SPATIAL VARIABILITY IN PLANT AND SOIL PROPERTIES ON NEW ZEALAND SEABIRD ISLANDS, AND THE EFFECTS OF INTRODUCED RATS

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Abstract

Seabirds are ecosystem engineers with two major impacts on island ecosystems: they bring large quantities of marine nutrients to the terrestrial environment in the form of guano, carcasses, feathers, eggs, and spilled food, and they disturb the soil surface. Burrowing seabirds can denude the soil surface of all seedlings and leaf litter, plowing them under and loosening the soil. However, seabirds are colonial, and burrows are not evenly spaced over the surface of an island, producing spatial variability within a single island that might reveal how seabird activities control island ecosystem function.

In this dissertation I review seabird island ecology in general, focusing on how introduced predators have reduced seabird populations, interrupting seabird activities and altering island ecology. I then describe three studies designed to quantify the effects of seabirds on soil and plant properties within individual islands and compare these patterns across islands varying in seabird density, especially where seabirds have declined because of invasive rats (*Rattus* spp.).

I used geostatistics to quantify the spatial variance in seabird burrows and various soil and plant properties (including soil and leaf N) within six islands of low, intermediate, and high burrow density. I found that burrow density was not a good predictor at within-island scales, and though the variance of some soil properties (pH, soil $\delta^{15}N$, and soil compaction) peaked on intermediate islands as expected, variables reflecting the soil N cycle (net ammonification and net nitrification potential, NH_4^+ and NO_3^-) continued to increase in variability on very high-density seabird islands. Ecosystem properties clearly responded to seabirds at different spatial scales, possibly because seabirds deposit guano at different spatial scales than they dig.

Using data within three rat-invaded and three rat-free islands, I used structural equation models to examine seabird influences on N cycling. I found some mechanisms that were constant across islands, such as seabird-related decreases in soil water and pH, but other mechanisms differed between invaded and uninvaded islands, suggesting that rats alter seabird control over island N cycles, thus manifesting an alternative island state which may or may not be reversible.

Finally, I investigated whether plants can use ammonia (NH_3 gas) volatilized from seabird islands, measuring NH_3 concentrations across 10 islands and within a single island where

I also experimentally manipulated plant N demand. Both rat-invaded and rat-free islands produced meaningful concentrations of NH_3 gas, and multiple plant species including *Melicytus ramiflorus* and *Coprosma macrocarpa* used it for up to 20% and 30% (respectively) of their total leaf N. Plant N demand modified NH_3 uptake, suggesting that plants located not on seabird colonies, but downwind, may benefit the most from this gaseous N source.

I suggest that future studies attempt to estimate thresholds of burrow density at which seabird-controlled ecosystem properties can recover from rat invasion.

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Chapter 1.

General introduction

Familiar with the waves, and free,
As if their own white foam were he:
His heart upon the heart of ocean,
Learning all its mystic motion,
And throbbing to the throbbing sea!

—E. B. Browning, *The Sea-Mew*

They burrowed wherever there was soil in which to burrow; some on the eroding gravel slides, where they were liable to lose their homes and families, others in dense thickets where they were liable to lose their lives...

As the dusk crept down on us, the air above our heads became thick with birds. Round and round they hurtled, wailing and muttering to their mates belowground… Birds were plumping to earth all around…

—Mary E. Gillham, *A Naturalist in New Zealand*

Seabirds are boundary creatures, both marine and terrestrial, connecting the air, land and sea. They depend upon the isolation of islands to protect their young, but island ecosystems depend just as surely upon the seabirds. Their marine diets provide the terrestrial environment with allochthonous nutrient subsidies (guano, carcasses, spilled food, failed eggs, and feathers) and their nests, whatever form these take, constitute a physical disturbance to local soil and plants (Mulder et al. 2011b). Island communities, from soil microbes to predators, depend upon the birds' activities; this is shown in the dramatic changes that ensue when seabirds go missing from the islands, usually after predator invasion (Drake et al. 2011; Towns et al. 2011). Rats

(*Rattus* spp.) are the most widespread island invader because of their proclivity to stow away in human cargo (Towns et al. 2011), and yet they are some of easiest to eradicate (Dunlevy et al. 2011), which can allow island seabird populations to rebound (Jones et al. 2011). Whether the return of seabirds allows the island ecosystem to fully recover, or whether it must be more intimately managed for full restoration, is of vital importance when managing scarce conservation resources (Jones et al. 2011).

