influenced by seabirds may be identified through the analysis of stable isotopes. Stable isotope analysis is an effective tool to provide ecological insights into nutrient and C source and cycling processes, diet, and trophic structure of communities (Hobson 1994; Anderson & Polis, 1999). Stable isotope ratio signatures of ^{15}N:^{14}N ($\delta^{15}N$) in soil can be used to elucidate patterns of nutrient cycling, fractionation, and source (Fry 2006). As seabird-derived N is biochemically cycled, heavy and light isotopes are interchanging through kinetic fractionation (e.g. ammonia volatilization) and mixing (e.g. deposition and uptake) (Mizutani et al. 1985; Wainright et al. 1998; Fry 2006). The nitrogenous compounds within guano are rapidly mineralized into inorganic forms where it may be used by plants, be leached through ground of surface water, or lost to the atmosphere through volatilisation (Lorrain et al. 2017; Kazama 2019). Marine-derived nutrients deposited by seabirds are typically enriched in ^{15}N as N is accumulated as fractionates through trophic systems (Minawaga & Wada 1984). As a result, soils, plants, and animals affected by allochthonous resource supply tend which suggest a reliance on this open source of N and C compared to terrestrially closed systems (Wainwright et al. 1998; Scheu 2002). Though the various aspects of the N cycle are complex, stable isotope analysis can be used to ascribe the various pathways of N gain, loss, and bioavailability of N to plants (Craine et al. 2015). Stable C isotope ratios $^{13}C/^{12}C$ ($\delta^{13}C$) can be used to determine C source, as photosynthetic pathways of plants are distinguished from another as reflected by different $\delta^{13}C$ values (Lajtha & Marshall 1994; Scheu 2002). Tracing spatial patterns and distribution of nutrients are often strong indicators of resource input and vegetation community shifts (Schlesinger et al. 2013). Using stable isotopes in ecological studies therefore is useful for elucidating trans-boundary nutrient transfer and geochemical cycling.

Wedge-tailed shearwaters commonly nest on landscapes with steep slopes, ridgelines, and plateaus that are easily reached following prevailing ocean winds (Warham 1990). Landscape position influences a range of soil properties and biochemical reactions like nutrient distribution, SOM decomposition and mineralisation (Brubaker et al. 1993). Incoming solar energy, water retainment, nutrient subsidy and soil stability may vary in relatively small surface areas, impacting distribution and cycling of soil nutrients (Hairston and Grigal, 1991). Erosion and runoff carry N and P and contribute to the accumulation of SOM, particularly in saturated or partly saturated catchment areas (Collins and Kuehl, 2001; Sahrawat 2004). Topographical features like landscape position are important factors to consider, yet the degree to which landscape position and soil type affect soil spatial heterogeneity is still poorly understood (Gallardo 2003; Zhang et al. 2011; De la Peña-Lastra 2021). Determining the underlying mechanisms driving nutrient distribution therefore is necessary to inform effective management frameworks.

High nutrient concentration in seabird colonies has been widely reported. However, the mechanisms for nutrient cycling as it relates to soil type and landscape factors have not been fully explored (De la Peña-Lastra et al. 2021). Many works describe seabird colony nutrients on shallow soils or rocky substrates, but few have reported values of nutrients in deeper soils and dunes (Grant et al. 2022). This study examined the spatial patterns of soil chemical concentrations in two well-drained dune landscapes colonised by Wedge-tailed Shearwaters.

The general objectives of this study were to: (i) Quantify soil nutrients both down the soil profile and spatially relating to landscape position to better understand the cycling of nutrients as it relates to the landscape, and (ii) use stable isotope signatures $\delta^{15}N$ and $\delta^{13}C$ to determine the extent of seabird derived nutrient compared with areas not intensely affected by seabirds. We hypothesised that colonial seabirds would have significant spatial impact on soil nutrient concentrations due to landscape redistributional processes. Applying ecosystem-based management by considering components of physical and topographical features (soil type, hydrology, slope etc.) will better inform the ecological functions of seabird landscape patterns (Van Dyke and Lamb 2020).

3.3 Methods

3.3.1 Site description

Broughton Island (138 ha) is the main and largest island of the Broughton Island Group of four surrounding islands (each < 40 ha) and is located approximately 16 kilometres northeast of Port Stephens, New South Wales (Figure 3-1). It is part of the Myall Lakes National Park and managed by the New South Wales National Parks and Wildlife Service (NPWS). The island has experienced a range of disturbance and occupation from aboriginal and post-European peoples, including fire regimes and introduction of invasive plants and animals, but has remained largely undisturbed compared to its mainland equivalent (Dodkin 1981). Today the island is recognized as a seabird sanctuary and recreational fishing area, and occupied by fewer than 10 residents and the NPWS in a cluster of huts. Broughton Island hosts thousands of migratory seabirds from the Pacific and Indian Oceans who use the island for breeding from August to May (Marchant & Higgins 2006; Carlile et al. 2012).

This study examined two well-drained aeolian dune systems colonised by breeding Wedge-tailed shearwaters (*Ardenna pacifica*). The inland sampling site was located on one of two major transgressive high dunes formed during the mid to late Holocene, which are characterised by rapidly drained aeolian sands reaching 17 m AHD in height (Tulau & Wilson 2018) (Figure 3-1). This dune covers 4.8 ha and is a major source of ground groundwater recharge, which accumulates at the base of the dune forming distinct soil and vegetation change defined by partially inundated peats and common reed *Phragmites australis* and fern *Calochlaena dubia* (Sommerville et al. 2018; Tulau & Wilson 2018). The second sampling location was on a coastal dune system consisting of a backdune with wedge-tailed shearwater colonies, a swale drainage region defined by ferns *Histiopteris incisa*, and a foredune with recently deposited sands, and these habitats have very little organic matter or profile development (Tulau & Wilson 2018).

[redacted]

Figure 3-1 Map of Broughton Island. Sampling sites are outlined in red on a central dune sampled in 2018 (western rectangle) and coastal dune sampled in 2019 (northern-central rectangle).

3.3.2 Field sampling design

Samples for the study were taken in two trips: one in October 2018 and one in September 2019. The first samples were taken in 2018 on the coastal dune (Figure 3-1). The second field sampling was conducted in September 2019 on the inland dune (Figure 3-1). Sampling dates were chosen when breeding seabirds are absent from the island in an effort to avoid damaging fragile burrows and minimising contact with seabirds, eggs or chicks as they nest in high densities. On the coastal dune, samples were taken from 5 transects which extended from areas categorised by areas labelled 'colony', 'histiopteris', 'swale' (denoted by 'swale_fd' for clarity in plots), and 'foredune' (Figure 3-2). The transect extended approximately 50 m where one sample was taken from each area per transect (4 areas per transect). Seabird burrows were principally concentrated at the top of the dune (colony), but were also present in smaller numbers in each area except for the foredune. The *Histiopteris* area was a very wet outflow area. On the inland dune samples were taken from 3 transects which extended from areas categorised by areas labelled 'top dune', 'mid dune', 'base dune' and 'swale' (Figure 3-2). The swale in this dune system was an inflow area which regularly is saturated with rainfall. Seabird burrows were again principally concentrated at the top of the dune, but were present on the mid dune and bottom of dune. There were no burrows in the swale area. For both sampling sites, on each transect, a 1 m^2 quadrat was randomly placed within each sampling area, where the distance along transect, elevation, and geographic coordinates were recorded with a handheld GPS. Soils were extracted using a stainless-steel corer at depth intervals of 0-5 cm, 5-10 cm, 10-20 cm, 20-30 cm, and 30-40 cm in the coastal dune and at depth intervals of 0-10 cm, 10-20 cm, 20-30 cm and 30-40 cm in the inland dune. Three soil cores within each quadrat were extracted and each depth class was thoroughly combined into one sampling bag.

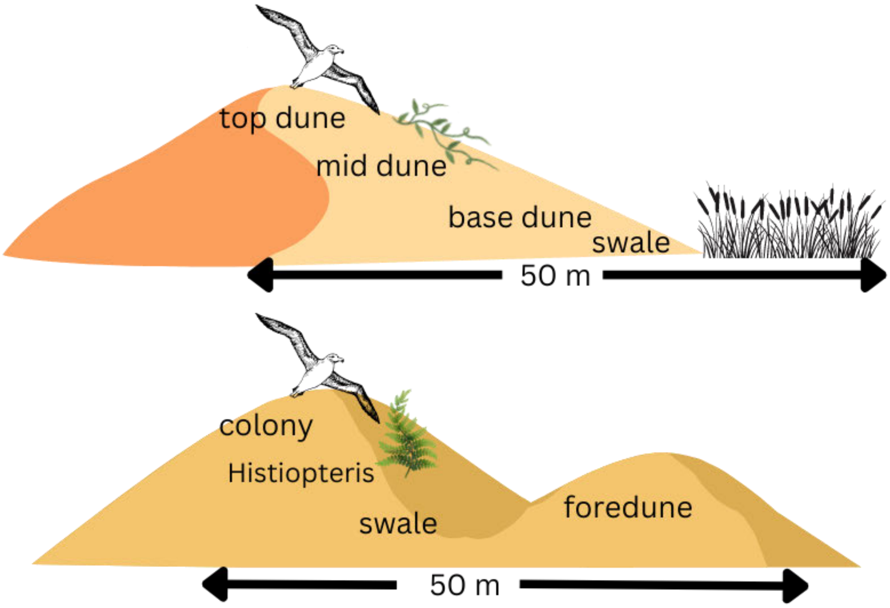

Figure 3-2 Graphical depiction of the landscape structure and sampling zones of the inland dune (top) and coastal dune (bottom).

3.3.3 Analytical processing of samples

Prior to analysis, soils were dried at 40 °C and passed through a <2 mm sieve. All instrumentation was used at the University of New England, Environmental Analysis Research Laboratory (UNE EARL). Soil pH and electric conductivity (EC) were tested using glass electrodes in a prepared 1:5 soil:water suspension. Nitrate (NO_3^-) were analysed by extraction using a 2 M potassium chloride (KCL) reagent and analysed with Skalar San^{++} continuous flow analyser (Skalar Analytical B.V., The Netherlands). TOC and TN concentrations were determined using Truspec CNS, LECO analyser (Truspec Corp, Michigan, USA), where the presence of carbonates were tested in each sample using hydrochloric acid (HCL); carbonates were not present in any samples.

Extractable phosphorus (ext. P) was determined following Colwell (1965), using a 0.5 M sodium bicarbonate ($NaHCO_3$) (pH= 8.5) extraction of each sample. Samples were shaken for 16 hours, filtered through Whatman No. 42 papers, and analysed immediately using Malachite Green Phosphorus determination method. This was done by adding and 750 uL of 1M H_2SO_4 solution (dispensed three times at 5-minute intervals of 250 uL) and malachite green/ PVA colour reagent. After 1.5 hours, absorbance was measured on a 630 nm spectrophotometer.

Soil isotope ratio samples of N and C ($\delta^{15}N$, $\delta^{13}C$) were prepared by grinding each sample through ball-mill grinder, achieving particle size < 200 μm and weighed into a 6 mm × 4 mm silver foil cups. Samples were analysed using a Sercon 20−22 (Cheshire, UK) continuous flow isotope ratio mass spectrometer (IRMS) by converting N and C into CO_2 and N_2 gas and comparing against a known standard. Results are presented as deviations from standards, expressed in the delta notation (δ) in units of parts per mille (‰):

$$\delta X= [(R_{sample}/R_{standard})-1] \times 1{,}000$$

Where X is ^{13}C or ^{15}N, and R is the molar ratio of $^{13}C/^{12}C$ or $^{15}N/^{14}N$. Carbon samples were compared relative to a known Vienna Pee Dee Belemnite standard, and nitrogen samples were compared against the isotope ratio of atmospheric N_2. Instrument precision was 0.1‰ for carbon and 0.3‰ for nitrogen.

3.3.4 Data analysis

To evaluate the differences among various soil parameters compared by each landscape position and depth, robust linear mixed models were fitted. All variables were tested for the normal distribution and homoscedasticity by visually inspecting Q-Q plots and residuals vs. fitted plots. Data were highly skewed and could not be transformed to fit the normal distribution, so robust linear mixed models were chosen to account for skewness using the *robustlmm* package (Koller 2016) in Rstudio (R Studio Team, 2022). Fixed effects in the models were the soil property, landscape area, upper depth and an interaction term of area and upper depth. The random effect set for the models was transect. The output from robust mixed models provides coefficient estimates, standard errors, and t-values. To obtain approximate p-values, ordinary mixed models were fitted using the *lme4* package (Bates et al. 2022) to extract Satterthwaite-approximated degrees of freedom for each estimated coefficient in the model. These Satterthwaite degrees of freedom were then combined with the robust mixed model t-values to obtain approximate p-values.

3.4 Results

'Area' and 'depth' were both significant factors influencing TOC, TN, and ext. P in both dune systems. All values are reported as the mean ± 1 standard error. TOC concentration was significantly higher in the swale area of both dunes (inland dune swale = 5.49 ± 0.78 %; $p< 0.001$, coastal dune swale 2.40 ± 0.31 %; $p<0.001$) and was significantly lower in the coastal foredune (0.38 ± 0.04 %; $p < 0.001$) (Figure 3-3). For TOC, there was a significant interaction between depth and area in both the inland and coastal dunes ($p< 0.001$, $p<0.001$). This was explained by the markedly steeper decrease in TOC down the profile in the swale soils in both dune systems (Figure 3-4). TOC typically decreased with increasing soil depth in both dune systems, but in top, mid, and base dune areas on the inland dune, TOC increased slightly at the 10-20 cm depth (Figure 3-4).

Soil TN on the inland dune had the highest concentration in the swale (0.36 ± 0.05 %) compared to significantly lower concentrations in the top dune (0.06± 0.01 %; $p< 0.001$) (Figure 3-3). The coastal dune had a significantly higher concentration of TN in the *Histiopteris* areas (0.20 ± 0.08 %; $p< 0.001$), and significantly lower concentrations in the foredune (Figure 3-4). In both inland and coastal dunes, TN concentration slightly decreased with increasing depth (Figure 3-4). There were again significant interactions between depth and area in both dune systems, explained by a more rapid rate of decrease in TN concentration in the inland swale ($p< 0.001$), *Histiopteris* ($p= 0.01$) and foredune ($p< 0.001$) (Figure 3-4).

On the inland dune, soil ext. P concentration was significantly higher in the swale (682.29 ± 127.18 mg/kg; $p< 0.001$) compared to other landscape positions (Figure 3-3). Subsurface accumulation occurred incrementally at each depth interval at the top of dune where ext. P concentration increased from 17.80 ± 5.02 mg/kg at 0-10 cm to 29.43 ± 12.12 mg/kg at 30-40 cm depth (Figure 3-4). Subsurface accumulation for the mid dune and base dune occurred in the 20-30 cm depth interval, then decreased with depth (Figure 3-4). The interaction between depth and area was significant in the inland dune ($p< 0.001$) which was explained by exceptionally high concentrations and subsurface accumulation in the 30-40 cm depth interval. On the coastal dune, ext. P was significantly higher in the *Histiopteris* area (31.78 ± 7.06 mg/kg; $p= 0.01$) and the swale area (30.01 ± 4.19 mg/kg; $p= 0.01$).

There was no effect of area or depth on NO_3^- concentration on the inland dune (Figure 3-3). Although subsurface concentrations of NO_3^- were found to be higher at 20-30 cm depth in the base dune (3.43 ± 0.98 mg/kg) and in the 10-20 cm depth (15.54 ±12.57) in swale of the inland dune, these values had large standard errors (Figure 3-4). On the coastal dune, the interaction of area and depth was significant for NO_3^- explained by the colony ($p< 0.001$) and *Histiopteris* ($p< 0.001$) area depth profile which showed higher rates of decrease compared to other landscape areas. (Figure 3-4).

Soil pH values on the inland dune remained relatively constant and showed no significant changes relating to landscape area, with mean values ranging from 4.78 ± 0.18 in the swale area to 4.97 ± 0.15 in the mid dune (Figure 3-3). The inland dune slightly decreased in pH with depth (Figure 3-4) but this change was not statistically significant. The coastal dune experienced more variable and neutral pH values on the landscape areas, particularly in the swale (6.54 ± 0.15) and foredune (7.79 ± 0.11) areas and were significantly higher in pH ($p < 0.001$ for swale and foredune). The pH of soils on the coastal dune became slightly higher with depth, and there was a significant interaction between area and depth, explained by *Histiopteris* which had a more consistent pattern of pH increase compared to other areas ($p = 0.04$) (Figure 3-4).

On the inland dune, the top, mid, and base dune ranged in EC from 40.37 ± 2.42 µS/cm to 48.05 ± 2.57 µS/cm in the base dune, but was significantly higher in the swale to 153.82 ± 19.88 µS/cm ($p > 0.001$) (Figure 3-3). The interaction between depth and area was significant ($p = 0.01$), explained by the decrease in EC with depth while other areas on the inland dune typically remained constant down the profile (Figure 3-4). The coastal dune had higher EC than the inland dune (Figure 3-4). In the coastal dune, the highest EC was in the *Histiopteris* area (246.73 ± 42.21 µS/cm) and the lowest was in the colony area (157.78 ± 10.28 µS/cm) (Figure 3-3).

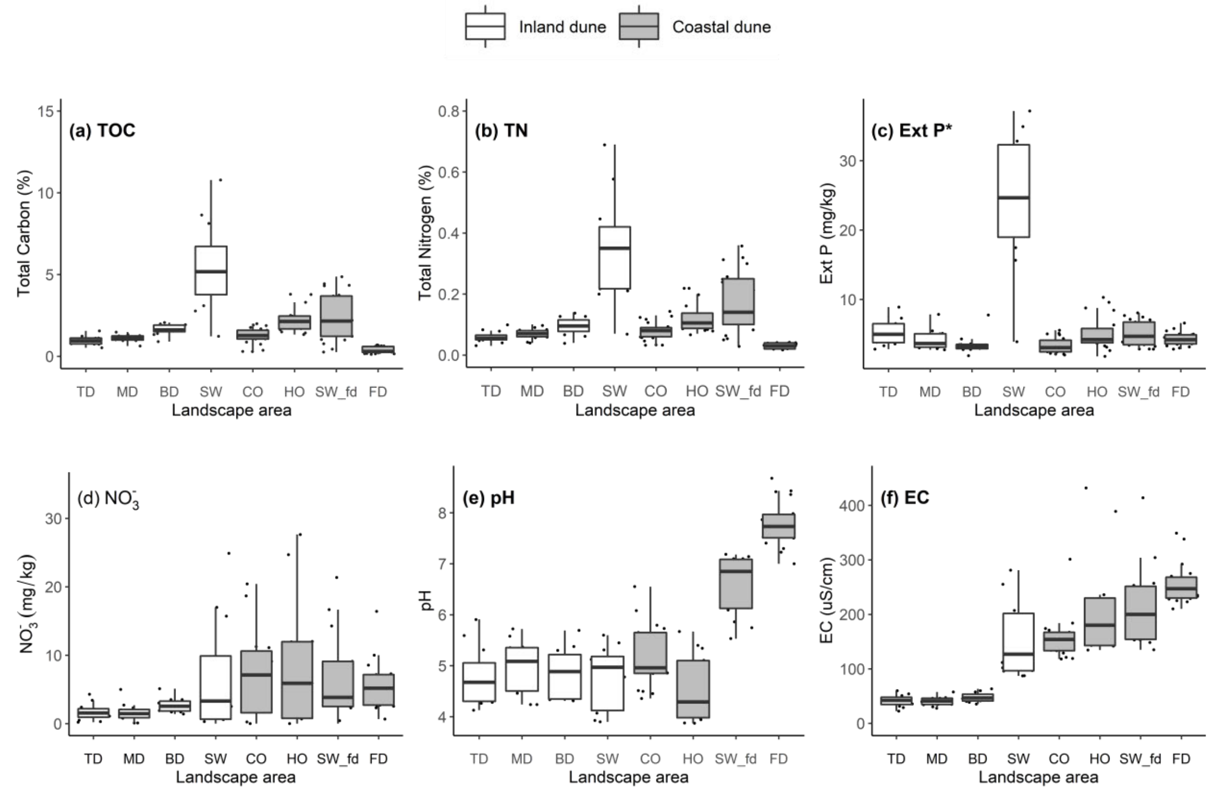

Figure 3-3 Effect of landscape position on soil properties in a Wedge-tailed shearwater colony (a-g). Boxplots in white are areas from the inland dune: TD= top dune, MD= mid dune, BD= base dune, SW= swale. Boxplots in grey are areas from the coastal dune: CO= colony, HO= histiopteris, SW_fd= swale_fd, FD= foredune. Values (excluding ext. P) represent untransformed averages from all depths (0- 40 cm). *Square root of all Ext. P values is displayed due to skewness of the dataset.

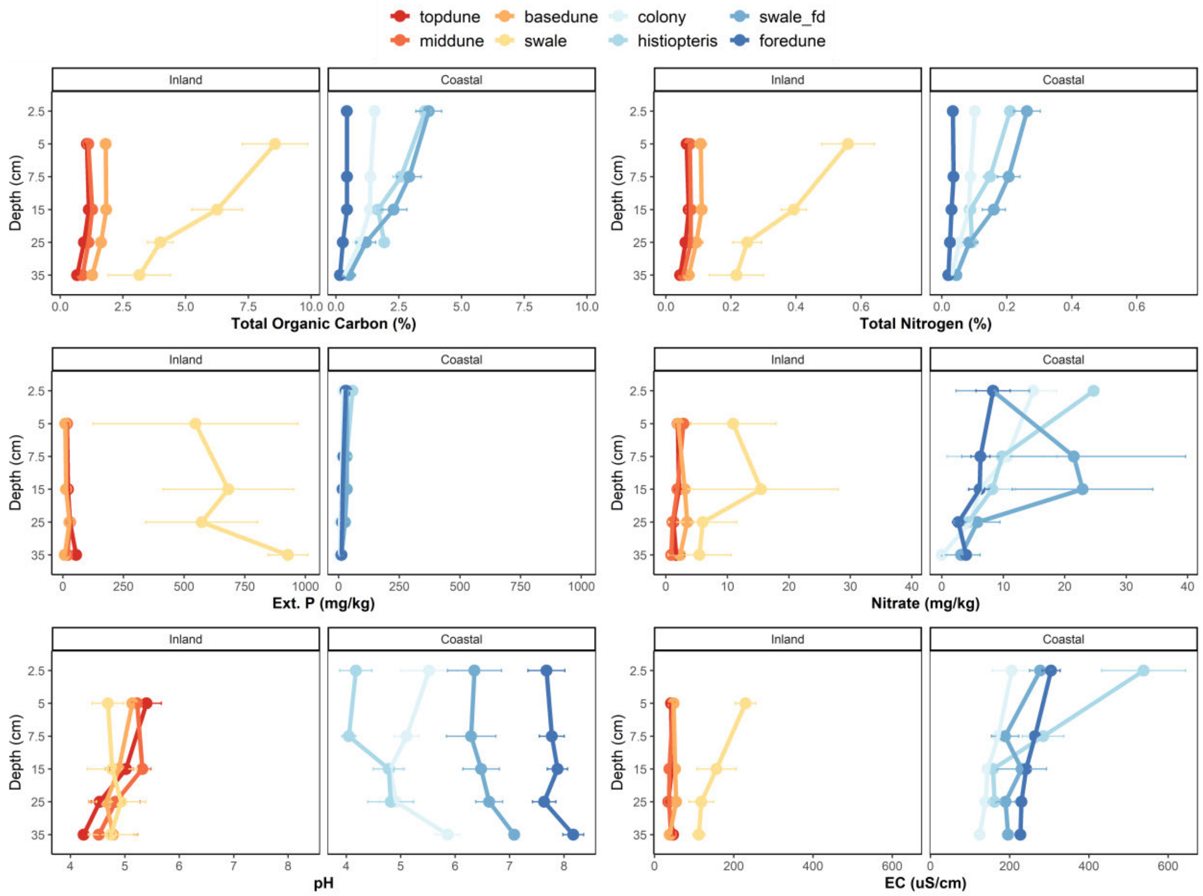

Figure 3-4 Comparison of soil chemical concentrations (mean ± 1 standard error) of each sample depth for each dune landscape position.