In Chapter 2, I review the state of seabird island ecology from a global standpoint, identifying patterns that rely upon system-specific attributes such as seabird identity, predator identity, or island climate, isolation, and vegetation type. I also discuss the various threats facing seabirds and seabird islands in a rapidly changing world. This chapter was the conclusion and synthesis of a book by the Seabirds and Invasive Predators on Islands (SEAPRE) network, representing researchers from island systems around the world (Mulder et al. 2011a), and thus provides a thorough introduction to the ecology of seabird islands in general.

Islands are discrete units of observation, with marine boundaries that make them ideal not only for seabirds, but for scientists (Vitousek 2002). Much research on the functioning of seabird islands has therefore compared them to similar but invaded islands, analogous to a “natural experiment” of seabird removal (in this ecosystem: Fukami et al. 2006, Grant-Hoffman et al. 2010a, Grant-Hoffman et al. 2010b, Mulder et al. 2009, Peay et al. 2013, Towns et al. 2009, Wardle et al. 2007, Wardle et al. 2009). However, we know that predators, especially omnivores like rats, have their own impacts on island communities and ecosystems (Towns et al. 2011, Drake et al. 2011) and also that individual island differences may constrain the effects of both seabirds and invaders (Chapter 2). Thus studying seabird impacts within a single island, while accounting for their variability at small spatial scales, may lend insight into the mechanisms by which seabirds control island ecosystem functioning. This knowledge may eventually help managers to restore island ecosystems.

The next three chapters describe work in a particular island system in northeast New Zealand (Table 1.1, Fig. 1.1, Fig. 1.2), blanketed in coastal broadleaf forest and colonized mainly by burrowing seabirds. These birds (petrels, diving petrels, storm petrels, shearwaters, and penguins; named in Table 1.2) are ecosystem engineers that tunnel into the ground up to 3 m, entering their nests only through a small (6-30 cm) entrance (Fig. 1.3). They trample or pluck any seedling nearby, plough the leaf litter beneath the surface, and loosen the soil to such an extent that large trees may topple (Chapter 2). Some of these islands also have current or recently eradicated populations of invasive European rats (*R. rattus* and *R. norvegicus*), which have dramatically decreased the local seabird populations.

Even on the most densely burrowed islands, however, seabirds do not space themselves evenly across the surface, usually preferring colonies with conspecifics and sometimes sharing burrows between species (Warham 1990). Seabirds have long, thin wings and use relative wind over the ocean, rather than thermal updrafts, to soar; thus they may need to gain height before rising aloft, especially in a forest (Fig. 1.4). Steep slopes and ridgelines or high plateaus are thus preferred habitat (Warham 1990). Thin spots in the canopy can also mitigate, but not entirely eliminate, the danger of uncontrolled descent through the trees in the dark (Fig. 1.5); tree canopies are thinner where burrow densities are highest and bird-related damage may reinforce this pattern (Mulder et al. 2009). Many seabird species are philopatric, returning not only to the same colony, but to the same nest year after year (Warham 1990). Consequently, burrowing seabirds are likely to have highly variable impacts within a single island. In this dissertation, I seek to quantify the effects of seabirds within individual islands, then compare these patterns across multiple islands, especially islands with and without invasive rats.

In the study described in Chapter 3, I used geostatistics to examine how burrow-nesting, colonial seabirds structure the spatial patterns of soil and plant properties (including soil and leaf N) on six islands that vary in seabird burrow density. At the *within-island* scale, I hypothesized that seabird impacts, represented by burrow densities, directly structure plant and soil properties over space, and also that seabird impacts are the result of their behavior rather than just coincidental to their choice of nesting sites (e.g., slope, aspect, elevation). *Among islands*, I reasoned that seabirds at very high densities may homogenize islands, but the effects of seabirds at very low densities will be spatially confined to a small colony; thus seabirds at intermediate densities will create the most spatial variability, including the greatest patchiness and the finest spatial grains.