Stable isotope signatures of δ^{13}C on the inland dune ranged from minimum (± 1 standard error) of -23 ± 1.30 ‰ to maximum -21.5 ± 0.32 ‰ in all landscape positions and there were no significant differences between landscape areas ($p < 0.05$) (Figure 3-5). In the coastal dune, δ^{13}C values were more variable, and the *Histiopteris* area had significantly different and more negative values (-24.48 ± 0.57‰; $p = 0.003$). Foredune areas were significantly different and had less negative values (-8.39 ± 1.57‰; $p<0.001$). Depth was not significant in the models for either the coastal dune or inland dune nor were interaction terms of depth and area (Table 3-2).

The inland dune was significantly more enriched in ^{15}N and in the mid dune ($p=0.01$). The swale had significantly lower δ^{15}N values compared with all other areas on the inland dune (0.32 ± 1.44‰) (Figure 3-5). There was a significant interaction between depth and area, (p=0.001), explained by depletion in $\delta^{15}N$ from 10-20 cm depth in the swale (Figure 3-6). The coastal dune had values range between 11.07 ± 0.36‰ in the colony and 10.06 ± 0.37‰ in the *Histiopteris* area, but these were lower in the foredune area (4.87 ± 0.68‰) (Figure 3-5). There was a significant interaction between depth and $\delta^{15}N$ in the foredune (p= 0.002) where $\delta^{15}N$ became depleted from the 10-20 cm depth interval (Figure 3-6).

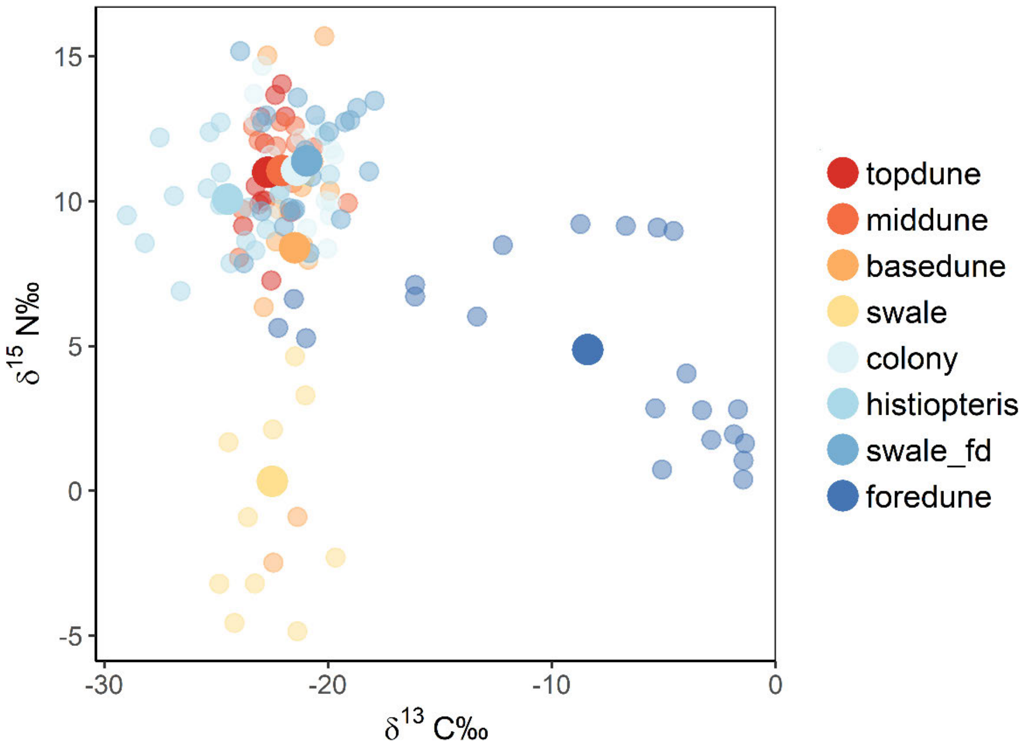

Figure 3-5 Isotope ratio values of $\delta^{13}C$ and $\delta^{15}N$ for each landscape area for inland dune (orange shades) and coastal dune (blue shades). Group centroids are represented by full coloured circles with all values in faded circles.

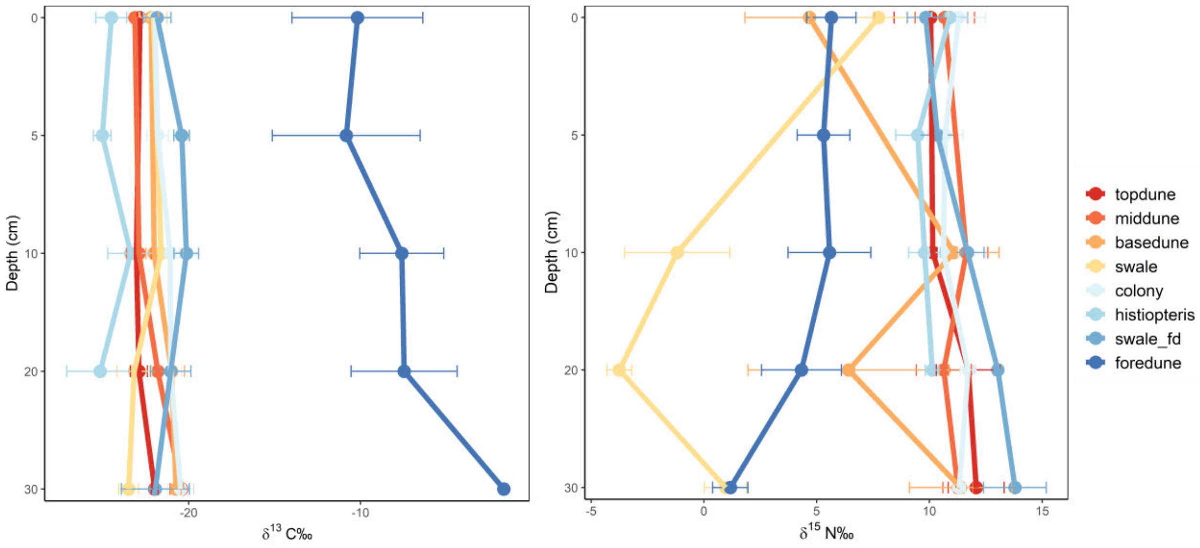

Figure 3-6 Comparison of isotope ratio values δ^{13}C and δ^{15}N (mean ± standard error) for each landscape area.

3.5 Discussion

This study described the movement of seabird derived biomaterials both down the surface of landscape and into subsurface depths on two dune systems with wedge-tailed shearwater colonies. The analyses considered the role of soil and terrain characteristics between landscape positions in driving spatial heterogeneity of soil chemical concentrations, and found significantly higher concentrations of C, N and P, pH, and EC in lower sloping areas compared to areas on the top of the dunes where seabird colonies are the densest. For this reason, we accept the hypothesis that lower dune regions would have higher concentrations of N, P and C despite seabird colonies being present and most dense in number at the higher dune regions. Many studies have demonstrated the enrichment of soil nutrients in seabird colonies by comparing seabird and non-seabird islands, or colony areas compared to areas with no colonies (Mulder et al. 2011; Grant et al. 2022). Contrary to comparison of point-source sites (i.e. directly within seabird colonies vs. outside colonies), this study found areas of accumulation downslope from colony areas, revealing novel insights into nutrient flow and distributions on seabird islands with sandy soils.

Soils in both dune systems are characterised by rapidly drained sands from which nutrients are leached and may accumulate with age, sloping into swale regions with different vegetation and may be partially saturated with rain and groundwater accumulation (Brown and McLachlan 2010; Tulau & Wilson 2018). With an average 1500 mm annual rainfall on Broughton Island, these dune systems have high likelihood of N and P moving through leaching and surface runoff. Nutrient supply, water regime, redox potential, accumulation and mineralization are external factors which also influence soil chemistry, and in this case, landscape and hydrological patterns influence the distribution and form of seabird-derived soil nutrients (Husson 2012). The significant interactions between depth and area occurring in swale regions for C, N, P indicated clear differences in the patterns of nutrient concentration down the profile compared to areas on the dune with evident movement with relation to position on the landscape.

TOC was higher in lower slope areas, though the dune soils did not reflect common marine or guano signatures of δ^{13}C (e.g. less negative, suggested by Mizutani & Wada (1988), thus high concentrations of TOC in the swale areas are more likely the result of the excess in plant available nutrients and water, stimulating plant productivity and biomass, which encourages organic matter accumulation and C sequestration (Arrouays et al. 1988; Leblans et al. 2014). The significant interaction between area and depth was a result of overall greater concentrations of TOC throughout the depth profile, indicating deep C storage in swales > 10 cm depth. Examining N and C stocks in plant biomass in these areas may have provided further insights into nutrient dynamics driving TOC accumulation. In both dune systems δ^{13}C fell in similar ranges except for the foredune, suggesting each landscape area has similar carbon dynamics, whereas foredunes have very little to no soil organic carbon or stable vegetation (Mizutani & Wada 1988; Tulau & Wilson 2018). Thus, it is more likely the greater concentration of C in the swales are due to edaphic and topographic conditions (i.e. C accumulation resulting from water and nutrient accumulation) rather than discernible C input from seabirds, and $\delta^{13}C$ in this case is not a reliable indicator of C source.

Nitrogen had similar patterns in lower slope areas of both dunes with concentration in depth and area. Transformation of guano-N behaves differently in mineral soils compared to bare rock, for instance during nitrification, and in this system, nitrogen leached on surface areas accumulating in swales, and nitrates were seen increased in some areas > 5cm depth (Blackall et al. 2008; Riddick 2012). Subsurface accumulation of nitrates occurred in the swale, but while the interaction of depth and area was significant, values had very high standard errors, and a higher number of samples may have increased the confidence in confirming subsurface accumulation. Stable isotope analysis was successful in confirming the N in the dunes were indeed sourced from seabirds because of their isotopic signature reflecting marine, therefore seabird source (Mulder et al. 2011; Craine 2015). Although TN was high in the swale region on the inland dune, since the isotopic values were close to 0‰, the fractionated N from guano may be explained by soil microbial activity, kinetic fractionation (for instance, urea production and the volatilisation of NH_4^+) or plant uptake between the dune and swale exhibiting more negative $\delta^{15}N$ values (Nadelhoffer & Fry 1994). Ammonia volatilisation is a pathway in which preferential heavier isotope ^{15}N is left behind in soil as lighter ^{14}N volatises to the atmosphere, thus leading to higher $\delta^{15}N$ values, further suggesting transformation in the dune areas (Mizutani et al. 1985).

Ext. P concentration was disproportionately higher in the swale than the dune, and increased in concentration with depth down the profile in both the dune and swale. Guano-P is typically mostly in the form of phosphates and insoluble P, and the bioactive nature of guano is highly labile compared to terrestrially derived P only available from geologic and soil weathering (Bitousek & Howarth 1991; Mulder et al. 2011). Although many terrestrial systems are P limited, the concentration of P in the inland dune and swale soils was in excess and increased below the root zone. P in soil is a strong indicator of guano-P as it is stable, lacks a gaseous phase, and may remain in soil for a number of years even in the absence of active seabird input (Anderson & Polis 1999; Hawke et al. 1999). Low retention of P in both organic and mineral soils from external inputs has been found (e.g. Hawke 2005; Blackall et al. 2007), however, in these dune systems, the ext. P found is largely labile and in excess from seabird input and is not limiting; rather it is leached down the soil profile, immobilised, and carried to the swale areas via hydrology. Results from Broughton Island suggest that P was indeed being translocated in the sub-surface zone with higher concentrations typically in the >2cm layers. Sub-surface hydrology would therefore appear to be a critical mechanism determining nutrient distribution on the island.

Soils were more acidic in areas directly affected by seabirds, and this effect is probably due to guano inputs through nitrification of ammonium (Mulder & Keall 2001). EC was significantly higher in the swales compared with the top of the dune, and the higher overall pH in the coastal dune can be explained by salt water influence since coastal landscapes and particularly the coastal dune will be more exposed to salt spray (Terra et al. 2004). The heterogeneity of soil chemical concentrations on the dune is likely a function of soil type and landscape, and while not measured, are likely to have an influence on associated vegetation patterns.

This research revealed novel insights to distribution of surface and subsurface redistribution from seabird nutrient subsidies on deep, well drained aeolian dune soils. The results from this study will contribute to filling the knowledge gap of understanding the impact of seabird nutrient subsidies according to soil and landscape features. The nutrient flows provided by seabirds are globally important, because they support far-reaching, cross-ecosystem areas on the islands they inhabit (Benkwitt et al. 2022). Effective management of seabird islands requires the knowledge of landscape, soil and nutrient dynamics as underlying drivers of plant assemblage make informed decisions for land use actions and conservation (Klingebiel 1961). Further research into diverse landscapes on which seabirds' nest is required in order to better understand the effects seabirds have on nutrient flow in island ecosystems.

3.6 Tables

Table 3-1 Summary statistics for each landscape area, number of samples (N), mean ± standard error from all depths.

Soil property	Area	N	mean	se
TC (%)	topdune	12	0.96	0.08
	middune	12	1.10	0.06
	basedune	12	1.64	0.10
	swale	12	5.49	0.78
	colony	21	1.23	0.11
	histiopteris	16	2.25	0.19
	swale_fd	21	2.40	0.31
	foredune	21	0.38	0.04
TN (%)	topdune	12	0.06	0.01
	middune	12	0.07	0.01
	basedune	12	0.10	0.01
	swale	12	0.36	0.05
	colony	21	0.08	0.01
	histiopteris	17	0.20	0.08
	swale_fd	21	0.17	0.02
	foredune	21	0.03	0.00
P (mg/kg)	topdune	12	30.67	6.07
	middune	12	19.80	4.39
	basedune	12	14.56	4.27
	swale	12	682.29	127.18
	colony	21	12.38	1.80
	histiopteris	19	31.78	7.06
	swale_fd	21	30.01	4.19
	foredune	21	19.34	1.95
Nitrate (mg/kg)	topdune	12	1.73	0.36
	middune	12	1.66	0.38
	basedune	12	2.69	0.30
	swale	12	9.46	3.67
	colony	14	7.51	1.74
	histiopteris	11	8.70	2.97
	swale_fd	15	13.47	4.81
	foredune	17	5.63	0.91

pH	topdune	12	4.80	0.16
	middune	12	4.97	0.15
	basedune	12	4.87	0.14
	swale	12	4.78	0.18
	colony	17	5.15	0.15
	histiopteris	13	4.53	0.18
	swale_fd	15	6.54	0.15
	foredune	18	7.79	0.11
EC (µS/cm)	topdune	12	41.49	3.10
	middune	12	40.37	2.42
	basedune	12	48.05	2.57
	swale	12	153.82	19.88
	colony	17	157.78	10.26
	histiopteris	13	246.73	42.21
	swale_fd	15	212.67	19.16
	foredune	18	256.17	8.96
$\delta^{13}C$	topdune	12	-22.69	0.17
	middune	12	-22.06	0.40
	basedune	12	-21.49	0.29
	swale	12	-22.58	0.48
	colony	21	-21.40	0.28
	histiopteris	19	-24.48	0.57
	swale_fd	21	-20.95	0.39
	foredune	21	-8.39	1.57
$\delta^{14}N$	topdune	12	11.00	0.60
	middune	12	11.05	0.47
	basedune	12	8.39	1.57
	swale	11	0.32	1.44
	colony	21	11.07	0.36
	histiopteris	19	10.06	0.37
	swale_fd	21	11.38	0.44
	foredune	21	4.87	0.68

Table 3-2 Results from robust linear mixed effect models on the effect of landscape area, depth, and the interaction of area and depth on soil chemical concentrations. Reference groups within the intercept term are base dune and upper depth. Interactions were not significant in $\delta^{13}C$ models. Bold p-values indicate statistical significance ($p < 0.05$).

		Estimate	**t-value**	**p-value**		**Estimate**	**t-value**	**p-value**
TOC (%)	intercept	1.92	8.04	**0.00**	upper depth	-0.02	-1.48	0.14
	top dune	-0.74	-2.29	**0.02**	top dune:depth	0.00	0.25	0.80
	mid dune	-0.68	-2.09	**0.04**	mid dune:depth	0.01	0.56	0.58
	swale	6.25	19.27	**0.00**	swale:depth	-0.18	-10.24	**0.00**
	colony	-0.32	-1.16	0.25	colony:depth	-0.02	-1.10	0.27
	histiopteris	0.83	2.65	**0.01**	histiopteris:depth	-0.04	-1.74	0.08

	swale fd	1.60	5.72	**0.00**	swale fd:depth	-0.09	-5.71	**0.00**
	foredune	-1.45	-5.21	**0.00**	foredune:depth	0.01	0.52	0.60
TN (%)	intercept	0.11	6.41	**0.00**	upper depth	0.00	-1.43	0.16
	top dune	-0.04	-1.89	0.06	top dune:depth	0.00	0.45	0.65
	mid dune	-0.04	-1.49	0.14	mid dune:depth	0.00	0.53	0.60
	swale	0.42	18.01	**0.00**	swale:depth	-0.01	-8.86	**0.00**
	colony	-0.01	-0.40	0.69	colony:depth	0.00	-1.01	0.31
	histiopteris	0.07	3.08	**0.00**	histiopteris:depth	0.00	-2.81	**0.01**
	swale fd	0.13	6.66	**0.00**	swale fd:depth	0.00	0.51	0.61
	foredune	-0.07	-3.72	**0.00**	foredune:depth	-0.01	-5.40	**0.00**
Ext P (mg/kg)	intercept	11.61	1.46	0.15	upper depth	0.00	0.01	0.99
	top dune	1.62	0.16	0.87	top dune:depth	0.97	1.80	0.07
	mid dune	3.39	0.34	0.74	mid dune:depth	0.15	0.28	0.78
	swale	223.09	22.23	**0.00**	swale:depth	21.86	40.75	**0.00**
	colony	5.56	0.64	0.52	colony:depth	-0.42	-0.83	0.41
	histiopteris	22.34	2.53	**0.01**	histiopteris:depth	-1.05	-1.73	0.09
	swale fd	23.63	2.73	**0.01**	swale fd:depth	-0.59	-1.14	0.26
	foredune	13.13	1.52	0.13	foredune:depth	-0.48	-0.94	0.35
NO_3^- (mg/kg)	intercept	2.33	1.25	0.22	upper depth	0.01	0.14	0.89
	top dune	-0.51	-0.20	0.84	top dune:depth	-0.03	-0.23	0.82
	mid dune	0.18	0.07	0.94	mid dune:depth	-0.08	-0.60	0.55
	swale	4.00	1.59	0.12	swale:depth	-0.14	-1.02	0.31
	colony	11.07	4.38	**0.00**	colony:depth	-0.46	-3.08	**0.00**
	histiopteris	16.42	5.89	**0.00**	histiopteris:depth	-0.79	-4.33	**0.00**
	swale fd	7.75	3.11	**0.00**	swale fd:depth	-0.24	-1.74	0.09
	foredune	5.01	2.20	**0.03**	foredune:depth	-0.17	-1.30	0.20
pH	intercept	4.90	17.06	**0.00**	upper depth	-0.02	-1.55	0.12
	top dune	0.28	0.87	0.39	top dune:depth	-0.02	-1.14	0.26
	mid dune	0.26	0.79	0.43	mid dune:depth	-0.01	-0.41	0.68
	swale	-0.36	-1.09	0.28	swale:depth	0.02	1.42	0.16
	colony	0.12	0.37	0.71	colony:depth	0.03	1.44	0.15
	histiopteris	-0.56	-1.61	0.11	histiopteris:depth	0.05	2.10	**0.04**
	swale fd	1.57	4.70	**0.00**	swale fd:depth	0.03	1.61	0.11
	foredune	2.86	9.53	**0.00**	foredune:depth	0.02	1.43	0.16
EC (µS/cm)	intercept	53.03	3.23	**0.00**	upper depth	-0.27	-0.32	0.75
	top dune	-11.69	-0.53	0.60	top dune:depth	0.34	0.29	0.77
	mid dune	-9.14	-0.41	0.68	mid dune:depth	0.10	0.08	0.94
	swale	155.48	6.99	**0.00**	swale:depth	-3.41	-2.87	**0.01**
	colony	122.46	5.96	**0.00**	colony:depth	-1.47	-1.24	0.22
	histiopteris	249.37	10.88	**0.00**	histiopteris:depth	-7.92	-5.23	**0.00**
	swale fd	166.76	7.60	**0.00**	swale fd:depth	-0.99	-0.80	0.43
	foredune	228.53	11.44	**0.00**	foredune:depth	-1.99	-1.72	0.09
δ^{13}C	intercept	-22.41	-30.54	0.00	upper depth	0.03	1.99	0.06
	top dune	-1.21	-1.58	0.12	top dune:depth			

	mid dune	-0.57	-0.75	0.46	mid dune:depth			
	swale	-1.15	-1.50	0.14	swale:depth			
	colony	0.66	0.94	0.35	colony:depth			
	histiopteris	-2.12	-2.96	**0.00**	histiopteris:depth			
	swale_fd	1.24	1.77	0.08	swale_fd:depth			
	foredune	16.28	23.37	**0.00**	foredune:depth			
δ^{15}N	intercept	7.40	6.25	**0.00**	upper depth	0.15	2.53	**0.01**
	top dune	2.69	1.70	0.09	top dune:depth	-0.07	-0.86	0.39
	mid dune	3.97	2.50	**0.01**	mid dune:depth	-0.15	-1.77	0.08
	swale	-4.43	-2.60	**0.01**	swale:depth	-0.30	-3.38	**0.00**
	colony	3.35	2.46	**0.02**	colony:depth	-0.12	-1.42	0.16
	histiopteris	2.85	2.05	**0.04**	histiopteris:depth	-0.17	-1.79	0.08
	swale_fd	2.42	1.77	0.08	swale_fd:depth	0.01	0.11	0.91
	foredune	-1.44	-1.06	0.29	foredune:depth	-0.26	-3.25	**0.00**

Chapter 4: Burrow nesting seabirds influence lower soil nutrient concentrations, stable isotope signatures, and invasive cactus growth on sandy soils

4.1 Abstract

The effects of seabird colonies on soil chemistry and plant communities were investigated by undertaking soil and plant surveys of wedge-tailed shearwater (*Ardenna pacifica*) colonies compared to adjacent landscapes with no seabird nests, but similar environmental features (slope, elevation, soil texture). Soils were tested for soil surface temperature (SST), total organic carbon (TOC), total nitrogen (TN), extractable phosphorus (ext. P), nitrate (NO_3^-), ammonium (NH_4^+), pH, and electrical conductivity (EC). Stable isotope ratios of $\delta^{15}N$ and $\delta^{13}C$ in soil were analysed to elucidate nitrogen and carbon sources. Plant species identification, species richness and vegetation cover were also surveyed. The results showed seabird colony soils had significantly lower TOC, TN, ext. P and pH compared to no-colony areas. Colony soils had higher variability of soil surface temperature, a greater percentage of bare ground and were characterised by the presence of invasive prickly pear (*Opuntia stricta).* Isotopic signatures of $\delta^{15}N$ and $\delta^{13}C$ in soils were significantly different between colony and no-colony areas, indicating nitrogenous marine enrichment in colony areas from ^{15}N (13.27 ± 0.20 ‰ colony, 11.57 ± 0.22 ‰ no-colony) and distinctive values of $1\delta^3C$ (-23.12 ± 0.16 ‰ colony, -19.37 ± 0.14 ‰ no-colony). Our soil chemical concentration results contrast with other studies finding more enriched soil nutrient status directly within colonies compared to surrounding areas. It is postulated that soils enriched with ^{15}N but lower in elemental concentration could be explained by burial and subsurface movement of marine-derived N via physical disturbance exerted on sandy dune soils, leaching, runoff, and/or ammonia volatilisation. The expansion of

seabird colony area into sedge dominated communities may shift characteristics to have greater abundance in shorter grasses and vines and potentially increase vulnerability to weed invasion. The results inform the recommendation for prioritising disturbed seabird colonies for control of weed species.

4.2 Introduction

Burrow nesting seabirds alter ecosystem properties on islands by subsidising soil nutrients via guano deposition and disturbing soil through subsurface nesting. Seabirds are considered to be biovectors of marine nutrients to terrestrial ecosystems through soil manuring with guano, which is rich in bioavailable nitrogen (N) and phosphorus (P) (Anderson & Polis 1999; Otero et al. 2018). Seabird colony areas are often observed to have higher concentrations of macronutrients (N, P, K) compared to landscapes with no seabird influence (Ellis 2005). Guano nutrient subsidies stimulate primary production, influence vegetation height, cover, and biodiversity in processes that are distinct from those in closed ecosystems (Anderson & Polis, 1999; Sánchez-Piñero & Polis 2000; Ellis et al. 2005). The bioavailable state of guano N and P influences all aspects of trophic systems (De la Peña-Lastra 2021; Gaiotto 2022), including soil biota (Fukami et al. 2006), terrestrial producers and consumers (Stapp & Polis, 2003), and surrounding marine environments (Kazama 2019; Finne et al. 2022). Seabirds are therefore integral components of nutrient cycling and trophic function on the islands they inhabit.

Burrow nesting seabirds are also considered to be ecosystem engineers because they excavate burrows to up to 2 metres depth with a nest at the base of the burrow. Much like other fossorial species, burrowing seabirds displace large amounts of soil through nesting activities, creating microhabitats where colonies are present (Butler 1995; Haussmenn 2017). Physical disturbance through burrow excavation modifies soil dynamics, including leaf litter inputs and carbon cycling (Bancroft et al. 2005a; McKenchie 2006). Furthermore, digging and trampling uproots existing vegetation, disrupts seed banks and seed dispersal, and suppresses germination success (Furness 1991; Smith et al. 2011; Orwin et al. 2016). Mechanical change to soils also influences plant systems and particularly plant community composition, diversity and richness (Bancroft et al. 2005b; Grant et al. 2022). Landscape alteration via erosion of excavated soils and patches of bare ground at active burrow sites can further enhance these effects (Butler 1995). Continuous seasonal excavation of burrows over many years can also alter soil physical properties, including water holding capacity and strength (Bancroft et al. 2005a), further influencing vegetation dynamics by modifying soil and plant nutrient status and other trophic interactions, altering carbon stocks and soil structure (Mulder et al. 2011; Loch et al. 2020).

The combination of high nutrient loads and soil engineering are understood to result in the distinct plant and soil characteristics observed within seabird colonies compared with those adjacent areas undisturbed by seabird activities (Bancroft et al. 2005b; Duda et al. 2020; Wait et al. 2005). Due to the life history and tolerance to thrive under intensely disturbed conditions from seabird activities, vegetation in these environments tends to be shorter lived, shorter in vertical structure, denser in number, and defined by annual plants and succulents (Grime 1973; White & Harrod 1997; Abbot et al. 2000; Bancroft et al. 2005b). Disturbed landscapes with high inputs of nitrogen and phosphorus create environments that are conducive to invasive weeds, particularly ruderal species (D'Antonio et al. 1999; Vidal et al. 2000; Hobbs 2000; Bartuszevige et al. 2006; Mulder et al. 2009). Seabird colonies may also have long-term impacts on plant community succession, where a reduction in tree and shrub taxa is often replaced by low lying species like ferns and grasses and may potentially benefit non-nitrogen fixing species (Boutin et al. 2011; Havik et al. 2014; Duda et al. 2020). The response of soil and vegetation to seabird colonisation depends on the characteristics of the receiving landscape and species behaviour (e.g. nesting ecology and density), biotic and abiotic results may vary

(Louw et al. 2019). Soil, climatic, and species-specific inputs can modulate the cycling process and spatial distribution of nutrients via guano (Anderson et al. 2008; De la Peña-Lastra 2020; Pascoe et al. 2022).

Stable isotope analysis in plants, animals and soils has been used to elucidate influences of seabirds on their environment, by determining the ratio of ^{14}N:^{15}N ($\delta^{15}N$) to identify nutrient source as a proxy for ecosystem function (Pascoe 2021; Gaiotto 2022) and ^{12}C:^{13}C ($\delta^{13}C$) for evidence of soil carbon cycles (Staddon 2004). Stable isotope analysis of C in seabird colonies has generated a wide variety of results, but some are used to trace marine sources of C in soil, whereas marine sources may be enriched (less negative) in $\delta^{13}C$ values (Mizutani & Wada 1988). Seabirds are at the highest trophic level on marine food webs and typically have enriched signatures of $\delta^{15}N$, which can be traced when guano, feathers, and carcasses are cycled through terrestrial systems (Goldsworthy et al. 2001; Hamer 2019). Deposition of guano and fractionation of N via ammonia volatilisation and microbial processes often result in higher nutrient concentrations and enriched, or more positive, isotopic signatures of $\delta^{15}N$ in soils associated with seabird colonies, and therefore are useful ecological studies for elucidating nutrient source from seabirds (Mizutani et al. 1985; Mizutani et al. 1988; Szpak et al. 2012; Otero et al. 2018; Pascoe 2021).

Broughton Island on the east coast of New South Wales (NSW), Australia has a history of disturbance from introduced plants and animals which have affected seabird population and native plant communities (Priddel et al. 2011; Carlile et al. 2012). Invasive rats and rabbits had resulted in suppressed seabird populations and altered vegetation communities through predation and grazing. An invasive mammal eradication program was done in 2009 in efforts to restore seabird breeding success and conserve native plant assemblages (Priddel et al. 2011).

Separate studies have observed the effects of seabirds on vegetation (e.g. Battisti & Fanelli 2021; Otero et al. 2021; De la Peña-Lastra et al. 2022), but the ecological relationships between the two factors, particularly invasive weed species, have not been fully explored. Furthermore, the role of soil type in explaining guano-driven nutrient fluxes has been understudied, yet is required to better understand seabird impacts on terrestrial systems (Grant et al. 2022). Many seabird soil nutrient studies have been located on high latitudes, rocky substrates for example on tundra (Zwolicki et al. 2013) and one in a dune system (Otero et al. 2015; De la Peña-Lastra et al. 2022). This study was located in a sub-tropical climate with well drained sandy soils and dense colonies of burrow-nesting wedge-tailed shearwaters: a unique combination of habitat and species to be observed. It was expected that this subtropical island with well-drained sandy soils would differ to other islands investigated elsewhere because of transportation of seabird-derived soil nutrients due to rainfall and movement through deeper, well-drained soils. Heavy nutrient loading and retention combined with physical disturbance from seabirds may increase the likelihood of seabird colony areas having particular vegetation, such as short-lived plants, invasive weeds, and annual plants (Bancroft et al. 2005b). The purpose of this study was to explore the effect of burrowing seabirds on sandy soil chemistry and plant communities in a recently predator-free (but weed present) island.

4.3 Methods

4.3.1 Site Description

Broughton Island is located 16 km NE of Port Stephens, NSW and is part of the Myall Lakes National Park estate. The climate on Broughton Island is classified as sub-tropical, with approximately 1,339 mm of annual rainfall (Data based on Nelson Bay, BOM, 2021). The island has both sedimentary and volcanic substrates but the most widespread soil types are associated with extensive, well drained sand sheets and sand dunes (Tulau & Wilson 2018). The most common vegetation type on the island consists of mosaics of low-lying shrubs, grasses, and sedge species (Sommerville et al. 2018). Prickly pear (*Opuntia stricta)* is the most common invasive weed and dominates in sand sheet landscapes particularly around seabird colonies (Sommerville et al. 2018; Hunter et al. 2020) (Figure 4-1). The island hosts dense migratory breeding seabirds which have expanded in breeding area since the removal of predatory invasive mammals in 2009 and the latest population estimate is 64,500 breeding pairs (Carlile et al. 2022).

Figure 4- 1 Periphery of colony. The bottom half of the photo shows transect area within the colony dense with ground level herbs, bare ground, and the invasive prickly pear (*Opuntia stricta)*. Immediate perimeter of the colony is shown in the top half of the photo with dense sedge and grasses. Photo taken by Mary Garrard.

4.3.2 Sampling design

Samples were collected December 2020 when Wedge-tailed shearwaters were present on the island laying and incubating eggs after arrival in late August aligned with typical behaviour for the annual breeding period. While we acknowledge the vulnerability of seabirds and eggs while in burrows, due to COVID-19 pandemic, travel to the island was only possible during this time in 2020. Stringent precautions were taken to avoid burrow collapse and/or interaction with birds or their nests. Three transects were extended from seabird colonies from three separate established colony locations extending to adjacent areas with similar elevation, slope and soil types (Figure 4-2; Table 4-1). Each transect was sampled at 5 m intervals where a 1 m^2 quadrat was randomly placed. Soils were extracted using a metal core at two depths: 0-10 cm and 10- 20 cm. Four cores were extracted within each quadrat and thoroughly combined to generate one representative sample for each depth increment. Soil surface temperature (SST) was measured using a probe placed into the surface layer of the soil and time of day was recorded during each measurement. GPS location along with elevation in mAC (metres above centroid) was recorded using a Trimble GPS unit (Trimble, Sunnyvale, CA). Plant species composition was recorded for each 1 m^2 plot by identifying each species present, and counting the number of each species per plot for species richness. Plant cover was measured using visual estimates of percent (%) into 6 categories: vines, herbs/ferns, *O.stricta*, grass/sedge, bare ground and surface litter. Plants which were evidently rooted within the quadrat or > 50 % within the quadrat were counted. Measurements of the tallest plant within the plot were taken from the soil surface to the tallest part of the plant using a tape measure from the soil surface to the top most part of the plant.

[redacted]

Figure 4-2 Map of Broughton Island displaying sampling transect locations.

4.3.3 Analytical processing

Soils were thoroughly combined, oven dried at 40 °C and passed through a <2 mm mesh sieve. To ensure consistent soil texture between areas, particle size analysis was conducted on soil samples using a hydrometer method described by the Standards Association of Australia (1976). Soil pH was determined using glass electrodes in a 1:5 soil:water suspension. Ammonia (NH_3) and nitrate (NO_3^-) were analysed following Rayment and Lyons (2011) extraction using a 2 M potassium chloride (KCL) reagent and analysed with Skalar San^{++} continuous flow analyser (Skalar Analytical B.V., The Netherlands). Bioavailable phosphorus (ext. P) was extracted following Colwell and Rayment and Lyons (2011). All extractions and analysis were carried out at the Environmental Analytical Laboratory (EAL) at Southern Cross University, Lismore.

Subsamples of soils were crushed to pass a sieve < 100 µm and analysed for total organic carbon (TOC), total nitrogen (TN) as well as stable isotopic ratio of ^{14}N:^{15}N ($\delta^{15}N$) and

^{12}C:^{13}C ($\delta^{13}C$) using a Thermo Fisher Delta V plus isotope ratio mass spectrometer (IRMS). The IRMS was coupled to an elemental analyser (Thermo Fisher Flash EA) via an interface (Thermo Fisher Conflo IV). Samples were compared to working standards of glycine, glucose and collagen to ensure accuracy. These were calibrated using international reference materials USGS64, USGS65 and *USGS64* (Schimmelmann et al. 2016). Precision for $\delta^{13}C$ was better than 0.15 ‰ and for $\delta^{15}N$ better than 0.3 ‰. at the Environmental Analytical Laboratory (EAL) at Southern Cross University, Lismore.

4.3.4 Statistical analysis

To test the effect of seabird colonies on soil chemistry (including $\delta^{15}N$ and $\delta^{13}C$) at two depth intervals, soil and plant data were fitted to linear mixed effects models using *lme4* package (Bates et al. 2015) in R version 4.2.0 (R Core Team, 2022). Area and lower depth were set as fixed effects. An interaction term for soil depth and area was included when it significantly improved the model per the ANOVA table and was removed from each model otherwise. Intercepts of transect number were set as random effects to account for potential variability between transects. Assumptions for each model were checked. The random intercept term for P had zero variance and the data was highly skewed, so an inversed transformation was applied to P.

Soil surface temperature (°C), species richness, and vegetation height (cm) were statistically compared using Welch's two sample t-tests in R version 4.2.0 (R Core Team, 2022). All data were inspected for skewness prior to conducting t-tests. Bare ground was not statistically analysed because no-colony areas had 0 % in all observations. Though this is likely due to a relatively small number of observations in the study, the t-test could not be performed.

To examine differences in vegetation composition using species presence/absence data, non-metric multidimensional scaling (nMDS) was applied using a Bray-Curtis distance matrix within the *vegan* package in R (Oksanen et al. 2020). Species which were most significant in structuring group communities were fitted to the ordination using envifit() where $p < 0.05$. ANOSIM was used to calculate the difference between groups (colony and no-colony) using 9,999 permutations.

4.4 Results

Both colony and no-colony areas had sandy soil types (sand fraction > 90 %) and flat slopes < 20°, confirming that within each transect, landscape features were equivalent (Table 4-1).

Table 4-1 Landscape characteristics of each transect. Slope, elevation, and soil texture represent the composite mean value of each recording at each site.

Site ID	**Elevation (m)**	**Slope (degrees)**	**Soil texture**	**Aspect**
Colony 1	17.5	2	sand	East
No colony 1	18.5	6	sand	East
Colony 2	13.5	6	sand	North/Northeast
No Colony 2	15.5	5.5	sand	North/Northeast
Colony 3	52	18	sand	North
No colony 3	52	18	sand	North

4.4.1 Soil chemistry

Both ‘area’ and ‘depth’ were significant factors determining soil properties on the sites sampled. TOC concentration was significantly lower in colony areas compared to no-colony areas (ANOVA: $p < 0.001$), and was significantly lower in the lower depths (10-20 cm) of both areas (ANOVA: $p < 0.001$) (Table 4-2, Figure 4-3). TN concentration was significantly lower in soils of colony areas compared to no-colony areas (ANOVA: $p < 0.001$), and was significantly lower in the lower depths of both colony and no-colony areas (ANOVA: p <

0.001). No differences were found in NO_3^- between colony and no-colony areas (ANOVA: p = 0.27). Ammonium concentration was significantly higher in colony areas (36.32 ± 4.68) compared to no-colony areas (23.10 ± 3.66) (ANOVA: p = 0.008). Colony soils were slightly more acidic (4.38 ± 0.12) compared to no-colony soils (4.87 ± 0.06 se) (ANOVA: p < 0.001) (Table 4-2; Figure 4-3).

Table 4-2 Summary of linear mixed effects models of colony area and depth on each soil chemical concentration. *p < 0.05, **p < 0.01, ***p < 0.001. $^{\#}$Results for P with an inverse transformation.

Variable	**Fixed effect**	**Estimate**	**Std error**	**t-value**	**p-value / significance**
TC	area	-2.44	0.54	-4.85	<0.001 ***
	depth	-2.08	0.54	-3.85	<0.001 ***
TN	area	-0.13	0.03	-4.40	<0.001 ***
	depth	-0.11	0.03	-3.99	<0.001 ***
P $^{\#}$	area	0.02	0.01	5.18	<0.001 ***
	depth	0.01	0.01	2.37	0.02 **
NO3-	area	1.38	1.22	1.125	0.27
	depth	-2.12	1.21	-1.75	0.09
NH4+	area	12.27	4.12	2.98	0.004 **
	depth	-13.95	4.10	-3.41	0.002 **
pH	area	-0.50	0.122	-3.99	<0.001 ***
	depth	0.07	0.12	0.53	0.60

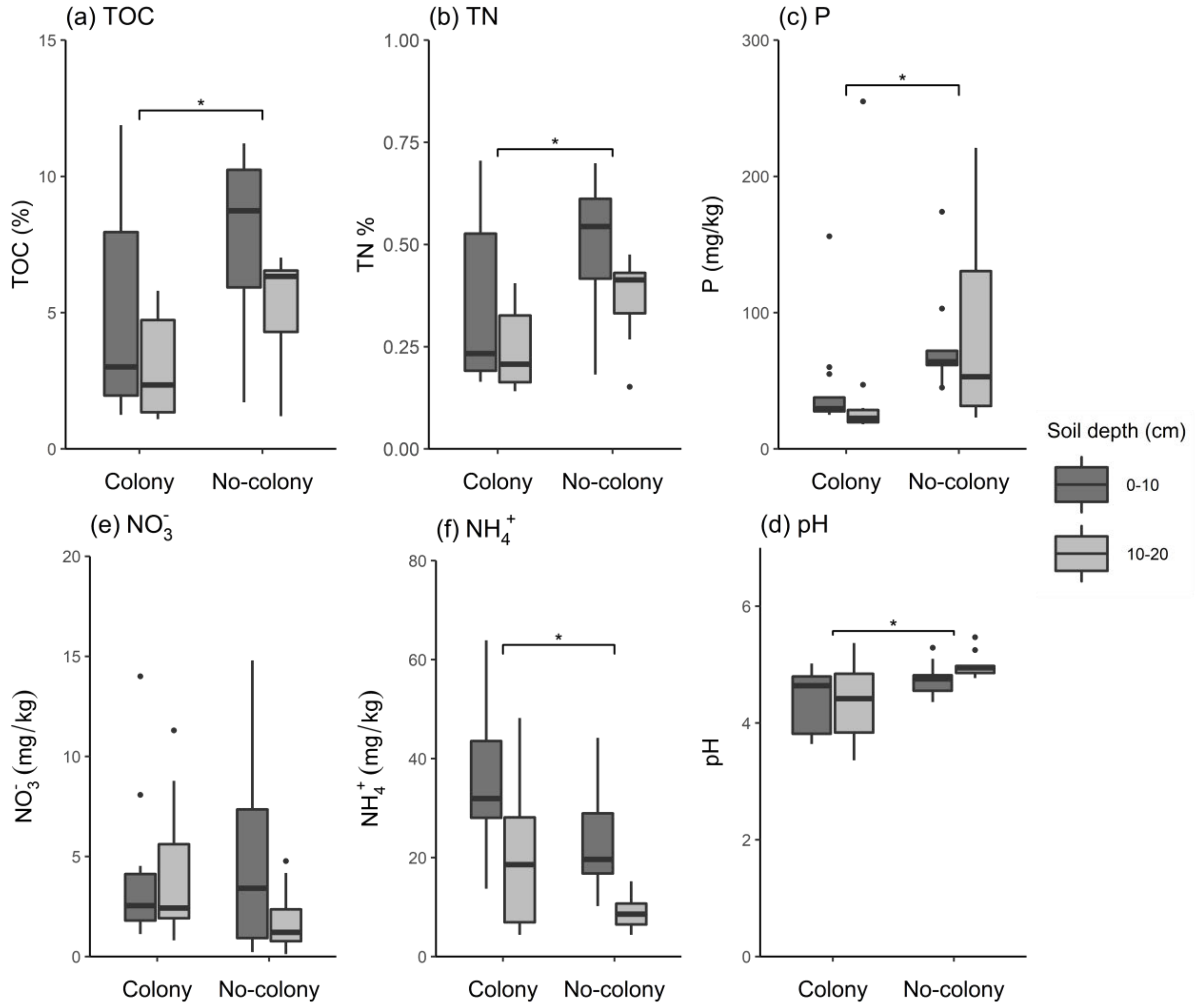

Figure 4-3 Soil properties between colony and no-colony areas with two soil depths: 0-10 cm (dark grey boxplots) and 10-20 cm (light grey boxplots). Variables a-d: TOC = total organic carbon, TN= total nitrogen, P= extractible phosphorus, NO_3^- = nitrate, NH_4^+ = Ammonium and pH. Lines within the boxplots indicate median values and bars maximum and minimum values. Outliers are presented as black points. Asterisks above groups demonstrate significant difference in variables from both depths in each area ($p < 0.05$).

4.4.2 Isotopic signatures of soil

Colony and no-colony soils were significantly different in $\delta^{15}N$ value with colony soils being significantly more enriched in ^{15}N compared to no-colony soils (ANOVA: F= 49.30, $p < 0.001$) (Figure 4-4). Colony soils had a mean (± standard error) $\delta^{15}N$ of 13.27 ± 0.20‰ while no-colony areas had $\delta^{15}N$ of 11.57 ± 0.22‰ $\delta^{15}N$ (Figure 4-4). There was no effect of depth on $\delta^{15}N$ values ($p> 0.05$). Isotopic ratio values of $\delta^{13}C$ resulted in mean value of -23.12 ± 0.16‰ in colony areas and -19.37 ± 0.14‰ in no-colony areas (Figure 4-4). There was a significant difference between colony and no-colony δ^{13}C values (ANOVA: F= 544.41, $p < 0.001$), but depth was not significant ($p > 0.05$).

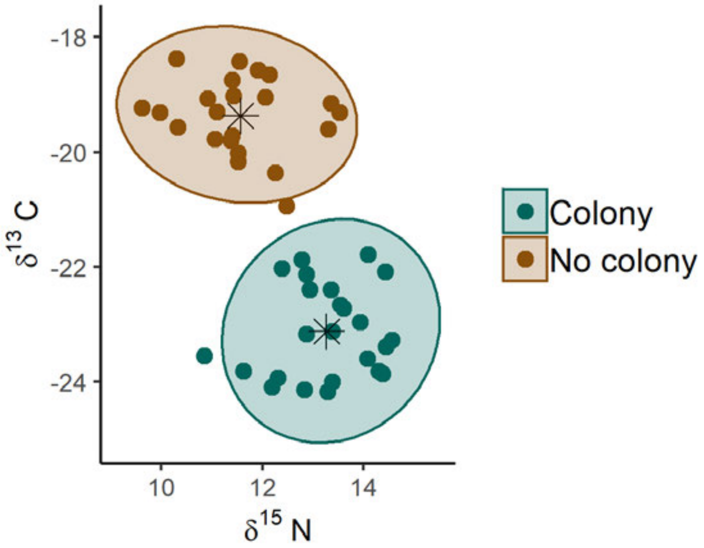

Figure 4-4 Scatterplot of δ^{13}C and δ^{15}N values from soils in landscapes with and without seabird colonies present. Ellipses represents the 95% confidence interval. Group centroids are represented by black asterisks.