Chapter 4 describes the direct and indirect effects of seabirds on island N cycling, at the within-island scale, and how these pathways are altered by rat invasion. I used structural equation models with soil and plant data from six islands, three invaded by rats and three rat-free.

Goals were to 1) identify the most important mechanisms by which seabirds affect components of soil N cycling, particularly net ammonification, net nitrification and the resultant inorganic pools, 2) explain how dominant pathways differ between uninvaded and rat-invaded islands, and by soil depth, 3) investigate the main mechanisms affecting plant leaf N and $\delta^{13}C$, a key indicator of plant water stress, 4) explore whether soil $\delta^{15}N$, as an indicator of cumulative seabird effects, can be used interchangeably with seabird burrow density in models relating seabirds to island ecosystem function.

In Chapter 5, I describe how I evaluated a specific mechanism by which seabirds affect island plants: foliar uptake of seabird-derived ammonia (NH_3 gas). I measured NH_3 gas concentrations and $\delta^{15}N$ values both on- and off-colony on ten seabird islands, including several where invasive rats have reduced local seabird densities, expecting higher NH_3 concentrations on rat-free seabird islands and especially on seabird colony sites. I also performed a nine-month-long field experiment in which I manipulated soil nutrient content, hypothesizing that plant demand for NH_3 gas would be greater when N was less available compared to other nutrients. I then used a stable isotope mixing model to quantify foliar uptake of NH_3 gas both across rat-invaded and rat-free islands and within my experimental plants, hypothesizing that NH_3 gas volatilization from seabird colonies is an important but overlooked plant N source.

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Table 1.1 The 18 islands studied, 2004-2006

Island	Code	Island group	Latitude (°S)	Longitude (°E)	Area (ha)	Distance from mainland (km)	Rat status	Burrow density (1 plot)[1] burrows m^{-2}	Burrow density (2-4 plots)[2] burrows m^{-2}
Green	GRN	Mercuries	36.64	175.85	2.5	7.2	rat-free	1.01	1.015
Middle (Atiu)	MID[GA]	Mercuries	36.60	175.84	13.5	8.3	rat-free	0.98	0.685
Archway	ARY	Poor Knights	35.49	174.74	6.3	20.7	rat-free	0.56	0.380
Tawhiti Rahi	TR	Poor Knights	35.45	174.71	158.2	21.7	rat-free	0.48	0.245
Ruamahuanui	RNI[GA]	Aldermen	36.95	176.09	32.4	19.9	rat-free	0.35	0.185
Ruamahuaiti	RTI[A]	Aldermen	36.97	176.06	25.5	18.1	rat-free	0.23	0.130
Aorangi	AOI	Poor Knights	35.48	174.72	107.1	20.6	rat-free	0.18	0.170
Aorangaia	AOA	Poor Knights	35.48	174.71	5.6	21.4	rat-free	0.13	0.110
Otata	OTA	Noises	36.41	174.58	16.8	14.9	rats	0.09	NA
Motueke	MOK[GA]	NA	36.82	175.80	6.2	1.2	rats	0.06	0.040
Aiguilles	AIG	Great Barrier	36.03	175.39	72.7	47.7	rats	0.02	0.005
Hauturu	HAU	Whangamata	37.12	175.53	10.3	0.54	rats	0.01	NA
Ohinauiti	OHI[GA]	Ohena Is	36.71	175.88	5.9	5.3	rat-free	0.00	0.035
Te Haupa	TEH[G]	NA	36.51	174.74	6.0	10.5	rats	0.00	0.025
Motukaramarama	MOA[A]	Coromandel	36.68	175.37	10.1	3.3	rats	0.00	0.000
Motutapere	MOE[A]	Coromandel	36.78	175.40	45.6	2.5	rats	0.00	0.000
Motuoruhi	MOI[A]	Coromandel	36.73	175.40	58.0	2.6	rats	0.00	0.000
Goat	GOT	NA	36.26	174.80	13.4	0.015	rats	0.00	0.005
Pakihi	PAK	NA	36.54	175.10	110.0	1.4	rats	0.00	0.000
Motuhoropapa	MOP[GAE]	Noises	36.41	174.57	8.6	13.6	rats	0.00	NA

[1] Burrow density calculated from the first plot sampled in 2004

[2] Burrow density as an average of 2-4 plots, reported by Grant-Hoffman (2010a)

[G] Geospatial sampling, Chapter 3-4

[A] Ammonia gas sampling, Chapter 5

[E] Field experiment, Chapter 5

Table 1.2 List of seabird species present

Order, Family	Species	Common Name(s)	Conservation Status[1]
Procellariiformes			
Hydrobatidae	*Pelagodroma marina*	white-faced storm petrel	LC
	Pelecanoides urinatrix urinatrix	common diving petrel	LC
Procellariidae	*Pterodroma macroptera gouldi*	grey-faced petrel, great-winged petrel	LC
	Puffinus bulleri	Buller's shearwater	VU
	Puffinus griseus	sooty shearwater, titi	NT
Sphenisciformes			
Spheniscidae	*Eudyptula minor*	little blue penguin	LC

[1] Conservation status according to IUCN Red List of Threatened Species 2010.1, accessed in March 2010: www.iucnredlist.org. LC=Least Concern; NT=Near Threatened; VU=Vulnerable

1.3 Figures

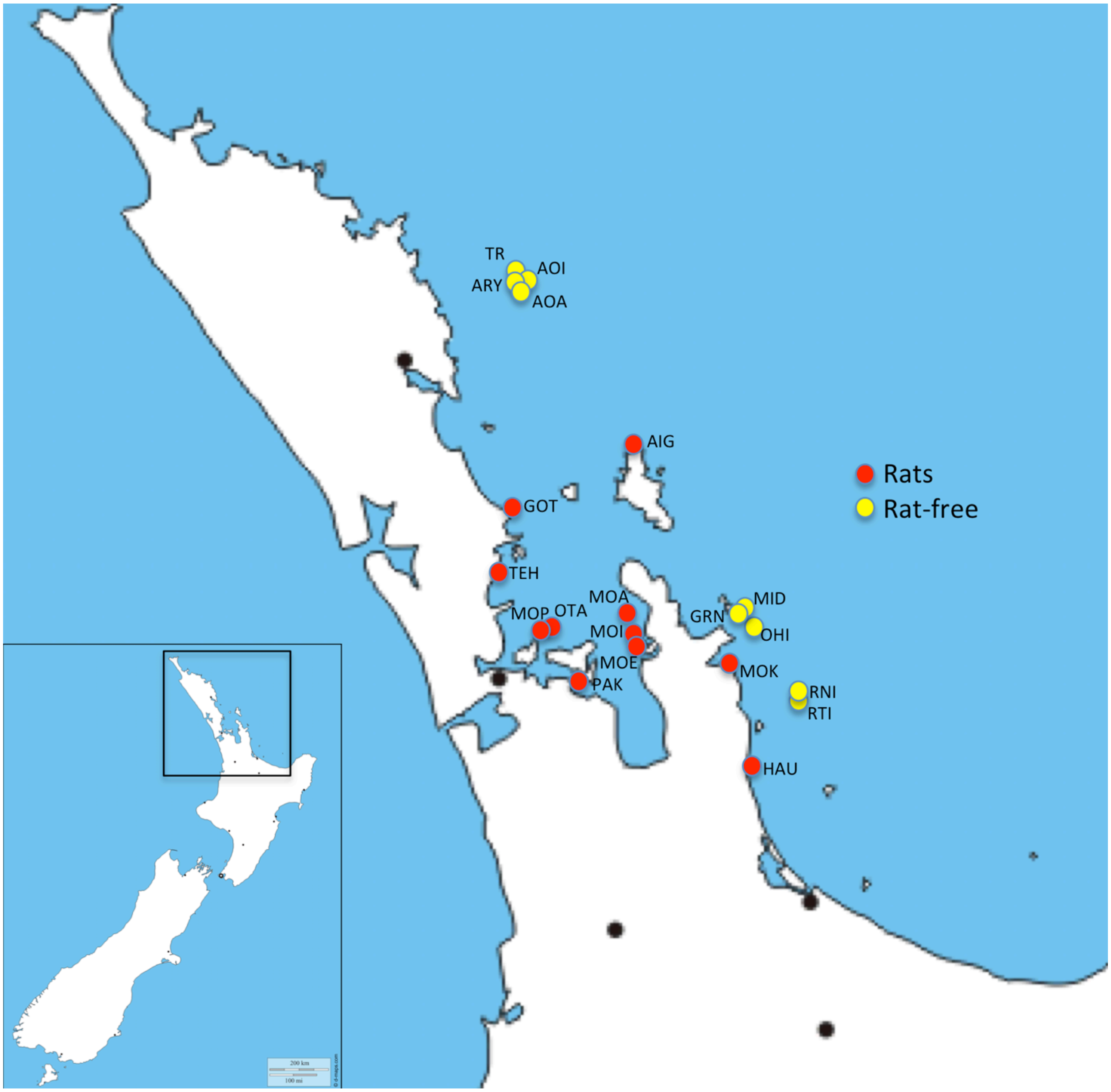

Fig. 1.1 Map of the islands studied. Islands invaded by rats are indicated in red, rat-free islands in yellow. Black dots indicate major New Zealand cities

Fig. 1.2 Topography of some of the islands studied. Top row: Ohinauiti. Second row: Ramahuanui and Atiu (Middle Mercury). Bottom row: Goat I. and Te Haupa (Saddle I.)

Fig. 1.3 Seabird burrows. Top row: diving petrels, sooty shearwaters. Second row: grey-faced petrels. Bottom row: grey-faced petrels and/or little blue penguins

Fig. 1.4 Climbing tree for diving petrels on Ohinauiti

Fig. 1.5 The dangers of an uncontrolled descent through the forest at night

Chapter 2.

The state of seabird island ecology: current synthesis and global outlook[1]

2.1 Introduction