4.4.3 Vegetation cover and composition

No-colony areas had no variability in bare ground cover (0% in each observation) and bare ground cover in colony areas were not statistically significant (Figure 4-5). Soil surface temperature was on average higher and more variable in colony areas than in no-colony areas but were not found to be significantly different (t= 1.02, p= 0.32) (Figure 4-5). Mean species richness was significantly greater in no-colony areas compared to colony areas (t= -2.38, p= 0.03), (Figure 4-5). Vegetation was significantly lower in height in colony areas compared to no-colony areas (t= 2.65, p= 0.02).

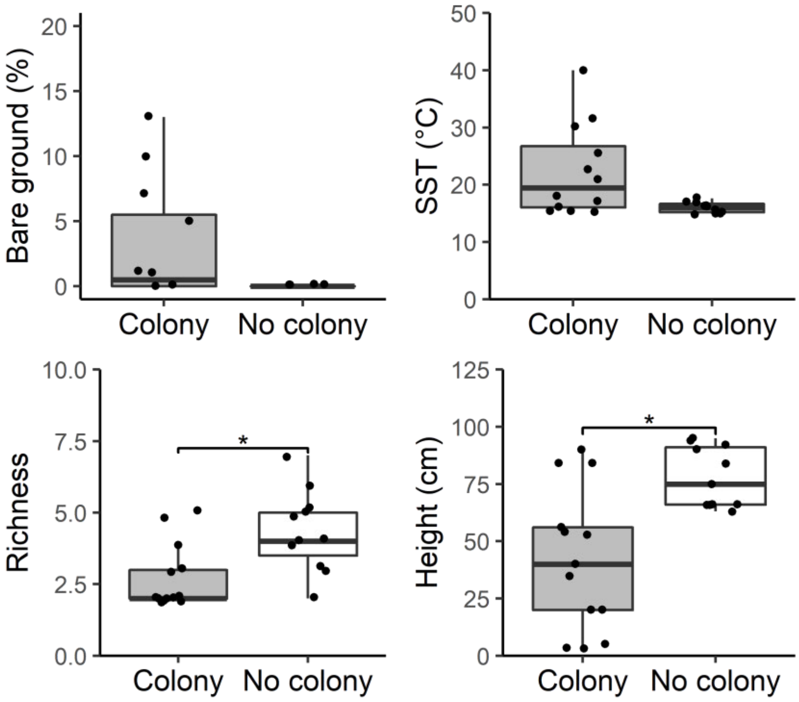

Figure 4-5 Bare ground, soil surface temperature, species richness, and the tallest species height in each transect for colony and no colony areas. Lines within the boxplots depict median values and vertical lines display the range. Points display raw observation values. Asterisks above groups demonstrate significant difference demonstrated by two sample t-tests ($p < 0.05$).

The vegetation cover in colony areas had an average of (mean ± standard deviation) 20.83 ± 0.11% cover in vines and 0% ferns compared to no-colony areas, which had 10.75 ± 0.09% cover of vines and 5.83 ± 0.07% cover in ferns. Colony areas had 28.75 ± 0.13% cover in herbs compared to no-colony areas which had 17.50 ± 0.11%. Colony areas had 10.00± 0.08% cover in surface litter and no-colony areas had 7.08 ± 0.21%. Colony areas had 29.25 ± 0.13% cover of *O. stricta* and no *O.stricta* cover was found in every observation from no-colony areas. Colony areas contained 12.25 ± 0.09% cover in grasses and sedge and no-colony areas had 67.75 ± 0.13% (Figure 4-6).

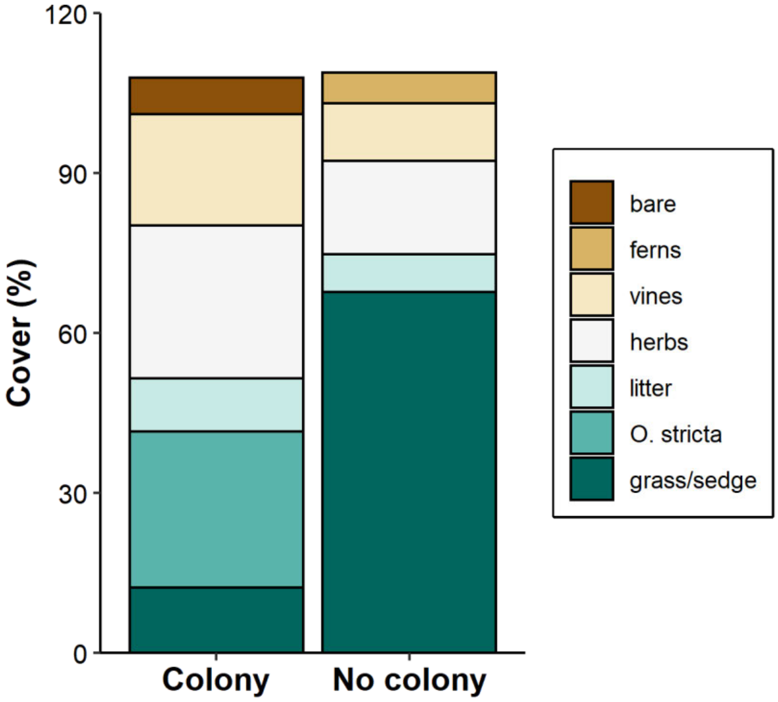

Figure 4-6 Mean percentage (%) of each measured vegetation category as well as surface litter and bare ground within 1m^2 plots on transects in colony and no colony areas.

The nMDS showed good ordination (stress= 0.11) and separation between colony and no colony areas (Figure 4-7). ANOSIM tests indicated significant difference between colony and no colony groups plant species (R= 0.7418, $p < 0.001$). As indicated by envifit(), 8 total species were significant in contribution to community compositions. For colony areas, *O. stricta* was the most significant species driving colony vegetation composition ($p = 0.001$) and *Commelina cyanea* (p = 0.001) (Figure 4-7). Species contributing most to no colony areas were perennial grass *Imperata cylincrica* and vine *Marsdenia rostrate (p* = 0.001, 0.005*)* (Figure 4-7).

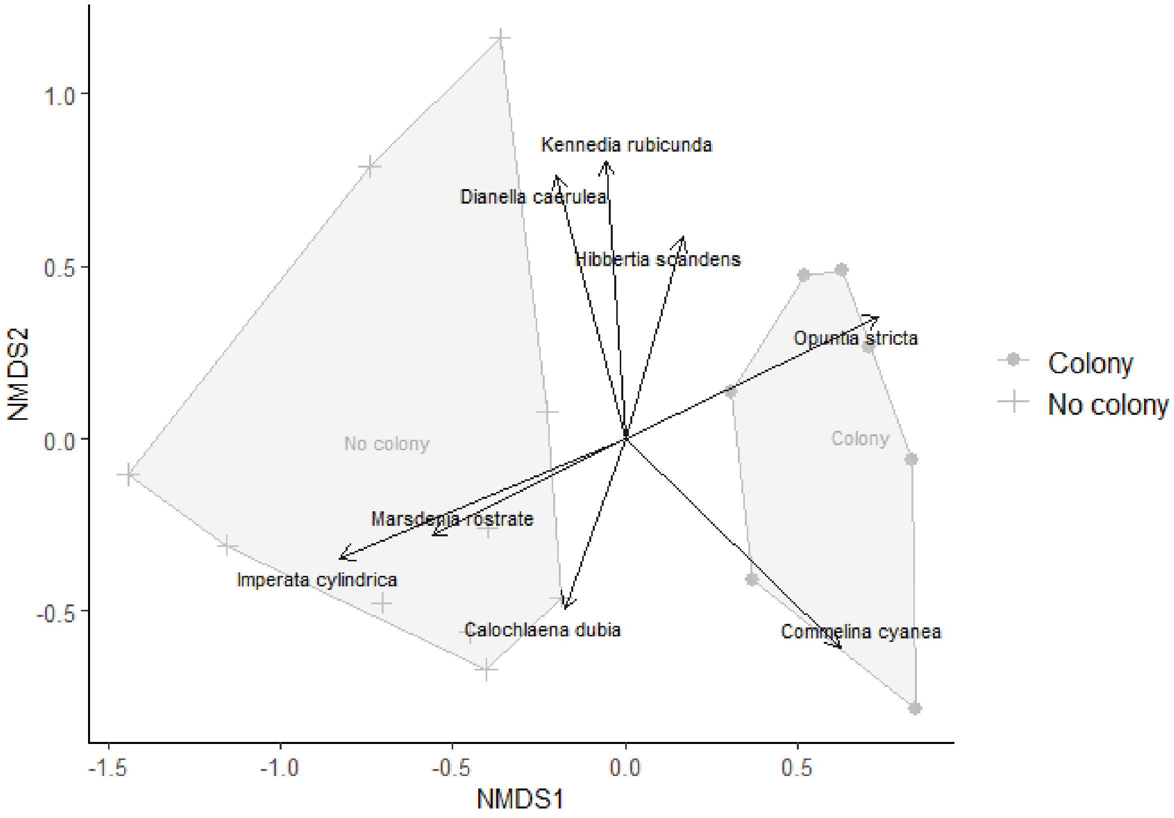

Figure 4-7 Non-metric multidimensional scaling (nMDS) of plant species assemblage in colony and no colony areas (stress = 0.11). Group centroids are represented by grey group names. Plant species names are significant species' maximum correlation with each group ($p < 0.05$). Longer arrow length represents stronger correlation to group.

4.5 Discussion

This study revealed the sandy landscapes occupied by seabird colonies have distinct soil nutrient concentrations, vegetation communities and soil stable isotope signatures compared to adjacent un-colonised areas with similar landscape characteristics. While the majority of seabird terrestrial research to date has found increased soil N and P directly within colonies and a decrease in soil nutrients with increase in distance from seabird colonies (Zwolicki et al. 2016), this study found contrasting results across a short distance (~50 m). The physical disturbance of seabird nesting activity and role of sandy, well drained soils, modify soil nutrients, plant structure and plant composition. Burrowing continually excavates a fresh layer of nutrient poor, aeolian sand, thereby influencing nutrient concentrations (Platt et al. 2016). The role of soil type and physical disturbance via burrowing is most probably driving the movement of N, C and P. Nutrient retention is commonly low in sandy soils and with rainfall N and P are lost from runoff and leaching, which can accumulate in drainage areas or nearby marine sources (Savage 2019).

Stable isotope signatures of $\delta^{13}C$ and $\delta^{15}N$ were significantly different between colony and no-colony areas. Despite the lower N concentration of N in colony soils, ^{15}N across colonies was significantly enriched by comparison with no-colony areas. Seabird colony soils are often found to be enriched in heavier isotope of nitrogen (^{15}N) due to the trophic position of seabirds and values are often used to determine N pathways and sources (Bedard-Haughn et al. 2003; Tabak et al. 2016). For example, Gaiotto et al. (2022) and Pascoe et al. (2021) found that isotopic enrichment of ^{15}N in soil decreased as distance from seabird colonies increased. Although colony soils had a lower concentration of total nitrogen they were enriched with heavier isotopic N (^{15}N) and this result therefore suggests that guano-derived N dominates, and is retained, in the soil system. The lower concentration of TN in seabird colony soils yet the enriched $1\delta^{15}N$ indicates the fractionation of light and heavy nitrogen atoms via various pathways, likely volatilisation of ammonia, leaching, and runoff, and confirms the source of N in soil is from seabirds (marine source). Our result of $\delta^{13}C$ is inconsistent with the idea marine-derived C in terrestrial matter would be more enriched (less negative) in ^{13}C (Mizutani & Wada 1988; Harding et al. 2004; Sabat et al. 2006). Unless, however, decomposition of organic C in seabird colonies differed from no-colony areas, perhaps exacerbated by burrow disruption to soil characteristics but this remains unclear (Wang et al. 2015). Given this complexity, stable isotopes of C in soil may not be a particularly good indicator of seabird C in this system, and the analysis of δ^{13}C in seabird systems should have a different approach for interpretation, for example, in elucidating microbial mineralisation or decomposition of organic C (Hawke & Vallance 2015; Zwolicki et al. 2016).

Seabird colonies were defined by vines and herbaceous plants dominated by the invasive *O. stricta* with patches of bare ground and variable soil surface temperature and low pH. Colony soils were generally more acidic than no-colony soils and could have an effect on vegetation tolerance, as uric acid acidifies the soil which can be toxic for some plant species (Boutin et al. 2011; Zwolicki et al. 2016). The physical engineering of seabirds displaces soil and uproots plants to maintain the integrity of borrows (Bancroft et al. 2005). It is apparent that the dual pressures of physical engineering and nutrient differences in colony areas drives significantly different vegetation which can survive in heavily disturbed environments, and is more conducive to weed species (Ellis 2005). *O. stricta* (family *Cactaceae*) is a perennial cactus commonly associated with heavily disturbed sites such as abandoned farmland and urban areas (Vilà et al. 2003). *O. stricta* is successful in heavily disturbed sites because it is long lived, can withstand high nutrient loads and low water content, can reproduce through fallen cladodes and has seeds that remain viable for decades (Wilder et al. 2021, Hunter 2015). It is postulated rabbits were a main cause of the spread of *O. stricta* once present on the island, as they would eat the fleshy fruits and deposits seeds through their droppings, though wind, land birds, and water also may disperse the seeds (Carlile et al. 2012). On many parts of the island, *O. stricta* marks the boundary of many seabird colonies, so they have established themselves and outcompeted the native community present beforehand. Taller grasses occurred in no-colony areas compared to lower level vines, herbs, and bare ground in colony areas. Prickly pear has been documented to encroach on seabird colonies and threaten nesting success on Mudjimba Island in Queensland (Dyer 2000). The presence of prickly pear did not seem to deter seabirds from colonising, but further research is needed to quantify the effects of prickly pear on seabird distribution.

These results are the first reported where seabird colony soils were more depleted in N, P and C directly in colony areas and more enriched in adjacent landscapes unaffected by burrow nesting seabirds. The function of acidic, sandy, and highly disturbed soils with rapidly lost soil nutrients drives distinct ground cover which is generally shorter, less diverse, and with patches of bare ground. Broughton island is experiencing an increase in seabird population (Carlile et al. 2022). As colonies expand we expect the disturbance and nutrient loading to favour the spread of *O. stricta* to dominate over low level sedge, grass, and fern species with shorter lived vegetation, and be more similar to seabird colony plant communities surveyed in this study. To mitigate the spread of *Opuntia stricta*, additional biocontrol within seabird colonies should be prioritised. Monitoring longer term floristic changes concurrently to seabird population flux is useful for understanding to the change of plants and disturbance on insular communities as seabird population densities change (Vidal et al. 2000; Duda et al. 2020).

4.6 Acknowledgements

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Chapter 5: Vegetation change and recovery following the eradication of rats and rabbits on Broughton Island, New South Wales

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5.1 Abstract

Invasive mammal eradications have shown success in insular communities which are threatened by grazing and predation on native species. Recovery of vertebrate populations in such situations are well documented, though more intricate ecosystem and vegetation dynamics are rarely monitored. After the successful eradication of *Rattus rattus* (black rat) and *Oryctolagus cuniculus* (European rabbit) on Broughton Island in 2009, a vegetation monitoring program was established by the New South Wales National Parks and Wildlife Service (NPWS) to assess the response of vegetation dynamics on three affected community types until 2016. Seven years following pest eradication, vegetation height and species richness significantly increased and bare ground cover decreased. Invasive weed cover showed no change over the survey period. Non-metric multidimensional scaling (nMDS) showed distinct species composition and cover between vegetation communities where environmental factors such as soil type, fire and nesting seabirds were also influential in community composition. An increase in woody species was found through ecological indicator species analysis, particularly within native *Themeda triandra* grasslands. The results from this survey show non-uniform,

but generally positive outcomes for vegetation from pest eradication, and continuation of the program would be useful to gauge ecosystem function and recovery. Continuation of surveys will contribute to developing a framework understanding dynamics of ecological recovery following invasive eradications on islands.

5.2 Introduction

Invasive mammals are one of the greatest threats to global biodiversity and account for significant losses of species diversity and native habitat worldwide (Doherty et al. 2016; Bellard et al. 2016). It has been estimated that 40% of all plant and animal species threatened with extinction are on islands, with threats primarily due to predatory pressures exerted by invasive mammals (Clavero & García-Berthou 2005; Doherty et al. 2016; Tershy et al. 2015; Russell & Kueffer 2019). As a consequence of the fragility of island plant and animal communities to disturbance, islands are considered to be biodiversity hotspots with high conservation value, and are strong candidates for conservation efforts (Sax & Gaines 2008; Kier et al. 2009; Holmes et al. 2019). In some circumstances, invasive mammals can replace the functional roles of native biota in terms of nutrient cycling, native habitat and trophic structure (Stone et al. 1992; Abe et al. 2011). To mitigate the detrimental effects of invasive mammals on native communities, eradication programs have become an increasingly popular conservation tool over the past five decades, with the dual aim of restoring island ecology and reducing rates of species loss (Towns & Broome 2003; Russell & Broome 2016; Segal et al. 2021).

Pressures from invasive species directly and indirectly impact components of island habitat and vegetation communities primarily through predation, grazing and trampling (Schweizer et al. 2016; Kearney et al. 2019). Introduced rats and mice are present on more than 80% of islands around the world and rapidly form dense populations (Atkinson 1985; Terborgh et al. 2001). Rats and mice are opportunist foragers and graze on fleshy fruits, seeds, and seedlings, impacting seed distribution and increasing competition with native animals for resources (Ruffino et al. 2011; Shiels & Pitt, 2014; Wotton & McAlpine 2015). Invasive rodents may also prey on insects, birds, and mammals, which can decrease or decimate population size, breeding success, nutrient pathways and pollination (Towns et al. 2006; Jones et al. 2008; Ruffino et al. 2009). European rabbits (*Oryctolagus cuniculus*) have been attributed as the most heavily cited species in Australia found to be harmful to native plant communities (Kearny et al. 2019; Finlayson et al. 2022). These herbivores graze upon ground-level plants, exposing soil to degradation and erosion by reducing herbaceous cover (Campbell & Donlan 2005; Eldridge and Myers 2001; Van Vuren & Coblentz 1987). Predation of seeds and seedlings also impacts vegetation patterns and food resources (Bird et al. 2012). Disturbance from invasive mammals alters the trajectory of secondary succession in native plant communities by altering plant biomass, diversity, richness and encouraging biotic homogenization of plant community composition (Olden et al. 2004; Suding et al. 2004; Mulder et al. 2009; Emery 2010). Predation of woody seedlings can suppress the growth of larger shrubs and trees, altering woody diversity and density (Campbell & Atkinson 2002; Cooke & McPhee 2007; Meyer & Butaud 2009). Disrupted patterns of seed dispersal and seedling success and may increase the recruitment of non-native seeds and seedlings competing with native flora (Shiels & Drake 2011; Miller-Ter Kuile 2020; Wotton & McAlpine 2015).

The pressures exerted by invasive mammals can result in prolonged periods of recovery even after eradication which depends on a range of environmental factors during both passive (natural) and active (intervened) restoration (Jones 2010; Holl & Aide 2011; Prior et al. 2018). Factors such as human influence, climate, and co-occurrence with established exotic plants can confound restoration goals and ecological states (Atkinson & Cameron 1993; Chapuis et al. 2004; Prior et al. 2018; Ritchie and Johnson, 2009). Landscape, climatic and plant community features can further complicate plant community response to invasive mammal eradication (Bartuszevige et al. 2006). These systems will likely require concurrent control of exotic plants and animals for maximum success (Calvino-Cancella 2011; Le Corre et al. 2015; Prior et al. 2018; Zavaleta et al. 2001).

Many post-eradication studies have shown how eradications can mitigate the rate of biodiversity loss on islands directly by preventing the predation of threatened plant and animal communities (Courchamp et al. 2011; McCreless et al. 2016; Holmes et al. 2019). The removal of invasive mammals has reduced seed predation promoted native plant abundance, biomass, and overall ecological recovery (Pender et al. 2012; Le Corre et al. 2015; Wolf et al. 2018; van Dongen et al. 2019). Post-eradication ecological studies have demonstrated restored habitat and increased abundance in native plant and animal communities (North et al. 1994; Kurle et al. 2021). Despite well-documented successful outcomes of eradications however, fewer than 10% of all successful rodent eradications in Australia have subsequently reported quantitative results of native recovery dynamics (Segal et al. 2021). Of these reported surveys, most focus on bird and mammal species, leaving vegetation response understudied in the literature (Segal et al. 2021; Jones et al. 2016; Schweizer et al. 2016). Pre-and-post-eradication monitoring would greatly assist our understanding of the efficacy of eradication programs and assist in the prediction and mitigation of adverse outcomes (Zavaleta et al. 2001; Courchamp et al. 2003; Bird et al. 2019). Such knowledge is vital in properly supporting ongoing management, effective resource allocation, and funding decisions (Holmes et al. 2019).

The aim of this study was to assess the biophysical outcomes of vegetation community structure and composition over 7 years following the eradication of rats and rabbits on Broughton Island, New South Wales, Australia. Fourteen transects were surveyed across a range of vegetation community types from 2009 – 2016. We examine the overall change of vegetation community dynamics, including species richness, abundance, cover, and height. We also examine potentially influential ecological drivers contributing to change, including indicator plant species, soil type, disturbance, and landscape characteristics. The results of this work will inform our understanding of how vegetation recovers in the absence of invasive mammals, and will help fill knowledge gaps regarding the response of island vegetation communities to management efforts.

5.3 Methods:

5.3.1 Site Description

Broughton Island (32.616° S, 152.314° E) is part of the Myall Lakes National Park and is the largest offshore island in New South Wales (NSW), with an area of 132 hectares (Figure 5-1). Though it is relatively limited in size, the island contains an assemblage of geologic substrates principally of felsic rhyolitic rocks with basalt intrusions, conglomerates, and sandstones (Matson & Chestnut 1975; Thom et al. 1981). Landscapes on Broughton Island include two central aeolian sand dunes with mosaics of shrubs and ferns, sandy beaches and foredunes, and endangered *Themeda triandra* (kangaroo grass) grasslands on coastal headlands (Somerville et al. 2018). Broughton island experiences a subtropical climate with temperatures ranging from an average minimum of 9.1 ℃ in winter to an average maximum of 27.3 ℃ in summer, and a mean of 1,339 mm of annual rainfall (Data based on Nelson Bay, BOM, 2021). Since its establishment of a National Park Reserve in 1972, the only structures on the island include a small cluster of fisher huts and a camping platform and is otherwise protected from external development.

[redacted]

Figure 5- 1 (A) Map of New South Wales and Broughton Island's location in relation to Sydney. (B) The departure location from the NPWS station at Nelson Bay to Broughton Island. (C) Transect locations of the monitoring project by vegetation community.

The island has experienced a range of terrestrial disturbance from human influence, fire and the introduction of invasive plants and mammals (Mooney et al. 2020; Carlile et al. 2012). Deliberate use of fire by both Indigenous and post-European groups has contributed to the homogenisation of much of the landscape's floristic composition (Hunter & Alexander 2000; Mooney et al. 2020). The most recent wildfire occurred in 2008, affecting primarily mixed grassland areas, which supressed grasses and shrubs but left *O. stricta* comparably undisturbed. No climatic or weather anomalies however were observed during the period of the survey. Historic introductions of feral animals including rodents, rabbits and goats have influenced native plant and animal assemblages from grazing and predation. Rabbits were found to forage on invasive cactus *Opuntia stricta* and increased their prevalence, and rats were preying on eggs and chicks of nesting seabirds, impacting populations and breeding success (Carlile et al. 2012; Carlile et al. 2022). Motivated by the disruption to plant and seabird communities, an invasive mammal eradication program was initiated in 2009 to target *Rattus rattus* (black rats) and *Oryctolagus cuniculus* (European rabbits) using aerially dispersed cereal pellets with brodifacoum (20 ppm), bait stations with pellets and carrots sprayed with rabbit haemorrhagic disease. The operation was done in efforts to restore seabird habitat and breeding success, and to promote growth of native plant communities (Priddel et al. 2011). The island was declared free of rats and rabbits in 2011 and to date there are no rats or rabbits present on Broughton Island.

5.3.2 Survey Design

Fourteen 20 metre transects were established in 2009 in the same year of the eradication program and was the first assessment of vegetation since the arrival of rats and rabbits on Broughton Island. Transects were located on three vegetation communities impacted by rats and rabbits: coastal dunes (hereafter, dunes) mixed grasslands, *Themeda triandra* grasslands (hereafter, themeda) (Figure 5-1). Because the entire island was affected by rats and rabbits, a control site was not available, though we acknowledge the associated limitations. Transects were surveyed in September from 2009- 2013 and again in September 2016. Each plant species was identified extending 4 metres on each side of the transect, where visual estimates of bare ground and individual species (grouped as native and non-native) cover were recorded to the nearest estimate of percent (%). Species richness was calculated by counting the number of different species found in each transect. on 4 m of each side of the transect. At every 1.0 metre interval extending 4m on either side of the transect and starting at 0 m, the tallest plant was measured from the ground surface to the tallest part of the plant to the nearest centimetre using a measuring tape. The beginning and end points of each transect were georeferenced, photographed, and marked with metal stakes. Twelve complete transects were included in analysis: dune= 2, mixed grassland= 6, themeda= 4 (Fig 1). Two of the 14 transects were abandoned and not included in analysis, one due to disturbance from significant human foot traffic, and one due to a large swell causing beach erosion. To account for external factors potentially influencing vegetation change, categories of known disturbances to each transect (2008 fire, surface nesting seabirds, and pervasive weed *Opuntia stricta*) and soil type of each transect location (derived from Tulau & Wilson 2018) were included in the dataset for analysis.

5.3.3 Statistical Analysis

To assess overall changes in vegetation parameters over the course of the survey period, response variables of height, richness, bare ground and invasive weed cover were analysed using mixed effect linear models by specifying ‘year’, ‘vegetation community’, and the interaction term of ‘year’ and ‘vegetation community’ as fixed explanatory factors, and ‘transect’ as a random effect variable using *nlme* package version 3.1-161 (Pinheiro et al. 2022) in R software version 1.4 (R Core Team 2022). All response variables were visually assessed to meet assumptions for each model, and where necessary were transformed. Due to the residual values, height was analysed using average values from each transect which significantly reduced heterogeneity and provided a better fit for the model. For weed cover and bare ground, the log transformation was used. Tukey contrast test for multiple comparisons of means was used for post-hoc comparisons using the *multcomp* package (Hothorn et al. 2008). Where variables had significant interactions, compound variables were created combining ‘year’ and ‘vegetation community’ for post-hoc tests.

To assess vegetation community assemblage over time and evaluate if external factors (fire, seabirds, or prickly pear) affected vegetation community groups, an ordination of plant community structure within and between the three vegetation groups was created from values of individual species cover (%) in nonmetric multidimensional scaling (nMDS) using a Bray-Curtis dissimilarity matrix with 999 permutations. All ordination functions were computed using the *vegan* package version 2.5-7 (Oksanen et al. 2020) in Rstudio (R Studio Team, 2020).

Environmental disturbances were included in the ordination to describe the influence of these variables on to potentially elucidate trends since eradication. To test whether there were significant differences between vegetation groups in the ordination, permutational analysis of variance (PERMANOVA) was then used to test the effects of vegetation community type, disturbance, soil type, transect and year on each vegetation community cluster using adonis() function. To test the null hypothesis that the dispersions of group means are equal (a condition to perform PERMANOVAs) betadisper() was used (Anderson & Walsh 2013). Significant PERMANOVAs ($p < 0.05$) were followed with pairwise tests using the PairwiseAdonis() function at 0.05 significance (Martínez Arbizu 2020).

To identify plant species significantly correlated to each group, species were fitted to the ordination and values of correlation with corresponding vegetation communities were computed using envifit() function in the *vegan* package. A subset of species with high correlation (and $p < 0.01$) significance was included in the ordination plot to avoid overcrowding of the visualisation by species with lower significance values. Indicator species analysis was performed using the same distance matrix created for the nMDS ordination and assessed using the indval() function in the *labdsv* package version 2.0-1 (Roberts 2019) in R (RCore Team 2022). The output from indval() provides indicator values representing fidelity and probability of presence for each species based on group clusters, which in this case are vegetation communities (Dufrêne & Legendre 1997). Species with the highest indicator values for each community (greatest relative frequency and relative average abundance in clusters) were extrapolated to assess their relative abundance in cover (%) over the survey period, and tested for significance by fitting them to linear models. The indicator species were found to meet assumptions of normally through the square root transformation.

5.4 Results:

Among each vegetation community, plant height was significantly greater in years 2011-2016 compared to 2009 (Tukey's test: P= < 0.001, < 0.001, 0.01 and 0.004 respectively) but no difference was found between plant heights in 2009-2010 (Tukey's test: P = 0.13) (Figure 5-2.a; Table 5-1). Dune and themeda communities experienced the most growth in height by 2012 where height (mean ± se) increased from 10.50 ± 2.05 cm in 2009 to 49.02 ± 4.18 cm in dune transect and 13.18 ± 1.44 cm in 2009 to 41.87 ± 4.57 cm (Table 5-2). There were no differences in values between vegetation communities in height nor interaction of the two response variables (Table 5-1). Mixed grassland communities experienced the greatest increase in plant height, where mean height increased from 20 ± 1.92 se cm in 2009 to 60 ± 2.56 cm in 2016 (Fig 5-2.a.). Species richness significantly increased between years 2009 and 2016 (Tukey's test: P = 0.05). Richness values did not vary between vegetation communities and ranged between the two years from in 8.0 ± 1.00 to 13.50 ± 1.50 se in dune communities, 9.5 ± 1.60 to 10.5 ± 1.5 se mixed grasslands, and had the greatest increase from 6.50 ± 0.29 to 14.75 ± 1.93 se in themeda communities (Figure 5-2.b).

Bare ground cover significantly decreased between the survey period (ANOVA: F= 9.70, p = < 0.001) and the interaction of vegetation community and year was significant (ANOVA: F= 2.80, p= 0.008), but significantly increased in dune communities in 2012 and 2013 compared to 2009 (Tukey's test: P < 0.01 & 0.01 respectively) and each year compared to 2009 cover in mixed grassland communities (Tukey's test: P < 0.01 for each comparison to 2009) (Figure 5-2.c). Themeda communities began with relatively little bare ground (≤ 0.8 % each survey year) and had no significant change in bare ground cover (Tukey's test P > 0.05). Invasive weed cover showed no significant changes between vegetation type or year (ANOVA F= 1.56, p= 0.19) (Figure 5-2.d).

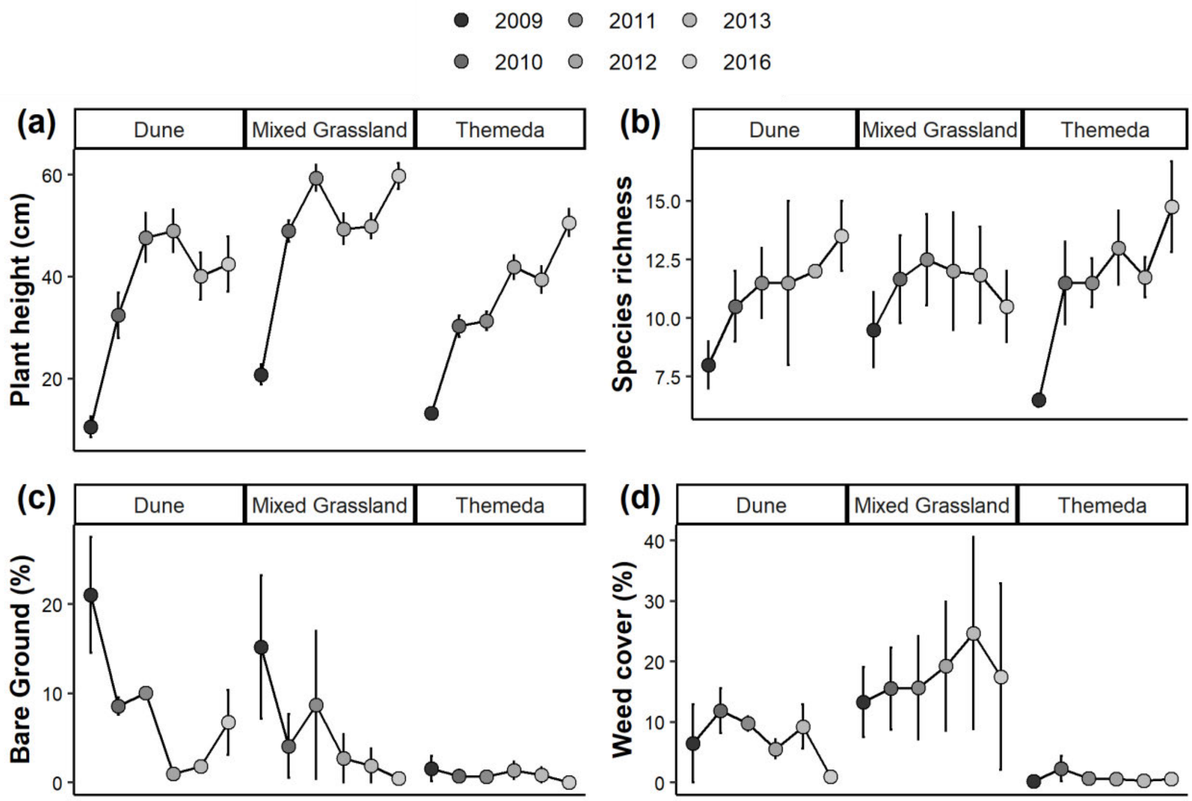

Figure 5- 2 Vegetation parameters showing mean ± standard error of (a) plant height (cm), (b) species richness, (c) bare ground cover (%) and (d) invasive weed cover (%) from each survey year from 12 transects. Points represent mean values from all transects within each vegetation group and black vertical lines represent the standard error of the mean.

Table 5-1 ANOVA table describing the effects of year, vegetation community, and their interaction on vegetation height, species richness, bare ground and invasive weed cover. Values in bold indicate statistical significance at $p < 0.05$.

Response	**Fixed effect**	***df***	**F-value**	***p***
Height	Veg community	2	2.76	0.12
	Year	5	26.15	**<0.001**
	Veg com: year	10	1.39	0.217
Bare ground	Veg community	2	2.05	0.18
	Year	5	9.71	**<0.001**
	Veg com: year	10	2.80	**0.01**
Species richness	Veg community	2	0.001	1.00
	Year	5	7.75	**<0.001**
	Veg com: year	10	2.01	0.06
Weeds	Veg community	2	1.96	0.20
	Year	5	1.56	0.19
	Veg com: year	10	1.07	0.40

Table 5-2 Mean values ± standard error for vegetation height (cm), species richness, bare ground cover (%) and invasive weed cover (%) from transects surveyed in dune, mixed grassland, and themeda vegetation communities.

		height (cm)					
		2009	**2010**	**2011**	**2012**	**2013**	**2016**
dune	mean	10.50	32.40	47.69	49.02	40.10	42.45
	se	2.05	4.44	4.74	4.18	4.65	5.38
mixed grassland	mean	20.79	48.97	59.37	49.38	49.94	59.75
	se	1.92	2.01	2.54	3.02	2.42	2.57
themeda	mean	13.18	30.29	31.29	41.87	39.45	50.58
	se	1.44	3.30	3.41	4.57	4.30	5.52
		Species Richness					
		2009	**2010**	**2011**	**2012**	**2013**	**2016**
dune	mean	8.00	10.50	11.50	11.50	12.00	13.50
	se	5.66	7.42	8.13	8.13	8.49	9.55
mixed grassland	mean	9.50	11.67	12.50	12.00	11.83	10.50
	se	3.88	4.76	5.10	4.90	4.83	4.29
themeda	mean	6.50	11.50	11.50	13.00	11.75	14.75
	se	3.25	5.75	5.75	6.50	5.88	7.38
		Bare Ground (%)					
		2009	**2010**	**2011**	**2012**	**2013**	**2016**
dune	mean	21.04	8.59	10.09	1.00	1.81	6.76
	se	14.88	6.07	7.13	0.71	1.28	4.78
mixed grassland	mean	15.21	4.09	8.69	2.73	1.91	0.46
	se	6.21	1.67	3.55	1.11	0.78	0.19
themeda	mean	1.56	0.72	0.69	1.38	0.84	0.00
	se	0.78	0.36	0.34	0.69	0.42	0.00
		Weed cover (%)					
		2009	**2010**	**2011**	**2012**	**2013**	**2016**
dune	mean	6.48	11.85	9.75	5.57	9.26	1.02
	se	6.48	3.69	1.15	1.58	3.63	0.67
mixed grassland	mean	13.28	15.54	15.70	19.25	24.70	17.51
	se	5.78	6.74	8.55	10.66	15.88	15.38
themeda	mean	0.24	2.31	0.66	0.63	0.28	0.62
	se	0.24	2.13	0.60	0.57	0.28	0.44

The nMDS showed distinct species assemblages within each of the three vegetation groups and represented a good 2-dimensional ordination with the stress value 0.181 (Figure 5-3). Beta dispersion analysis showed each factor except year was significantly different in dispersion and variance (F= 56.123, $p < 0.001$), thus rejecting the null hypothesis of equal dispersion (Table 5-3). PERMANOVA (adonis()) showed vegetation community type and disturbance had a significant effect on species composition, and explained 34 % and 19 % of the variation in community composition, respectively (Table 5-3). While the PERMANOVA differences may have been influenced by the non-homogenous dispersion indicated via the betadisper analysis, inspection of the ordination indicates the PERMANOVA differences are most likely due to differences in community composition. Communities with seabird influence were significantly different to those that had experienced fire ($R^2 = 0.30$, $p = 0.001$), prickly pear ($R^2 = 0.40$, $p = 0.001$) or no disturbance ($R^2 = 0.30$, $p = 0.001$) (Figure 5-4). All post-hoc pairwise comparisons for each vegetation community were significant at $p < 0.05$. Soil type, transect and year were also significant factors in explaining vegetation composition, but with very weak correlation values (R^2 = 0.07, 0.03, 0.04, respectively) (Table 5-3).

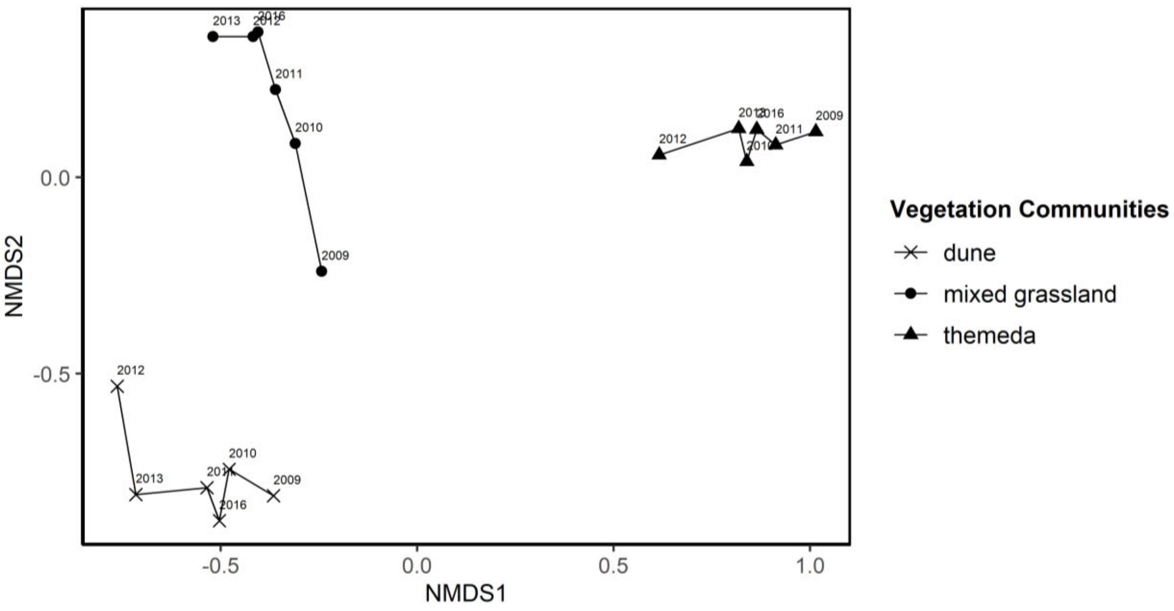

Figure 5- 3 Non-metric multidimensional scaling (nMDS) plot of plant community assemblage centroids in each vegetation group sampled through survey years using Bray-Curtis dissimilarity. Stress = 0.18.

Table 5-3 Multivariate homogeneity of group dispersion analysis (Betadisper), and permutational multivariate analysis of variance (PERMANOVA) using adonis(). [1.] Adonis factor terms are added sequentially. [2]. Betadisper transect squared distances were negative and changed to zeroes.

Factor	**Betadisper**				**Adonis**[1]	
	F-value	***p***		***Df***	***p***	**R**^{2}
Veg com	4.73	<0.001		2	0.001	0.34
Disturbance	4.73	0.004		3	0.001	0.20
Soil type	9.74	<0.001		3	0.001	0.07
Year	0.45	0.81		1	0.001	0.03
Transect[2]	2.17	0.03		1	0.001	0.04

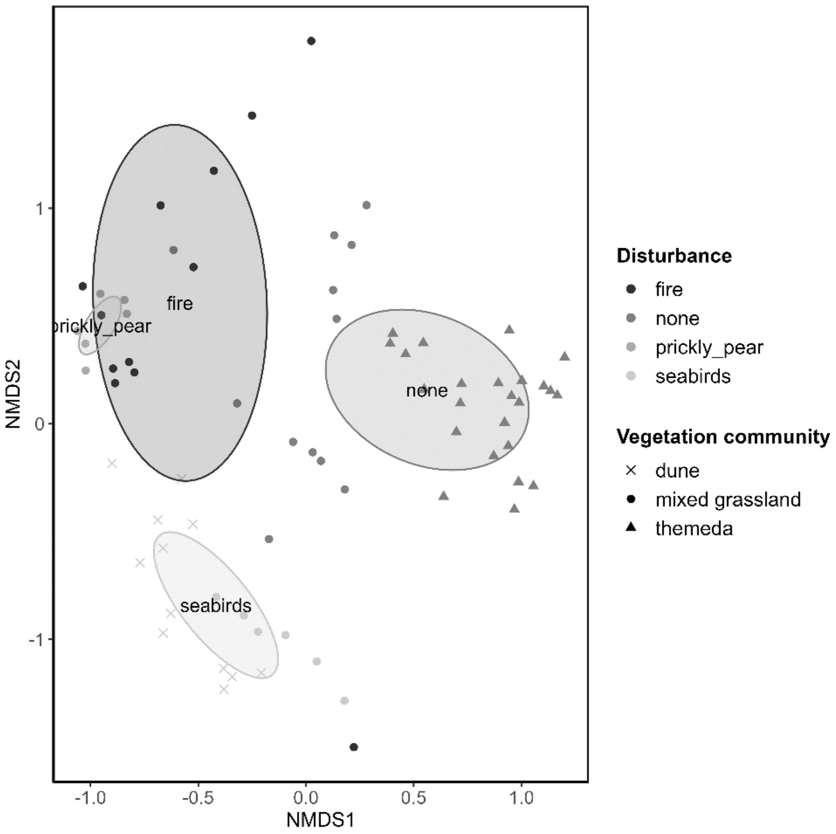

Figure 5- 4 Nonmetric multidimensional scaling (nMDS) of species presence using cover (%) for transects sampled in dune (x), mixed grassland (circle), and themeda (triangle) communities using Bray-Curtis dissimilarity (stress= 0.18). Transects with disturbance factors of fire, prickly pear, and seabirds are identified by shape. Names of disturbance type are superimposed as the cluster centroid with ellipsoids encircling the standard deviation of each disturbance group.

Out of 72 plant species recorded during the survey period, 31 plant species were identified as significant contributors to explaining differences in community composition with indicator species analysis based on cover (%) with 15 species with significance value of 0.001 (Figure 5-5). Dune community indicator species identified *Carpobrotus glaucescens* (indicator value= 0.81, p= 0.001) which had no significant changes overtime (ANOVA: F= 1.35 p= 0.29) and *Opuntia stricta* (indicator value= 0.30, *p*= 0.03). There was a slight decreasing trend in *O.stricta* cover with time, although no years were significantly different from each other (ANOVA: F= 0.73, p= 0.61) (Figure 5-6). In mixed grassland communities, native grass *Imperata cylindrica* was identified as an indicator species (indicator value= 0.66, p= 0.001) (Figure 5-5) but had no significant changes overtime (ANOVA: F= 0.45, p= 0.81) (Figure 5-

6). The indicator species identified for themeda communities was *Themeda trianda* (indicator value= 0.93, *p*= 0.001). The cover of *T. triandra* decreased by 22% between 2009 and 2016, though was not statistically significant (ANOVA: F= 0.13 p= 0.99) (Figure 5-6). Woody shrub species *Westringia fruticosa* was also identified as an indicator species in themeda communities and increased in cover over time though was not statistically significant (ANOVA: F= 1.01, p= 0.45) (Figure 5-6).