Islands are excellent model ecosystems because they are discrete units, allowing replication at the island scale. They often have restricted, but highly unusual or endemic floras and faunas, with naturally low immigration / emigration rates due to their isolation from other land masses (Vitousek 2002). Island biodiversity and levels of endemism probably depend upon island size, geology, and isolation, among other variables (MacArthur and Wilson 1967).

Breeding seabirds can change the character of an island considerably, depending upon their numbers and behavior (Smith et al. 2011). Many seabird species nest in dense, noisy, smelly colonies located on steep slopes or windy, hard-to-reach cliffs in some of the most isolated locations in the world. Some nest on top of the ground, cementing their nests with guano, others dig underground burrows, and still others nest in trees or in the crevices of cliffs. Some forage in the shallows around the coast while others travel thousands of miles and spend weeks at sea before returning to land. However, all seabirds eventually bring marine nutrients back to land, depositing guano, feathers, spilled food, eggshells, and even carcasses in the terrestrial environment (Smith et al. 2011). Seabird island communities depend upon these nutrient inputs.

Many seabird islands have been directly modified by anthropogenic global change, including pollution and land uses like guano mining, logging, and agriculture (Anderson and Mulder 2011). However, introduced seabird predators have had the most devastating effects on seabird island communities and ecosystem functioning (Towns et al. 2011b, Drake et al. 2011).

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[1] Published as: Durrett, M.S. and C.P.H. Mulder. 2011. The state of seabird island ecology: current synthesis and global outlook. Pp. 393-424 in C.P.H. Mulder, W.B. Anderson, D.R. Towns and P.J. Bellingham, eds. Seabird Islands: Ecology, Invasion, and Restoration. Oxford University Press, New York.

By preying upon eggs, chicks, and even adult birds, predators exclude seabirds from these islands, along with the marine nutrients they bring, dramatically altering plant community composition and ecosystem functioning (Mulder et al. 2011b, Ellis et al. 2011). This alters energy transfers to higher trophic levels and marine feedback loops (Kolb et al. 2011, Young et al. 2011, Russell 2011). Eradicating these predators is the first step toward restoration of island ecosystem dynamics (Dunlevy et al. 2011), but sometimes other steps are needed to restore seabird densities and thus return the island to its natural state (Jones et al. 2011). This process requires the collaboration of many institutions and individual stakeholders (Towns et al. 2011a).

Seabirds are considered to be indicators of global change in over 100 scientific articles (Durant et al. 2009). Because seabirds depend upon marine ecosystems for the food resources that ensure their survival, they spend most of their lives at sea. However, many roost on land between foraging trips, and all return to land to breed. Thus every seabird's fate is directly tied to the state of both the marine and the terrestrial ecosystems. Global change, in the broadest sense, threatens seabird populations by land and by sea, and seabird islands will suffer from any decline in seabird densities. However, islands are also directly at risk from habitat destruction, pollution, and climate change, which in turn threaten seabirds on their breeding grounds.

In this chapter, we describe emergent trends in seabird island ecology and the effects of global change on seabird and seabird islands. Where possible, we indicate relationships that are generally true among all seabird islands, and to what extent ecological relationships depend upon system-specific attributes such as seabird identity, predator identity, or island climate, isolation, or vegetation type. We also discuss the threats facing seabird islands in a changing world, and suggest a way forward for understanding and conserving seabird islands in the future.

2.2 Seabird Effects on Island Soils and Vegetation

Seabirds impact island communities and ecosystem processes primarily through two different mechanisms: by depositing large quantities of marine-derived nutrients, and by imposing physical disturbance (Smith et al. 2011). In this section we synthesize the impacts of these two types of activities on soils and vegetation in order to address the general questions raised in Anderson and Mulder (2011). First, to what extent are the impacts 1) predictable across island systems and 2) dependent primarily on seabird density? Second, to what extent are these general relationships modified by system-specific characteristics such as seabird identity, climate or vegetation type, and geographical location (i.e., distance to the mainland)? Finally, we identify questions that we cannot answer with the data currently available and some approaches to resolving these.

2.2.1 Effects of seabird nesting density

The density of nesting seabirds is consistently linked to soil and plant nutrient concentrations, although its predictive ability varies with island system (Mulder et al. 2011b). Nest density was correlated with an exponential increase in the concentration of nitrogen (N) and phosphorus (P) in the soil, as well as a decrease in soil pH, in most island systems (each relationship was linear on a log-log scale). Soil $\delta^{15}N$ increases strongly with nest density, indicating an increase in the proportion of marine-derived N in the soil. We did not identify a "ceiling" nest-density above which soil properties remained constant. Compared with changes in soil chemistry, plant responses to nutrient additions are far less predictable based on seabird nest density. Like soils, plants incorporate more seabird-deposited N (shown by foliar $\delta^{15}N$) with increasing seabird nest density. However, foliar N concentrations increase only up to moderate bird densities of about 600-1000 nests ha^{-1}. At higher nest densities, foliar N concentrations stabilize or decline, probably due to N-saturation.

Phosphorus is far less soluble than N and lacks a gaseous phase, so soil P concentrations are more tightly coupled to seabird nesting densities than soil N concentrations. There were too few reported relationships between nesting densities and plant P concentrations to draw reliable conclusions. Phosphorus may persist in the soil for many years (Hawke et al. 1999), so even islands currently without seabirds may benefit from the "legacy effects" of now-extinct seabird colonies—possibly outsupplying the vegetation's demand for P. Unfortunately, island history with respect to seabird densities and human land use is usually unknown, and better paleoecological methods are needed to investigate the importance of legacy effects.