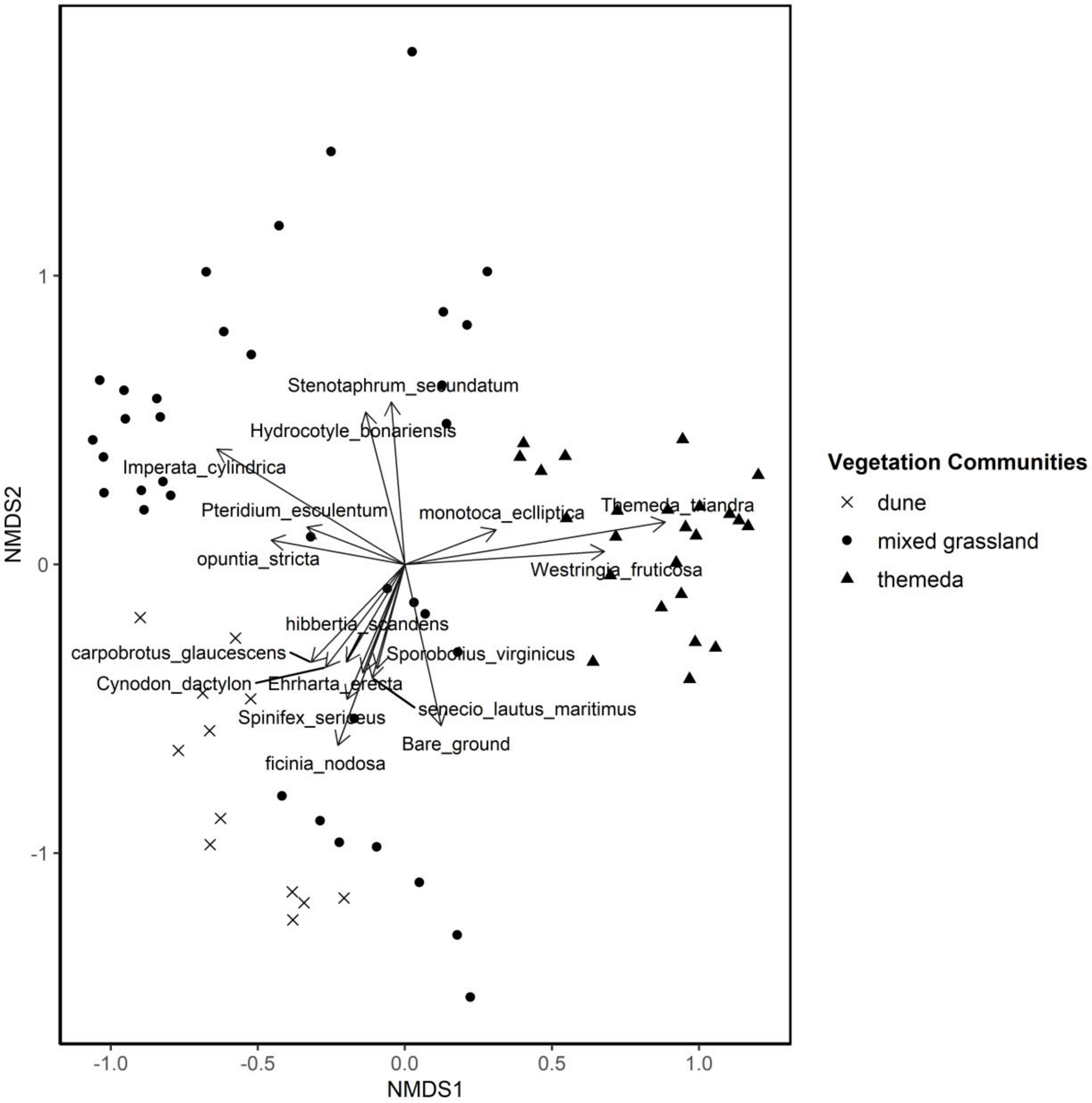

Figure 5- 5 nMDS Ordination plot showing significant species vectors ranking p ≤ 0.01 (Stress= 0.18). Species names with the longest arrow are stronger in correlation of composition to their group identifier.

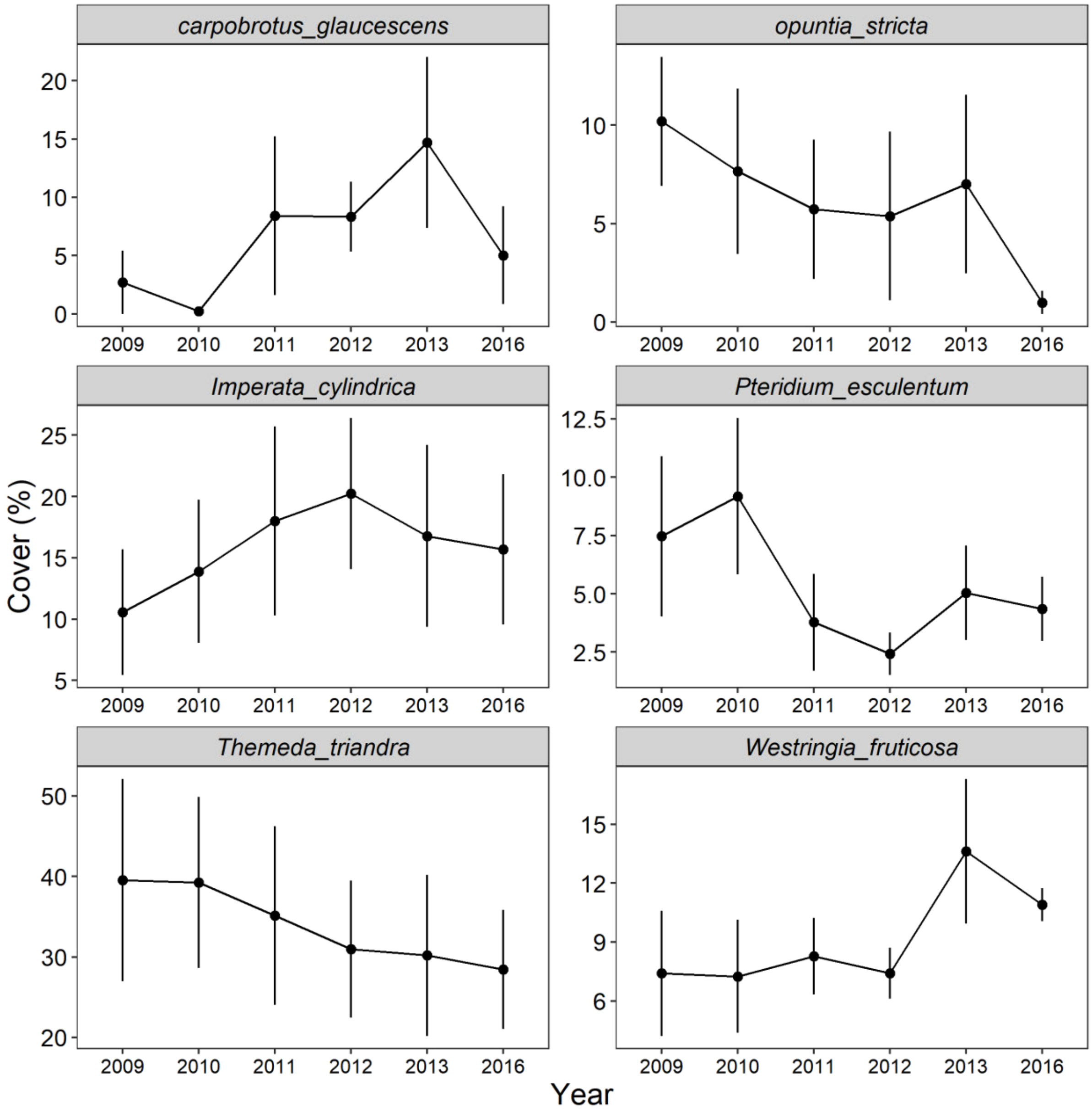

Figure 5- 6 Plot of indicator species cover recorded each year of the survey in all transects. Points represent the mean cover value and vertical lines represent standard error of the mean.

5.5 Discussion

In this study we sought to assess changes in vegetative characteristics among a range of vegetation zones following the eradication of rats and rabbits on Broughton Island. The trajectory of change was not uniform among vegetation communities; however, this finding highlighted confounding environmental drivers like landscape, disturbance, and co-occurrence of invasive plants and animals in affecting recovery patterns. Since the removal of invasive mammals in 2009 on Broughton Island, three vegetation communities experienced linear increases in plant height, species richness, and ground cover. Vegetation height increased as plants revegetated and had time to reach maturity in the absence of seedling predation (Travset et al. 2014). Species richness increased presumably as the halt to seed and seedling predation from grazing facilitated the growth of plant species that had been preferentially supressed. Ground level herbs, vines and grasses vegetated areas of bare soil relatively quickly and were able to increase in cover as time since eradication increased with both native and non-native plants. This illustrates the fact that eradication of grazing mammals only removes one pressure exerted on a native ecosystem, and does not independently provide a mechanism for suppression of weed species (Mulder et al. 2009).

Incorporating the environmental factors of ‘disturbance’ and ‘soil type’ into the analysis provided a more robust evaluation of underlying drivers of change in vegetation community structure. The nMDS ordination and analyses of variance showed distinctness in vegetation community composition and disturbance factors driving vegetation composition. The ordination plot strongly suggests that while dispersion is different between groups, the displacement of groups supports the PERMANOVA findings as well. For example, there were strong differences between vegetation communities. The significant correlation between bare ground and seabird colonies probably reflects a number of factors mediated by seabirds as well as rats and rabbits. For example, dune systems are suitable habitat for burrow nesting seabirds, who through trampling, digging, and high nutrient loads contribute to soil exposure and structural complexity of vegetation (Bancroft et al. 2005; Wait et al. 2005; Yoshihara et al. 2010). Secondly, dune systems consist of aeolian sand on sloping landscapes, which when grazed can be susceptible to soil exposure (Hesp et al. 2010). However, over time, bare ground and plant height significantly increased in dune communities after eradication, even with seabird disturbance, suggesting an overall change in structure and ground cover. Factoring drivers of disturbance to vegetation monitoring in this way can underpin ecological succession and explain anomalies to general and broad scale patterns of vegetation recovery.

Interactions between invasive plants and mammals may leave a legacy effect on the weed distribution and ecological relationships even after one factor is removed, and may require additional management efforts to control (Corbin et al. 2012). Without dual methods of control (i.e. mammal eradication only), invasive plant species have an opportunity to increase in abundance, particularly in areas in which they were already established. Rabbits on Broughton Island fed on the fleshy fruits of *O. stricta* and spread the seeds through their droppings, spreading this plant species to the perimeter of their feeding range (Traveset et al. 2014; Hunter et al. 2021). With the combined management of rabbit removal and chemical/biological control, this pervasive weed decreased in these transect areas. It is important to note however, *O. stricta* remains a dominant and persistent weed species across sandy soil communities on Broughton Island (Hunter et al. 2021).

Broughton Island therefore experienced positive effects on vegetation community structure characteristics between 2009 and 2016, though the long-term successional benefits from the removal of rats and rabbits remain to be observed. The survey was relatively small in scale and focused on changes among a variety of micro-habitats on one 114 ha island. A real benefit to this method of post-eradication vegetation survey is the ability to define the underlying processes hindering restoration goals within small locations (Hughes et al. 2011). On the other hand, small-scale trends could be highly variable when different vegetation units are surveyed at such small scale and may confuse the representation of ecosystems as a whole (Ogden and Rejmánek 2005; Thomson et al. 2022). Additionally, no control unit was available as the entire island had been affected by rats and rabbits. Baseline vegetation quality data was not available prior to the eradication, and both of these components can make interpretation of vegetation change more challenging. Incorporating vegetation monitoring as a component in post-eradication surveys both before and after eradication will help fill the knowledge gap in how island ecosystems recover without predatory pressures exerted. Many islands continue to exist with significant populations of invasive mammals where eradication would optimise ecosystem function and promote biodiversity (Holmes et al. 2019). A deeper understanding of the recovery of complex island ecosystems to invasive mammal eradication will refine future projects and closer align conservation goals with outcomes to gain scope on ecological recovery and effectiveness of management.

5.6 Acknowledgements

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Higher Degree Research Thesis by Publication
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STATEMENT OF AUTHORS' CONTRIBUTION

We, the Research Master/PhD candidate and the candidate's Principal Supervisor, certify that all co-authors have consented to their work being included in the thesis and they have accepted the candidate's contribution as indicated in the *Statement of Originality*.

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STATEMENT OF ORIGINALITY

We, the Research Master/PhD candidate and the candidate's Principal Supervisor, certify that the following text, figures and diagrams are the candidate's original work.

Type of work	Page number/s
Figure 5-1	76
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Figure 5-5	86
Figure 5-6	87

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Chapter 6: Modelling the habitat suitability of expanding and new wedge-tailed shearwater *Ardenna pacifica* colonies on Broughton Island, New South Wales

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6.1 Abstract

Wedge-tailed shearwaters, *Ardenna pacifica,* breed on offshore islands of eastern Australia and reliably return each year on migration routes. Introduced predatory mammals on islands are one of the greatest threats to seabirds on land and have led to reduced breeding success and populations. To mitigate these threats, invasive mammal eradication and habitat restoration projects have been employed, yet subsequent surveys of seabird populations can be limited in scope and difficult to conduct. To identify patterns of surveyed colony habitat and identify unoccupied habitat, a habitat suitability model was developed for Broughton Island, an island with a dense *A. pacifica* population which has recently been subject to a successful pest eradication program. The model was created using weighted overlay analysis where environmental layers were rated by importance in nest-site selection and an output map displayed pixel values representing areas most to least suitable for *A. pacifica* habitat. The model indicated nearly 40% of the island contained highly suitable habitat and only 20% unsuitable habitat. The model was validated using existing population survey as assessment points

and showed the model was overall 72% accurate in identifying habitat. The largest contiguous areas of highly suitable habitat were populated by expanding colonies, and smaller colonies recently formed in relatively isolated, moderately suitable habitat. It is likely that newly pioneered colonies formed as a result of competition within established colonies and availability of predator-free habitat. Integrating GIS-based surveys using high resolution digital layers to model habitat suitability can be a supplementary tool to seabird conservation efforts.

6.2 Introduction

Migratory seabirds travel large distances on seasonal migration routes between breeding and non-breeding locations and many populations use offshore islands to nest. Offshore islands provide optimal habitat for breeding seabirds because of their geographic location, absence of natural predators, and proximity to pelagic food resources (Kier et al., 2009). Seabirds not only benefit from islands as safe breeding habitat, they also play important roles within terrestrial trophic systems and drive ecosystem function via the deposition of marine nutrients primarily through guano deposition (Anderson & Polis, 1999; Sánchez-Piñero & Polis, 2000; Ellis, 2005).

Wedge-tailed shearwaters (*Ardenna pacifica)* are migratory marine birds that occur across the Pacific and Indian Oceans and are commonly observed on both eastern and western coasts of Australia during Austral summer (Marchant & Higgins, 1990; Brooke, 2004). Their use of offshore islands is solely to construct burrows which may reach 2 metres long and lay one egg per season (Marchant & Higgins, 1990). Nesting season occurs during March to January until the fledging emerges in November or December (Byrd et al., 1983). Like many other seabird taxa, *A. pacifica* are a gregarious species that engage in colonial nesting. *A pacifica* have high nest-site fidelity, where most individuals return to the same burrow each year (Kharitonov & Siegel-Causey, 1988; Warham, 1990).

Colonial living is an essential part of seabird breeding ecology, and information on habitat quality, individual quality and demographic characteristics are important factors in determining where seabirds choose to nest in existing colonies (Kildaw et al., 2005). Nest-site selection is influenced by factors such as philopatry (using the same nest), natal philopatry (returning to where the individual was born) or information on habitat quality (Kildaw et al., 2005). Healthy colonies exhibit signs of high habitat suitability, safety from predators, and food availability, encouraging recruitment of new members (Forbes & Kaiser, 1994; Boulinier & Danchin, 1997). Conspecific attraction is a major determinant of why seabirds may prefer lower habitat quality within established nesting sites compared with colonizing new, uninhabited sites which are of higher suitability (Kildaw et al., 2005). For example, colonial seabirds show preference for nests in the centre of the colony but population pressure from competition for burrow sites and efficiency can weaken individual breeding success (Dyer & Hill, 1990; Carter, 1997; Hoi et al., 2006). Because of their high observed philopatry and low reproductive rate, seabirds in newly formed breeding colonies are infrequently measured or documented (Coulson, 2002; Jones, 2011; Kappes & Jones, 2014). Whether seabirds choose to stay in established colonies or form new colonies depends largely on costs and benefits determined by the health of the individual and the population as a whole (Schrieber & Burger, 2001; Kildaw et al., 2005).

Seabirds also rely on terrestrial and oceanic aspect for determining where to nest. Most colony locations are within close proximity to pelagic foraging ranges (Davoren et al. 2003). *A. pacifica* colonies are often found on steeper slopes and ridges which are beneficial for landing and take-off in prevailing winds (Pennycuick, 1982; Warham, 1990; Spear & Ainley, 1997). Soil and substrate are important habitat features for construction of burrow nests, where deeper soils with low moisture and medium strength provide both ease of excavation and sturdiness (Neil & Dyer, 1992; Carter, 1997). It is unclear the degree to which vegetation type influences nesting choice, though Bancroft et al. (2004) suggested specific site selection within a colony (e.g. centre or perimeter of colony) is more important than vegetation type. As vegetation composition is largely driven by soil biogeochemical properties, it is suggested that surface and population dynamics are the principal drivers of nest site selection (Neil & Dyer, 1992; Carter, 1997).

Like many other seabird species, *A. pacifica* have life-cycles characterized by longevity and low fecundity (laying one egg per year) and, as a result, can be vulnerable to slow population recovery when subject to disturbance and predation (Weimerskirch, 2001; Jones, 2011). Introduced mammals have created a suite of challenges for seabird breeding success and habitat quality on islands, which has led to population decline, and in some cases, local extinction (Atkinson, 1985; Towns et al., 2006). Introduced mammal species like rodents and feral cats (*Felis catus*) are particularly threatening to island biodiversity, vertebrate extinctions, and disruption of ecological function (Tershy et al., 2015; Doherty et al., 2016; Russell & Kueffer, 2019). Management of native habitat and biodiversity threats is therefore critical for supporting seabird breeding success and ecosystem function (Jones et al., 2016; Russell & Kueffer, 2019).

To mitigate the detrimental impacts to seabirds and their habitat on islands, various conservation strategies such as invasive mammal eradications, social attraction mechanisms, and habitat restoration projects have resulted in subsequent seabird repopulation and growth (Aguirre-Muñoz et al., 2011; Jones et al., 2012; Brooke et al., 2018; Herrera-Giraldo et al., 2021). Applying integrated GIS (geographic information system) techniques as supplemental tools for planning, predicting and monitoring of terrestrial occurrences provides an opportunity for higher accuracy and efficiency of resources (Borrelle et al., 2015). For example, habitat suitability models are effective in identifying relationships between species' presence and ecological parameters and can influence decisions in conservation management (Rayner et al., 2007; Troy et al., 2014; Legrand et al., 2016; Troy et al., 2017).

The aim of this study was to identify suitable nesting habitat for *A. pacifica* on Broughton Island, New South Wales, by overlaying various spatial datasets of environmental parameters. This research can provide scope on using GIS to identify areas which may be priority for conservation projects, such as habitat restoration and monitoring (Troy et al., 2017). Although the seabird population on Broughton Island has been expanding in area and population following a pest eradication in 2009, this method can be expanded similar islands in the coastal New South Wales undergoing active seabird habitat restoration.

6.3 Methods

6.3.1 Study area

Broughton Island (32.616° S, 152.314° E) is part of the Myall Lakes National Park estate and is the largest offshore island in New South Wales (Figure 6-1). The island is located 2.5 km offshore and 16 km northeast of Nelson Bay (Port Stephens) (Figure 6-1). Broughton Island experiences a subtropical climate with mild winters and warm summers, where mean annual temperatures range from a minimum of 9.2 °C and maximum 27.3 °C (BOM, 2022). Rainfall averages 1342.5 mm per year (BOM, 2022). The nearest wind database at Nelson Bay indicates that mean wind speed reaches between 12.5 – 21.7 km/hr in the spring and summer months when seabirds are present, and wind direction is predominantly north-northeast (BOM, 2022).

[redacted]

Figure 6- 1 Maps of Broughton Island, located 2.5 km from the nearest mainland point off the eastern coast of New South Wales, Australia.

Despite its size of 138 hectares, Broughton Island boasts a distinct assemblage of geological formations and soil types. The solid geology of the island includes rhyolitic rocks with basalt intrusions, conglomerates and sandstones (Thom et al., 1992). The most common soil and landscape types are defined on moderately well drained plateaued sand sheet mosaics beneath sedge and grassland communities dominated by spiny-headed mat-rush *Lomandra longifolia* and blady grass *Imperata cylindrica*. The coastline comprises sandy shorelines and foredunes, rock outcrops and steep cliffs. Drainage swamps have formed at the base of high dunes which are annually inundated (Tulau & Wilson, 2018). Endangered kangaroo grass *Themeda triandra* grasslands exist on the headlands, particularly to the east at Pinkatop Head, the highest elevated area (91 m ASL) (Hunter, 2018). It is postulated that the island contained more woody, littoral rainforest species but through the use of fire by both Aboriginal and European peoples, and the introduction of plants and animals, the current vegetation cover on the island has changed to be comprised predominantly of grasses and sedges (Dodkin, 1981).

Breeding *A. pacifica* colonies are abundant on the island beginning in August when adults return from their annual migration route to clean burrows and form pairs, and remain until early May when chicks fledge. Wedge-tailed shearwaters are the most abundant seabird species on Broughton Island. In a population survey conducted in 2009, there were estimated to be over 55,000 breeding pairs (Carlile et al., 2012). The most widespread and dense populations are located on both high aeolian sand dune systems. A decade after the successful eradication of rats and rabbits, the area which seabirds have colonised has expanded and total population estimated to have increased to 64,500 breeding pairs (Carlile et al., 2022).

6.3.2 Data acquisition and pre-processing

To acquire datasets necessary for the model, each environmental layer was selected to satisfy as many environmental parameters *A. pacifica* encounter during all phases and activities of breeding and with the advantage of use of existing spatial datasets. Elevation, slope and aspect were obtained from a digital elevation model (DEM) at 2 m resolution. Slope and aspect layers were derived from the DEM by using spatial analyst tools from ESRI ArcGIS 10.6.1. Wind speed and directional data were obtained from the Australian Government Bureau of Meteorology (BOM) station in Nelson Bay for 2000-2021 and adjusted to Austral spring, the season in which *A. pacifica* arrive for breeding. Due to the low resolution of the extrapolated pixel values (n=2 pixels to cover the area of Broughton Island), wind speed and direction were not used as factors in analysis. Vegetation vector layers were obtained from the New South Wales National Parks and Wildlife Service (NSW NPWS) from surveys conducted in 2018 where vegetation community zones were mapped and described (Somerville, 2019). Soil layers were obtained from the New South Wales Department of Planning and Environment (Tulau & Wilson, 2018) where each soil area was categorized on the basis of its parent material and general formation, texture, drainage and associated vegetation community. Buildings and public trail vector layers were created using aerial images from Google Earth to identify locations and create features. Distance from buildings and public trails were generated using ESRI Euclidean distance tool to measure the distance from every cell and converted into an output raster. All spatial layers were rasterized and snapped to 2 m resolution and spatial extent, and were projected to coordinate reference system GDA 1994 MGA Zone 56.

6.3.3 Weighted overlay analysis and model validation

The model was created during July of 2022. Decision-making criteria for environmental layers and their contribution to the model were based upon literature on *A. pacifica* breeding behavioural ecology, nest-site selection, flight and foraging patterns along with advice from local field rangers. Soil and vegetation layers were classified as the most suitable in areas least likely to be inundated with rainfall and in soil types which are easy to construct yet sturdy enough to keep burrows in form. Elevation and slope were of the most importance because of flight and foraging patterns and distance above sea level. Pixel values from every layer were re-classified from least suitable to most suitable from 1 to 3. Each classified layer was put into the weighted overlay analysis where influence (%) was incorporated in computation of the final output suitability map (Table 6-1). The suitability model was built using Model Builder tool in ArcGIS 10.6.1 (ESRI 2018) (Figure 6-2).

Table 6-1 Environmental variables used in the weighted overlay analysis and their data sources.

Variable	Influence	Least favourable	Moderately favourable	Most favourable	Source
	(%)	(1)	(2)	(3)	
Soil type	40	Poorly drained peats and sand sheets, shallow soils (<50 cm), rock outcrops, rocky headlands, cliffs, sandy beaches	Moderately well drained sand sheets	Dunal sands and well drained sand sheets	Tulau & Wilson, 2018
Vegetation community	30	Wetland, swamp and soak communities, bare rock	Sedgeland and foredune grasslands	Fern and coastal grasslands, coastal shrublands	NPWS, 2018
Elevation (m)	10	0-5	5-10, 40-70, 70-91	10-40	2 m DEM
Slope (°)	5	0-5, 55-90	5-20, 45-55	20-45	2 m DEM
Aspect	5	-	North, northeast, northwest, east, south	Southwest, southeast, west	2 m DEM
Distance to trails (m)	5	0-1	1-4	4- max	NPWS trail map
Distance to buildings (m)	5	0-5	5-15	15- max	NPWS aerial image

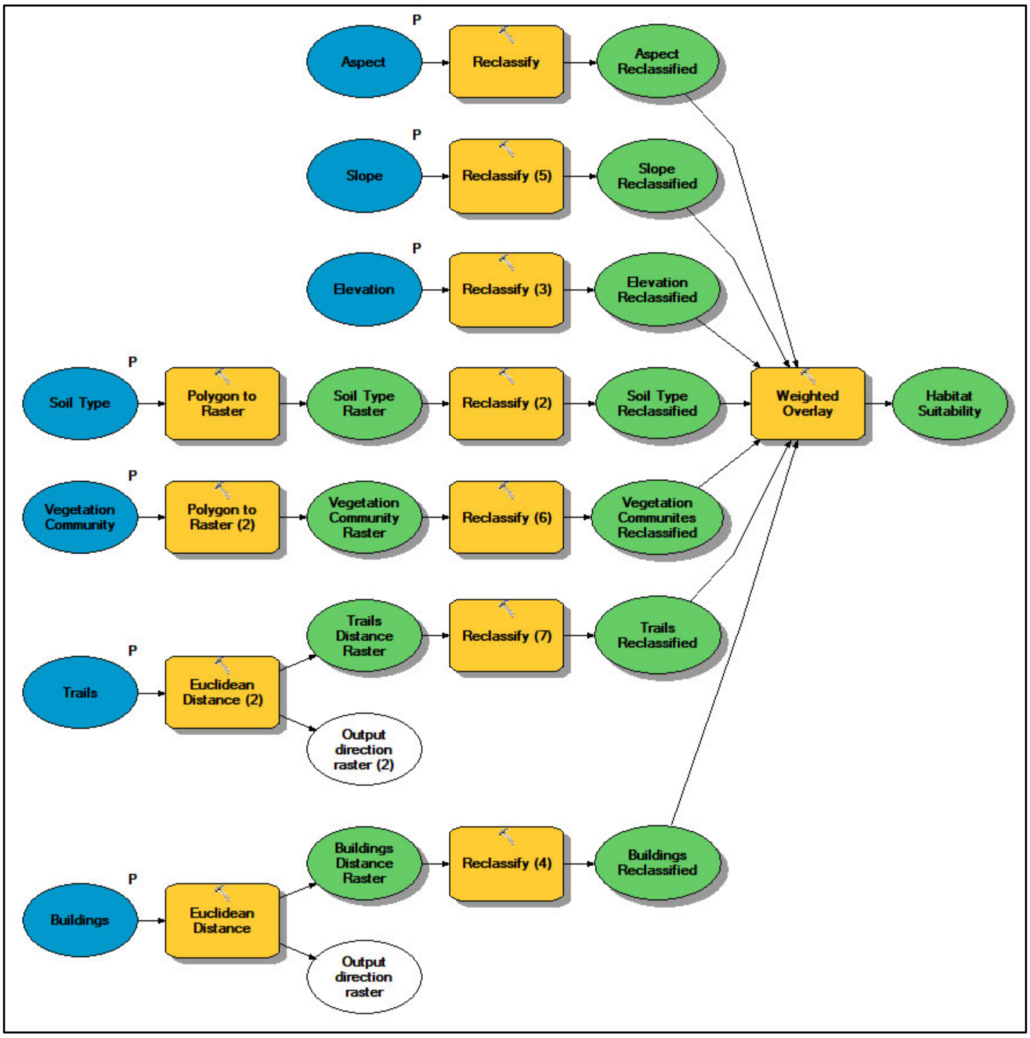

Figure 6-2 Weighted overlay geoprocessing model design for habitat suitability analysis. The 'blue' colour represents different input layers with P indicating model parameters; 'yellow' as geoprocessing task performed; and 'green' as model outcome after each task.

To determine the accuracy of the model, a confusion matrix was used which produced metrics on classified and observed values. The observational data available for this assessment was derived from an *A. pacifica* colony boundary map from 2018 by Carlile et al. (2022). The assessment itself was difficult to conduct due to limited ground truth information (i.e. species presence was only information for areas of high suitability). To run the assessment, three model derived suitability categories (unsuitable, medium and highly suitable) were reclassified into two categories: unsuitable (which combined unsuitable and moderately suitable

classes) and highly suitable. For post-classification accuracy assessments, a 1000 stratified ground truth samples were created, equally distributed within the unsuitable/highly suitable classes. Suitable points were within the mapped colony boundaries by Carlile et al. (2022), and unsuitable points were in the areas with no colonies mapped. The reference points were then compared with the classification results at the same locations and a 2x2 confusion matrix was produced. The accuracy parameters included a producer's accuracy (PA), which indicates the reference points correctly categorised compared to the model's user's accuracy (UA), which indicates how much of the model agrees with reference points correctly categorised, an overall accuracy (OA) and a Kappa coefficients (K).

6.4 Results

The spatial distribution individual reclassified environmental layers are displayed in Figure 6-3, which were used in the weighted overlay analysis for habitat suitability modelling. In the soil suitability layer, the highest suitable areas were defined by well drained soils to high sandy dunes and the suitability class covered a large proportion of the island. Least suitable soils were from shallow soils on rocky substrates with low suitability on the east of the island, and the surrounding beaches and cliffs on the perimeter of the island (Figure 6-3.A). Highly suitable vegetation communities were defined by sedge and grass plant species (Figure 6-3.B). Unsuitable areas were defined by drainage swamps with water tolerant or partially water tolerant plant communities (Figure 6-3.A). A majority of the island fell within suitable elevation above sea level, where unsuitable areas included steep cliffs at the highest edges of the island (Figure 6-3.C). Unsuitable slope areas were located on steep cliffs greater than 70 degrees as well as flatlands and coastal beaches, surrounding much of the perimeter and inner areas of the island (Figure 6-3 D).

Figure 6-3 Habitat suitability layers for *Ardenna pacifica* (A-G) of soil, vegetation, elevation (m ASL), slope (°), aspect, distance to public trails (m) and distance to buildings (m), respectively.

The final output of habitat suitability map showed nearly 80% of the island to be suitable habitat for *A. pacifica* colonies, where 41.0% (53.7 ha) was classified moderately suitable and 38.75% (56.8 ha) highly suitable (Figure 6-4). Least suitable areas accounted for only 20.25% (28.1 ha) of the total terrestrial cover, on many of the steep cliffs, beaches at sea level and areas partially inundated with water. Areas with highest suitability fell within areas with rapidly and moderately well-drained soils. The largest contiguous areas for high suitability were located on two high dunes ranging from 10–30 m with northwest and south eastern facing slopes.

Figure 6-4 Habitat suitability ratings from not suitable to highly suitable for *Ardenna pacifica*, generated from a weighted overlay analysis of environmental factors. Astrisks denote areas of dense colonies on two aeolian dune systems.

The colony survey locations from Carlile et al. (2022) validated the accuracy of the model output based on established colonies residing on the areas of highest habitat suitability, as well as newly pioneered colonies existing on suitable habitat (Figure 6-5). The overall accuracy of the model was 72%, indicating good agreement between the predicted suitability values from the model and true values from seabird colony surveys (Table 6-2). However, the kappa value (0.43) was low, which indicated a more random classification. As no reference ground truth data were available for moderately suitable class, the sample points for moderately suitable areas were classified as unsuitable. This has reduced the overall model accuracy.

[redacted]

Figure 6- 5 Accuracy assessment points of highly suitable and unsuitable (moderately + unsuitable) areas for *Ardenna pacifica* on Broughton Island. Green points represent the occurrence points categorised as highly suitable, derived from areas mapped by Carlile et al. (2022). Red points represent non-occurrence points categorised as unsuitable. Highly suitable habitat determined from weighted overlay analysis is blue area.

Table 6-2 Confusion matrix of colony points within predicted classes of suitability.

Ground truth	**Unsuitable**	**Suitable**	**Total**
Classified as			
Unsuitable	361	146	507
Suitable	139	354	493
Total	500	500	1000
Producer accuracy (%)	72.3	71.0	
User accuracy (%)	71.2	72.0	
Overall classification accuracy (%)	72.0		
Kappa value	0.43		

Newly formed colonies occur on model derived moderately suitable areas excluding the colony to the western side of the island which occurs in highly suitable area (Figure 6-6). On the eastern side of the island, these colonies are located on *T. triandra* grassland communities with shallow loamy and volcanic soils (Tulau & Wilson, 2018). They are on steep slopes and at higher elevation compared with existing colonies. Colonies were in close proximity to higher suitable land; however, they appear to be isolated from existing populations (Figure 6-6). Unoccupied areas of highly suitable habitat occur on adjacent areas to existing colonies, particularly on sand sheets with sedge and grassland mosaics (Figure 6-6).

Figure 6- 6 Habitat suitability map of *Ardenna pacifica* on Broughton Island. Occurrence points are derived from Carlile et al. (2022), where circle represent existing colonies and red triangles represent new colonies.

6.5 Discussion

The habitat suitability model successfully indicated areas most suitable, moderately suitable, and least suitable to *A. pacifica* breeding colonies on Broughton Island by using weighted overlay analysis in GIS. Most of the island was suitable for breeding habitat and a majority of observational points fell within highly suitable habitat, which showed good model prediction accuracy. The results supported the optimal model design with thorough investigation of environmental factors and decisions on relative importance of each input parameter that contributed to preference for nesting site selection. There still however were occurrence points that fell within moderately suitable areas as well as non-occurrence points which fell into highly suitable habitat, which reduced the model accuracy. This model could be improved by having more ground truth data defining highly, moderate, and unsuitable habitats.

The model, when compared to occurrence points, showed a large patch of unoccupied space with highly suitable habitat. Broughton Island has experienced an increase in *A. pacifica* population since the eradication of mice and rabbits via expansion of existing colonies and forming new colonies (Carlile et al., 2022). The increase in colonised habitat from seabirds has been attributed to successful removal of invasive predatory mammals and has been similarly observed on islands around the world (Priddel et al., 2011; Jones et al., 2016). It is possible that vacant habitat may be colonised on the outer margins of existing colonies in highly suitable habitat if rate of immigration increases, conspecific attraction persists and quality of individual species fitness appears high (Forbes & Kaiser, 1994).

Despite the model showing vacant highly suitable habitat, smaller colonies formed in moderate to high quality habitat separate from existing colonies. There are a few possible explanations as to why the habitat may not appear suitable to seabirds (potentially inexperienced birds), or why newly recruited seabirds may have formed new colonies. Existing colonies with high densities can decrease breeding success due to over-crowding and competition (Carter, 1997; Schumann et al., 2013). It is possible that over-crowding within individual nests facilitated individuals to colonise new suitable habitat areas. For example, Carlile et al., (2022) demonstrated that while colonized area increased on Broughton Island, individual density had decreased. This suggests that one or a combination of factors made the benefits of colonising new areas outweigh the risk of nesting in an established colony. Habitat quality information may vary temporally and influence immigration to new colonies (Oro & Ruxton, 2001).

It is unclear what caused the movement of *A. pacifica* to new colony sites or if they are inexperienced birds. Although the risk of forming new colonies can deter individuals from nesting and facilitate the migration to new colonies, once formed, such colonies often expand at a rapid rate (Kildaw et al., 2005; Brooke et al., 2018). Newer seabird colonies could potentially continue to develop and expand if they have reproductive success. Due to the complex nature of seabirds' long-life cycles and low reproductive rate, it is difficult to document population and demographic trends of seabirds (Weimerskirch, 2001). Further monitoring of population density and area of colonisation is needed to determine if new immigration colonies will transition to continued natal recruitment and philopatry (Dunlop & Goldberg, 1999). *A. pacifica* reach sexual maturity between three to five years, a delay in population density on newly formed colonies is expected (Byrd, Moriarty & Brady, 1983). Seabird populations can also be compromised by various external phenomena such as climate change, related to oceanic warming and El Niño-Southern Oscillation (ENSO) cycles disrupting oceanic productivity and therefore prey availability and foraging patterns (MacArthur & Wilson, 1967; Wang & Fiedler 2006; Bost et al., 2009; Buxton et al., 2014).

Identifying suitable habitats for seabirds at a local level can help managers anticipate where a) new colonies may form and b) existing colonies may expand. Moreover, allocating resources to these areas for encouragement of breeding success will further fulfil management and conservation goals. Understanding global seabird behavioural patterns is necessary for conservation of seabird species and their habitats. The restoration of seabird colonies is necessary to facilitate the functioning of island systems because their role in nutrient subsidies and engineering is so significant (Croll et al., 2005; Croll et al., 2016). Employing habitat suitability modelling on relatively small spatial scales presents an opportunity for land managers to map critical locations at a finer scale. The habitat suitability modelling and the integration of multiple environmental factors in this study support the usefulness of spatial modelling applications in seabird conservation (Lavers et al., 2010). The tool can be used to identify patterns and trends of existing species distribution, and also inform managers about the locations of potential unoccupied habitat. For instance, the results from this study suggest the map is 72% accurate at determining where highly suitable habitat occurs on the island. The method can provide a cost-effective, robust method of habitat modeling.

6.6 Acknowledgements

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STATEMENT OF AUTHORS' CONTRIBUTION

We, the Research Master/PhD candidate and the candidate's Principal Supervisor, certify that all co-authors have consented to their work being included in the thesis and they have accepted the candidate's contribution as indicated in the *Statement of Originality*.

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STATEMENT OF ORIGINALITY

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Chapter 7: MaxEnt modelling for predicting suitable breeding habitat of Wedge-tailed shearwater colonies on Broughton Island, Australia

7.1 Abstract

Habitat conservation is critical to the success of breeding seabirds under threat, and machine learning approaches to assessing habitat suitability is a useful tool to optimise conservation strategies. Broughton Island, a nearshore island off the coast of New South Wales (130 ha) experienced an invasive mammal eradication in efforts to restore native ecological function and seabird breeding success. A maximum entropy model (MaxEnt) was used to determine areas most suitable for wedge-tailed shearwater habitat by inputting environmental spatial layers including soil and vegetation type, elevation and slope. The results of the model were also used to identify potential unoccupied areas of suitable habitat, and assess the terrestrial traits important to breeding colonies and nest-site selection. The model showed good accuracy with AUC of 0.80 ± 0.02. Areas with the highest suitability were occupied by the largest existing colonies and defined by high sloping dunes with well drained sands and mosaics of fernland and grasslands. Medium-high to medium suitable habitat extended adjacent to occupied areas with high suitability. Areas on the Eastern side of the island showed low suitability with three small colonies exist, and factors not included in the model such as behavioural traits or microclimate could potentially explain this result. This MaxEnt model corroborates similar findings from a habitat suitability model made using GIS which showed habitat preferences to soil and vegetation communities are more important factors in habitat selection than some physical terrestrial features like elevation, slope and aspect. Assessing habitat suitability by integrating multiple data layers can aid in ecological decision making by

identifying species-and-site-specific habitat niches to identify priority conservation areas.. A broader scope to this research can be extended to other islands in the region undergoing post-eradication habitat monitoring.

7.2 Introduction

The offshore islands of New South Wales are globally important areas for migratory seabirds. Wedge-tailed shearwaters (*Ardenna pacifica*) annually migrate from the northern pacific and utilize offshore islands off the coast of Australia to nest, lay eggs, and raise chicks (Marchant & Higgins 1990). Wedge-tailed shearwaters (hereafter WTSW) are among seabird species with strong nest fidelity and colonial nesting behaviour, so habitat quality has a large effect on breeding success (Forbes & Kaiser 1994; Danchin 1998; Bried & Jouvetin 2002). Habitat features including local food availability, predator avoidance, soil strength and vegetation type for sturdy burrow construction, and topography for takeoff and landing are important to seabird nest-site selection (Neil & Dyer, 1992; Carter, 1997; Schumann 2013). Nesting seabirds are integral to island ecosystem function, as nutrient subsidies via guano significantly enhance the productivity of terrestrial and marine biotic communities (Fukami et al. 2006; Graham 2018). Conserving seabird habitat on islands is therefore critical to the success of breeding seabird populations and maintaining ecosystem services from nesting activities (Tershy et al. 2015; Holmes et al. 2019).

Island ecosystems are globally threatened by a suite of impacts including biodiversity loss from the introduction of invasive plants and animals (Spatz et al. 2017b). Island species are particularly vulnerable to disturbance compared to mainland areas because they serve as niche habitat for many highly specialised, endemic and threatened species (Myers et al., 2000; Kier et al., 2009). Invasive mammals are among the greatest threat to seabird survival due to predation and habitat modification and their presence is attributed to seabird population decline and both local and global extinction (Blackburn et al. 2004; Jones et al. 2008; Dias et al. 2019). In fact, at least 70% of global seabird populations have declined since 1950 as a consequence of threats both at sea and on land (Croxall et al. 2012; Paleczny et al. 2015). Seabird population surveys following mammal eradications have demonstrated the successful recovery of seabird populations, however passive recovery of seabirds is less predictable than integrating additional interventions to enhance restoration success (Kappes & Jones, 2014; Spatz et al. 2017b; Brooke et al., 2018).

Species distribution models (SDM) are a tool which can assist in predicting potential colonisations and extinctions of a species in an environment (Venne & Currie 2021). Machine learning approaches to ecological models like maximum entropy models (MaxEnt) are increasingly popular in the field of ecology and are useful in predicting geographic distributions and habitat niches (Elith et al. 2006; Qazi et al. 2022). Species distribution models (SDMs) correlate species occurrences with environmental characteristic and can quantify the relationships of species distribution with present and future scenarios (Peterson et al. 2011). Many seabird species behaviours remain poorly understood and the identification of key aspects of seabird ecology and mechanisms of nest-site selection can assist in developing and applying measures of conservation (Rodríguez et al. 2019). By using SDMs to identify suitable habitat, conservation benefits are optimized by the output of locating priority areas for species protection.

This study utilized population surveys conducted in recent years to include in a habitat suitability model using MaxEnt software (Phillips et al. 2022). This technique takes a multifaceted approach, collating real time and environmental data that can be used to identify geographical areas to conserve where a species may occur. The integration of data analysis and expert environmental surveys can produce strong results which support robust decision making by managers to achieve optimal conservation goals (Guisan et al. 2013; Miller et al. 2019). Invasive mammal eradications on Australian islands have encouraged recovery of nesting seabird colonies, but the trajectory of demographic changes following population recovery is largely unknown. Increasing the knowledge of habitat and nesting preferences of seabirds will enhance conservation actions (Rodríguez et al. 2019).

In this study we utilise MaxEnt to model the suitability of habitat for WTSW on Broughton Island to (a) elucidate the environmental characteristics associated with their preferential breeding habitat and (b) identify uninhabited areas of suitable habitat which can be shared with managers to prioritize habitat conservation in these areas. The output of the model was used to assess the relationship between spatial distribution of nesting colonies and environmental characteristics, underpin the topographic mechanisms of nest-site selection, and to identify potential unoccupied habitat where populations may expand. Areas located from the model output can be used by land managers to identify high priority areas for WTSW conservation.

7.3 Methods

7.3.1 Site Description

Broughton Island (32.616° S, 152.314° E) is the largest offshore Island in New South Wales (NSW) and is part of the Myall Lakes National Park in NSW, Australia (Figure 7-1). There are no permanent residents on the island and structures are limited to a small number of fisher huts and a camping platform on a southern beach. The island is primarily vegetated by grass, fern, and sedgeland with sand sheets and sand dunes

(Somerville et al., 2018; Tulau & Wilson, 2018). The island also has sandy beaches and rocky cliffs and headlands, reaching 91 m above sea level (ASL) at its highest point. Prior to becoming part of the National Park estate in 1972, Broughton Island experienced a range of disturbance from frequent burning and introduction of feral animals including rats, mice and rabbits (Carlile et al., 2012). These disturbances resulted in negative impacts on native vegetation and resident seabirds including supressed seabird breeding success from predation (Priddel et al. 2011). Invasive mammals were successfully eradicated and the island was declared free of rats and rabbits in 2009 and seabird population projects have continued subsequently (Priddel et al. 2011; Carlile et al. 2012). At present, WTSW are the most common seabird nesting on Broughton Island and the most recent survey conducted in 2018 estimated 64,500 breeding pairs assuming 50% burrow occupancy (Carlile et al., 2022).

[redacted]

Figure 7- 1 Map of Broughton Island, located approximately 14 km from Port Stephens, New South Wales, Australia.

7.3.2 Data acquisition and processing

Species occurrence records of WTSW were sourced from survey data collected by Carlile et al. (2022) which described colony boundaries across the island. The areas of the colonies were populated with points using ArcGIS software to represent occurrence points with a minimum distance of 2m to avoid pseudo-replication. A total of 1,000 random points were generated within the polygon colony across the island where active seabird colonies exist. These were used as occurrence points of WTSW on Broughton Island for the base MaxEnt model.

Environmental variables selected for the model were selected based upon relevance to seabird nest-site selection and data availability. Elevation was sourced from a digital elevation model (DEM) at 2m resolution. Slope (degrees) and aspect (degrees) were derived from the DEM (Figure 7-2.A and 7-2.B). The soil type spatial dataset was derived from Tulau & Wilson (2018) which described 8 soil types across the island (Figure 7-2.C). Vegetation classes were derived from a vegetation survey conducted by NPWS which described 19 unique vegetation communities (Somerville et al., 2018). Classes were consolidated to 8 classes with similar traits in dominant vegetation (e.g. grassland, fernland, sedgeland) (Figure 7-2.D). Due to the small size of the island, variables like wind and temperature, while acknowledged to be likely contributors to seabird nest site selection, were excluded due to limited data resolution across the island. Each environmental layer was snapped to 2m resolution using the DEM and projected to coordinates GDA MGA Zone 56.

[redacted]

Figure 7-2 Final input layers for the MaxEnt model A. elevation B. Slope (°), C. Soil type (derived from Tulau & Wilson 2018), and D. vegetation communities (derived from Sommerville et al. 2018).

7.3.3 Species distribution model

To avoid overfitting the model and to increase the precision of results, collinearity was checked between all variables using the *ENMTools* package (Warren et al. 2022). No variables were found to be significantly correlated so they remained in the base model. To determine MaxEnt feature settings for the best model fit and complexity, *ENMeval* package version 2.0.2 (Kass et al. 2021) was used in R version 6.1 (R Core Team, 2022) and Rstudio (Rstudio Team 2022). This package runs all possible combinations of user-defined settings and produces Akaike information criterion corrected for small sample size (AICc) values which were used to determine the optimal feature settings and regularization multiplier.