Despite the extremely wide range of plant species and growth forms found on our focal island systems, some seabird effects on plant communities were similar across all systems. The low pH and very high soil N associated with seabird colonies can induce phytotoxicity in many plant species, and the accompanying physical disturbance discourages slow-growing species—thus conferring an advantage to fast-growing plants that can quickly make use of seabird-deposited nutrients. In our analyses, plant families associated with seabird colonies were Apiaceae, Brassicaceae, Chenopodiaceae, Poaceae, and Solanaceae (see Ellis et al. 2011 for complete results). These families include many species with high growth rates, high seed production, and an annual or biennial life cycle—consistent with our findings that such growth forms respond most strongly to seabird-deposited nutrients (Mulder et al. 2011b). Ultimately this pattern can arrest succession indefinitely on seabird islands.

In every system that we tested, seabirds were associated with a decrease in plot-scale and island-scale plant species richness (Ellis et al. 2011). Seabirds determine plant species composition by excluding some species, facilitating others, and even, in some cases, dispersing seeds (e.g., gulls); our results strongly suggest that they exclude more plant species than they facilitate. It is important to note that while seabirds reduce species richness at the *island* scale, they probably increase species richness of the *regional* species pool by providing habitat for plants that depend on seabird colonies, e.g., coastal species of *Lepidium* in New Zealand (Norton et al. 1997), though we could not test this hypothesis statistically. Therefore, excluding seabirds from islands *via* invasive predators is likely to increase the local species richness by removing an important species "filter" while decreasing the regional species richness through habitat loss for species adapted to high seabird densities. We will return to this idea later in this chapter when considering how to restore such systems.

2.2.2 Effects of seabird identity

While nutrient inputs are tightly linked to seabird nesting density, the impacts of physical disturbance are strongly associated with seabird identity, especially nesting behavior. Surface-nesting seabirds tend to increase total N concentrations and $\delta^{15}N$ in soil and plants, while burrow-nesters tend to increase total soil carbon (C) concentrations. This is likely the result of where (on the nest or at sea) and how much the birds defecate. Surface nesters deposit N-rich guano purposefully on their nests, compacting the soil. Burrow-nesters, in contrast, rarely defecate inside the burrow, but actively plough leaf litter beneath the surface, consistent with increasing soil C concentrations. This additional carbon can increase water-holding capacity (as was found for the arid Gulf of California islands) but when such tillage is too extreme, the soil may become fine and friable instead (as in the Northeastern New Zealand islands).

Seabird nesting behavior also influences plant community composition. The proportional representation of various plant growth forms within an island system depends upon seabird presence, but which growth forms increase and decrease can be attributed to the disturbance regime promoted by particular seabirds (Ellis et al. 2011). For instance, terns and gulls in the Gulf of Maine nest on the surface and are associated with fewer trees and shrubs, either because they reduce those growth forms or because they choose more favorable habitat in which to nest. On the other hand, petrels in northeastern New Zealand burrow under the forest canopy, trampling and actively destroying herbaceous seedlings around their burrows, thus selecting for fast-growing, woody species that tolerate root disturbance (Grant-Hoffman et al. 2010).

2.2.3 Effects of island climate and vegetation

Although seabird density predicts N deposition to some degree, the climate and geology of the specific island system can also strongly influence the ultimate fate of seabird-deposited N. The relationship between seabird nesting density and soil N concentrations was weaker than that with soil $\delta^{15}N$, raising the possibility that much of the extra N deposited by additional nesting seabirds may actually be lost from the terrestrial system, either through leaching and runoff or by volatilization to ammonia gas (Mulder et al. 2011b). Particularly in island systems with high rainfall or rock substrate, N runoff may create an important allochthonous resource pulse for the surrounding marine system (Young et al. 2011). Higher summer mean temperatures were associated in our analyses with decreasing soil pH and increasing soil $\delta^{15}N$, consistent with greater ammonia volatilization (Mulder et al. 2011b). Both of these fates for extraneous seabird-deposited N are likely, though the magnitude and consequences of these potential N fluxes remain understudied; however, see Young et al. 2011 regarding runoff to marine systems, and Lindeboom (1984), Erskine et al. (1998), and Wilson et al. (2004) regarding ammonia volatilization from seabird colonies. Differences in soil nutrient immobilization may partially explain the variability in plant nutrient response to seabird density.