The habitat suitability model was created using MaxEnt software version 3.4.4 (Phillips et al. 2022). The base model was initially run with all variables, but aspect achieved only a very low percent contribution (<1) and permutation importance (1.7), therefore it was removed from the model in the subsequent run. Because the entire island was surveyed for WTSW, a bias file was not considered necessary to the model. The model was evaluated with 10-fold cross-validation replicates using 10,000 background points. Model performance was assessed using the area under curve (AUC) of the receiver operating characteristics (ROC) (Elith et al. 2006). The AUC ranges from 0 to 1, where values >0.9 show excellent model performance and values <0.5 are termed insufficient (Swets 1988; Thuiller et al. 2005). Response curves were assessed to elucidate relationships between predicted species presence and environmental variables. The jackknife test was selected as an output of the model for alternative estimates of variable contribution importance in predicting the distribution of WTSW.

7.4 Results

The feature selection in MaxEnt was done on the basis of delta AICc of 0, which was linear, quadratic, hinge and product features with a regularisation multiplier of 1. The output of the final run had an area under curve (AUC) of the receiver-operator characteristic (ROC) curve was 0.80 ± 0.019 standard deviation, indicating good accuracy of the model. High AUC values indicated reliability of model predictions, suggesting the optimal selection of variables in this model led to good prediction results.

The output of importance of predictor variables to the MaxEnt model showed soil and vegetation were proportionally greater in influence, contributing 50.8% and

29.9%, respectively, to the distribution model (Table 7-1). Elevation also influenced the model, contributing 13%. Slope was the least important factor in WTSW habitat with 6.2% contribution to the model. Models based on the contributions of the environmental variables showed that soil (56.2%) and vegetation (36%) had the greatest impact, following with elevation (5.4%) and slope (2.4%) (Table 7-1).

Table 7-1 Percent contribution and permutation importance of all predictor variables used in the MaxEnt model. Permutation importance shows the variable contribution from the training points from each predictor while all others are held constant. Percent contribution is calculated based on the path the MaxEnt code used to achieve the optimal solution.

Variable	Percent contribution (%)	Permutation importance
Soil	56.2	50.8
Vegetation	36.0	29.9
Elevation	5.4	13
Slope	2.4	6.2

The model’s jackknife test of variable importance showed soil had the highest test gain when used in isolation and decreases the gain the most when it is omitted from the model (Figure 7-3). This indicates soil had the most useful information in the model that was not present in other variables, and was the most important predictor of WTSW habitat distribution. The jacknife test also showed considerable change in vegetation and elevation when these variables were used in isolation (Figure 7-3). Slope had the lowest and moderate gain when used in isolation (Figure 7-3).

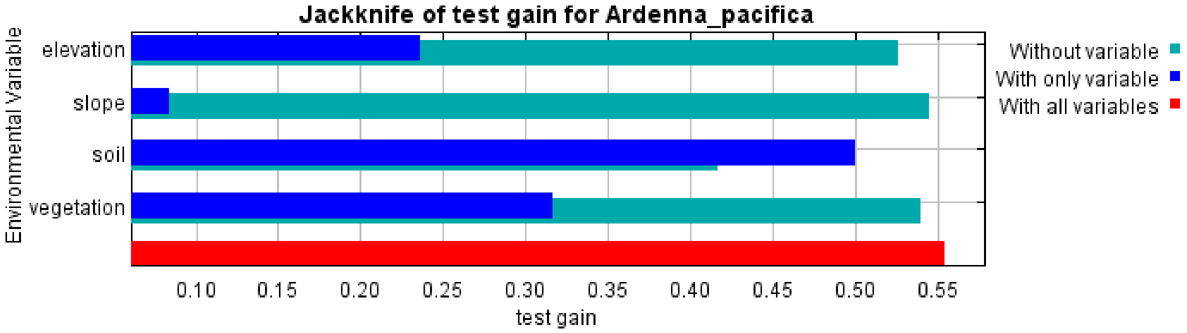

Figure 7-3 Jackknife plots of test gain for relative importance of each variable in the MaxEnt model.

Several soil types were found suitable for WTSW habitat, each of which consisted of sandy soils from foredunes, high dunes and sand sheets (Figure 7-4). The soil types with the lowest predicted suitability included peats, shallow soils, and rocky headlands and cliffs. Vegetation communities which had the highest predicted suitability included a range of shrubland, grassland, forest, and fern/grass mosaics. The predicted suitability for elevation was highest within the range 11m- 24m ASL, where unsuitable predicted elevation was below 5 m and above 40 m ASL. The predicted suitability for slope was relatively flat and was between the range of 4.5° and 12°, and had the lowest slope suitability of all values > 40° (Figure 7-4).

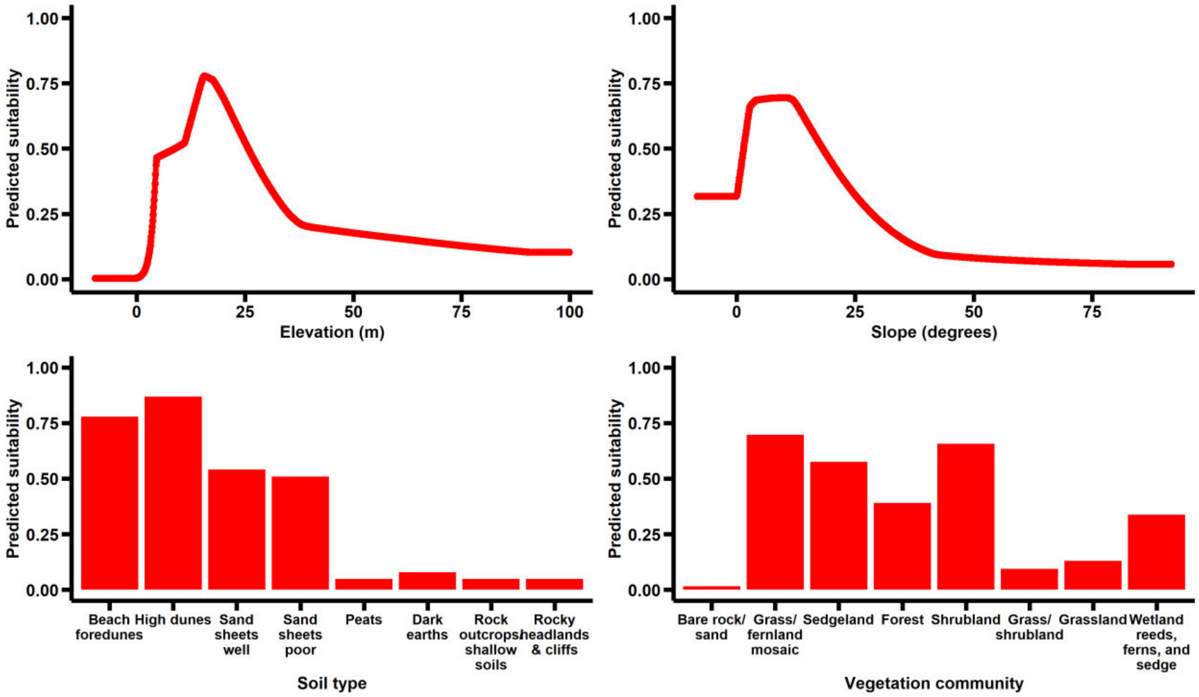

Figure 7- 4 Response curves of mean logistic prediction from 10 replicate runs from each variable while other variables remain constant.

Areas which had the highest suitability were located on high dune systems with fernland mosaic on the sloping sandy dunes in the central sections of the island (Figure 7-5). All areas of highest suitability for WTSW were occupied and these colonies extends to contiguous areas with medium-high suitability predominately on lower elevated and sloping sand sheet landscapes (Figure 7-5). Areas with medium to medium-high suitability were vacant on the central eastern and western sides of the island. Three colony areas on the eastern side of the island were located on areas with lower suitability, these areas are generally associated with volcanic soils scattered with elevated headlands dominated by *Themeda triandra* grassland. The outer perimeter of most of the island had the lowest suitability for WTSW, and these areas are largely defined by elevated rocky cliffs on the southern and eastern edges, and rocky/sandy beaches on much of the northern stretch of land (Figure 7-5).

[redacted]

Figure 7- 5 Habitat suitability index for wedge-tailed shearwaters on Broughton Island. Occurrence points are active nesting locations surveyed by Carlile et al. (2022) used for the distribution modelling. Areas of high suitability occur in red, areas of moderate suitability are in yellow, and areas of low suitability are in blue.

7.5 Discussion

Our results elucidated the most important topographical features for the distribution of WTSW based on the MaxEnt model. Soil type had the highest test gain when used in isolation and included the most useful information and importance to the model. The choice of seabirds for habitat type as soil is most important in habitat selection, is most likely because they rely on ease of excavation and strength in soil to maintain integrity of the burrow (Warham 1990; Neil & Dyer 1992). Vegetation type was an important factor in the model as well, and within-island seabird colonies have historically been categorised by vegetation community (Floyd & Swanson 1983). It is unclear the degree to which vegetation over soil is important in nest-site selection, but rather a combination of these factors (Pagenaud et al. 2022). For example, burrow nesting seabirds modify plant material through physically trampling and digging into the soil to construct nests (Bancroft et al. 2005; Ellis et al. 2011). Vegetation therefore may be important because the seabirds themselves are modulating the vegetation, making vegetation and seabird disturbance co-variates.

Mostly suitable elevations for species distribution occurred along most of the inland terrain and highly elevated coastlines had lower suitability. Slope was not an important contributing variable to the model nor did it show importance in the distribution of WTSW on Broughton Island. This was a surprising result because WTSW commonly rely on relative wind on slopes and ridges for take-off and landing (Warham 1977; Warham 1990). Steep slopes are also utilized from seabirds as a means of predator avoidance (Eveillard-Buchoux & Beninger 2022). Deep, well-drained and well-structured soils like dunes and sand sheets can maintain integrity of burrows (Marchant & Higgins 1990).

The most suitable areas for WTSW nesting on Broughton Island were already occupied by existing colonies. Colonies on the two large central dunes had been documented initially by Lane (1976). The expansion and continuation of active colonies on these landscapes indicate high suitability and favourability of both high dunes from WTSW (Danchin et al. 1998; Doligez et al 2003). The results from Maxent software confirm the results of Garrard et al. (2022), where a weighted overlay analysis was done using GIS and manually giving weighed importance percentages to each layer in terms of importance for nest site selection. The MaxEnt output map identified vacant habitat in medium suitable areas, confirming our hypothesis that suitable habitat for WTSW exists on Broughton Island. Carlile et al. (2022) described area of colonised land has increased between 2009 and 2018. If trends of WTSW expansion continue we expect areas with medium suitability may populate, particularly those adjacent to the two central dunes with highest suitability.

Assessing and predicting population trends of seabirds can be complex, and many interacting variables are at play after a predator is removed (Paleczny et al. 2015; Buxton et al. 2014). Colonies which are located in areas with low suitability according to the MaxEnt model and their occurrence in these locations may be explained by an external variable. Nest-site selection of seabirds on islands is also influenced by population dynamics (Schippers et al. 2009) such as conspecific attraction and quality of individuals within the colony (Kildaw et al. 2005), and offshore pressures such as food availability or climate variability (Smithers et al. 2003; Virgili et al. 2017). Additional offshore threats remain impacting seabird populations and range occurrence out of the control of land management such as pollution and bycatch (Chambers et al. 2011; Gorta et al. 2018; Dias et al. 2019). Hence, other variables such as metapopulation information, local and offshore climate data may be contributing factors to nesting distribution in areas unsuitable to this topographic model, and would be useful to consider other variables to future species distribution models. Expanding this work to a broader geographic range would require a lower resolution of topographic variables (e.g. soil and vegetation) but in exchange would allow for climatic variables (e.g. mean annual temperature, precipitation, etc.) and would provide more robust results in current and future projections of seabird distribution.

We have demonstrated the integration of seabird surveys and habitat modelling using various environmental data to identify WTSW habitat suitability and probability of occurrence on Broughton Island. The results also helped to better understand the environmental characteristics which are desirable to a species, and to predict the potential for species occurrences and distributions (Elith et al. 2011). Integration of data sources from ground surveys and habitat suitability models alike can help maximize conservation gains, and support funding opportunities for practitioners. Incorporating machine learning techniques like MaxEnt modelling to seabird conservation actions will optimize outcomes by identifying species-specific features of habitat and areas of high priority for seabird habitat (Rodriguez et al. 2019).

Chapter 8: Summary of Conclusions

The work presented in this thesis demonstrates a multi-faceted approach to elucidating ecological processes of seabird islands through the lenses of soils, plants, habitat features and environmental change. The integration of techniques required for these approaches (field surveys, analytical chemistry, geospatial analyses) provided a range of approaches to extend our understanding of the complex variables responsible for ecosystem function and the outcomes were novel and robust. The result of this work is important, in that it has shown the diverse effects of seabirds on their environment, and demonstrated how to anticipate ecological behaviour in a changing environment by quantifying these changes. Furthermore, novel insights were revealed into the behaviour of soil chemistry in sandy ecosystems which have not documented in the literature before, filling a significant knowledge gap with respect to seabird island ecology. The research into the themes and conclusions generated have real-world value, having applications relating to seabird habitat and landscape preservation, and can be used as a reference for islands with similar ecological conditions and overarching conservation goals. In the sections below, the general conclusions from each chapter are discussed, as well as the limitations of this research and proposed future research directions in the field.

8.1 Soils

Seabirds play an important role in the cycling of C, N and P in terrestrial ecosystems, however the mechanisms which control the spatial distribution have not been well understood, and were a key factor guiding the framework of the research presented in this thesis (Otero et al. 2018; Doughty et al. 2020). As a result of this research aim, Chapters 3 and 4 generated novel insights into the distribution and movement of soil N and P which were in contrast to many papers describing seabird colony soils enriched with N and P elsewhere. Previous work on seabird colony soils has been on shallow and rocky substrates, but Chapters 3 and 4 demonstrated how seabird colony areas had lower surface soil nutrient concentration as a consequence of burrowing, soil type, topography, surface disturbance and sub-surface soil processes. Nutrient subsidies had however resulted in high nutrient values in soils downslope, indicating the impacts of seabird on the wider ecosystem, affecting all levels of the trophic system. The results suggested impacts from nutrient subsidies from guano deposits are found in greatest abundance downslope from areas with freely drianed soils, to low areas with poorly drained soils and closer to water tables. This research is therefore the first to describe in detail how burrowing seabirds on islands with deep and sandy soils in a subtropical climate, affect their environment, thereby giving new insights into the mechanisms driving ecosystem function and the management implications for such islands.

Considering landscape type and topography as a key pathway for seabird nutrient cycling and distribution is an important part of planning and management for predicting patterns of plant productivity, carbon sequestration, and nutrient losses. The response of soils and plants was demonstrated to differ directly within a colony to downslope and surrounding regions. This result illustrates how seabird nutrient subsidies are spread on surface and subsurface spatial gradients, enriching soils without direct seabird colonies. It is now understood how incorporation of soils data is essential to fully examine and understand environmental impact and fate of guano-derived nutrients in different systems.

Stable isotope analysis was an integral part of this research and the results will contribute to the growing knowledge of using these values to trace seabird impacts and the fate and behaviour of seabird nutrient subsidies in terrestrial ecosystems. Though seabird islands may take several decades to significantly recover from the inhibition of seabird nutrient subsidies on the environment from invasive species, the monitoring of soil nutrient distribution and stable isotope abundance are effective strategies to better understand drivers of ecosystem function (Jones 2010). By assessing signatures of $\delta^{15}N$, the nutrients in and around seabird colonies determined to be largely derived from seabird (marine) sources, and confirmed seabird derived inputs as a significant source of nutrient delivered to downslope areas of accumulation on large dune systems. Stable isotope analysis allowed for a more sophisticated and accurate assessment of the source of N and transformations of N as it was cycled through the soil systems. Results suggest that nitrogen in seabird colonies is largely derived from marine sources but that its burial and presumably leaching in the sub-soil is the most significant process in these systems resulting in enrichment with marine N at lower, inflow parts of the landscape. The results found through carbon isotopes were less conclusive. Although there was some indication of marine derived C in these systems, the potential confounding inputs from terrestrial vegetation mean that this technique may not be the most insightful for detecting seabird influence in such systems.

8.2 Plants

The results from Chapter 4 showed distinct differences in vegetation communities between areas with and without seabird colonies on the same landscape. It is recognized that seabird colony vegetation is distinct, largely due to high nutrient loads and physical disturbance, but the mechanisms behind plant assemblage, and particularly weed invasion are not well understood (Ellis et al. 2011). The results revealed in Chapter 4 show contrasting results, where soils with lower nutrient content but distinct vegetation communities persisted. Physical disturbance has an important role in driving the physical features of plant assemblage (height, species type, richness) and encouraging bare ground by pulling roots, trampling surface plants and physically redistributing fresh sand via digging. Invasive weeds, particularly prickly pear, were associated with seabird colonies, and thrive in seabird colonies due to the disturbed environment. Based on the conclusions reached in Chapters 4 and 5, effective suppression of weeds should be prioritised in seabird colonies, particularly those likely to expand.

8.3 Invasive species

Active restoration projects such as invasive mammal removal has seen promising success on islands where native plants and seabirds are conservation priorities (Vanderwerf et al. 2014; Jones et al. 2016). The functional roles of ecosystem components can be replaced by invasive mammals, and the results of restoration efforts may take time or include several methods of control to experience positive effects (Courchamp et al. 2003). Chapter 5 provided evidence of both positive and negative impacts on plant communities after invasive rat and rabbit removal. While vegetation communities experienced overall positive results in height, species richness and plant cover, factors such as invasive weeds and continued disturbance via nesting seabirds may confound the desired outcome. For instance, in Chapter 4 the effect on seabird colonisation and invasive weed presence was discovered due to differences in soil chemistry and disturbance compared to un-colonised (and undisturbed) areas. Continued monitoring of vegetation is recommended to deeper understand the mechanisms driving vegetation change after the removal of rats and rabbits, and additional interventions to restoration projects may be required.

The predation on seabirds by invasive pests can significantly impact populations and breeding success, and decrease nutrient subsidies provided by guano deposition (Smith et al. 2002). Long-lived seabirds like wedge-tailed shearwaters are highly sensitive to adult mortality, and restoration of populations may take a great deal of effort from managers, however is necessary to restore ecosystem function and biodiversity (Jones 2010). Broughton Island has experienced changes in environmental function as a result of invasion and eradication, and assessing habitat features and spatial ecology of seabirds in Chapters 6 and 7 provided insights into the behaviours of colonising seabirds in a newly predator-free island by identifying habitat and extracting environmental features of existing and newly formed seabird colony locations.

8.4 Spatial analysis

Two habitat suitability models described in Chapters 6 and 7 had successful outcomes and corroborated key findings. Each model successfully located areas of highest suitability of *A. pacifica* colonies, identified vacant suitable habitat, and described the habitat features of the most populated areas on Broughton Island. The result of newly formed seabird colonies in less suitable areas suggests something of habitat or individual quality drove the same species to form a new colony, and the population dynamic and spatial ecology is something to be explored further (Lewison et al. 2012). Identifying areas on the island which have a high suitability of habitat is useful for environmental planning, since we understand the clear connection between terrestrial disturbance, nutrient input, and preferential weed growth in seabird colonies, this provides precise locations for which managers can anticipate this change and therefore take desired action.

Although both Chapters 6 and 7 had similar research aims, habitat was defined using background knowledge and applied through GIS (Chapter 6), and mechanically defined by the MaxEnt model via a machine learning algorithm (Chapter 7). Both of these approaches have independent strengths and weaknesses, but both were effective in determining habitat characteristics on Broughton Island. GIS-based strategies have broad applications and can incorporate a wide range of environmental features depending on project needs, however in weighted analysis the environmental features are subjectively defined, whereas MaxEnt determines suitability by using presence/absence data of the species. Similar studies have been able to achieve similar goals of identifying habitat and assessing habitat features in nest site selection using MaxEnt (e.g. Massaro et al. 2017), however the models were similarly unable to use climate data due to low resolution and relatively small size of island study area. Individual islands like Broughton Island do not cover much geographical space, and therefore lower resolution datasets are not able to be utilised such as climate data (e.g. temperature, rainfall, wind strength), which invariably are important factors influencing the distribution of a species. On the other hand, GIS strategy was appropriate and useful because of the local knowledge of the island and ability to use high resolution categorical data (i.e. vegetation community and soil type) in analyses, where larger scale terrestrial studies would use different strategies for classification. In conclusion, GIS strategies for habitat modelling are recommended for smaller islands with locally derived datasets available, and empirical models such as MaxEnt are recommended for perhaps a chain of islands, or offshore region, where climate variables would allow for current and future scenarios.

8.5 Limitations and future directions

Along with most other research projects planned during 2020-2022, the impacts of the Covid-19 pandemic restricted a bulk of the planning and field sampling opportunities during the period of candidature. As such, the licensing between other island park managers and uncertainty of planning between travel to the coast and on boat, other islands were unable to be sampled, which would have greatly expanded the datasets and area sampled for this research. Fortunately, there were short and last-minute windows where sampling on Broughton Island could occur. Despite the major delays and setbacks of field sampling, unexpected opportunities and alternative ecological strategies were taken. For example, the use of GIS-based analysis and machine learning models based on environmental data from Chapters 5 and 6 provided a reliable, accurate, and reproducible method for identifying areas of land with high and low suitability for WTSW, and elucidating environmental variables most important for habitat selection. The output from these chapters proved an excellent way to utilise and combine existing datasets (many of which are publicly accessible) with virtually no financial resources or travel involved. The direction the research took required an entire new skillset for processing spatial data, proficiency in GIS and remote sensing software (Esri ArcGIS, MaxEnt, and ENVI), computing and interpretation of geostatistics. For larger extents of geographic space, MaxEnt is recommended because of the inclusion of climate datasets which can be used to predict future scenarios. However, GIS applications in habitat modelling are recommended when spatial datasets are available on high resolutions with categorical variables relating to specific environments of the study site (e.g. soil type, slope, etc.).

There are a number of islands in New South Wales where expanding this work would greatly benefit conservation goals. Now is an excellent time for field and geospatial monitoring because active pest eradications are now widespread among managed islands, particularly those managed by the National Parks and Wildlife Service. An opportunity exists to track and monitor the impacts of migratory breeding seabird species on the protected Islands of NSW and how recovering populations concurrently affect soil and vegetation characteristics. Particularly with spatial modelling of habitat suitability, climate statistics can be applied to these models on a larger resolution which would be incredibly useful to determine current and future scenarios to map suitable habitat, and therefore priority zones for conservation of nesting seabird habitat. Other islands, for example Muttonbird Island, South Solitary, North Solitary are excellent sites to expand this work, as they have a range of human disturbance (structure, invasive plants and animals) and management (invasive plant control, invasive mammal eradications, restoration projects).

There is a world of information waiting to be revealed on the unique and ever-changing offshore islands of New South Wales. The research reported here has created a foundation for consideration of sandy landscapes and disturbance giving complex and informative results (e.g. the relationship between seabirds and invasive prickly pear, and the heterogeneity of nutrients in and around seabird colonies), a foundation exists which can be expanded upon to extend our understanding to other islands and deepen the understanding between ecological relationships, the effectiveness of management in terms of conserving seabird habitat and controlling invasive species. Collaboration between the research sector and the governmental sector

(National Parks and Wildlife, Department of Environment and Planning, etc.) greatly benefits well-intentioned scientific communities, conservation managers and the ecosystems of concern. The partnership between these roles should continue in order to make informed decisions on research framework and ecological decision making– where both roles support one another.

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