The run-on effects of extreme climates on nutrient deposition may also modify seabird impacts on plant communities. Nutrient-limited islands appear to depend most upon seabird nutrient deposition, responding strongly in foliar N concentrations and in plant community composition (e.g., high-rainfall, low-decomposition systems like the Aleutians; Croll et al. 2005). Therefore these systems may be particularly vulnerable to rapid, bottom-up shifts in ecosystem function caused by seabird decline. However, such responsive plant communities, if biodiversity remains intact, may also be able to recover in tandem with seabird populations. In contrast, some extreme climates may select so strongly for certain plant growth forms, such as slow-growing cacti and rain-responsive forbs on the arid Gulf of California islands, that the seabirds' role narrows to selection of species *within* growth forms. These vegetative growth forms may remain more stable due to climate, but individual plant species may still depend upon seabird nutrient and disturbance regimes that alter soil chemistry and microclimate.

2.2.4 Effects of island geography

An island's distance from the mainland also modifies the relationship between seabird presence and the proportion of non-native plants on the island. In our analysis, this effect mainly depended on an island's isolation from humans and other seed dispersers. Where seabird islands are located far from the mainland or access-limited (often the reason for the seabirds' survival), there are fewer non-native species than on non-seabird islands—although some weeds, e.g. *Poa annua*, are probably dispersed by the birds themselves. In these systems, non-seabird islands probably experience more human traffic and/or the effects of invasive animals that may disperse non-native plants (see below). However, in many cases isolation does not limit island access, and once non-native plant species are established, they thrive on seabird colonies. These species are often members of the plant families described above, with a tolerance or preference for high-nutrient, disturbed soil.

2.2.5 Directions for future research

The largest gap in our understanding of seabird island soils and plants is productivity: under what conditions do seabirds increase or decrease primary production, which will sustain higher trophic levels? Standardization of data collection would allow cross-system comparisons, as well as more advanced modeling. Relative abundance data should also be standardized to provide estimates of diversity and dominance, which could shed more light on what specific taxonomic groups are promoted by seabirds, and at what life stages they are promoted or excluded. Experimental manipulations and measurement of species-based traits (e.g., leaf area) are needed to reveal the mechanisms behind the promotion or inhibition of particular species or guilds; for example, how do mycorrhizal fungi and N_2-fixers respond to seabird colonies? Data from conspecifics or closely related species in different island systems may be able to answer questions about the generality of seabird effects on soil and plants. Similarly, systems with multiple seabird species living in monospecific colonies could be used to tease apart the effects of seabirds from the effects of climate and geography. Finally, legacy impacts of former seabird colonies and past land use management actions are a great unknown in many systems, but cross-disciplinary work with archeologists or anthropologists may illuminate these, providing a broader ecological context in which to place a particular island or island system.

2.3 Invasive Predator Effects on Island Communities and Ecosystems

Many native vertebrate, invertebrate, and plant species have been driven to local or global extinction as a result of non-native predators (Towns et al. 2011b, Drake et al. 2011), strongly implicating animal introductions in the global biodiversity crisis. All the major seabird predators discussed herein are known to decrease seabird populations, reducing nutrient inputs and seabird-related disturbance regimes, which in turn alter plant nutrition and community composition, with consequences for higher trophic levels (Table 2.1). In this section, we first examine what is common to all seabird islands: the threat of invasive predators. We describe broad groups of invasive predators that act similarly on island communities and ecosystems, both directly and indirectly, as well as the predator-specific traits that modify these effects, and the prey-specific traits that increase vulnerability for different native prey populations. Finally, we identify the areas where our predictive ability is limited by insufficient research.

2.3.1 Threat of predator invasion

Wherever humans have traveled throughout history, so too have our animal companions, whether as pests, pets, or livestock. The spread of exotic species escalated dramatically with the European explorations of the eighteenth and nineteenth centuries, usually with the best of human intentions. Animal gifts of cats, pigs, and goats were a kind of cultural exchange, particularly on South Pacific islands, while the release of furbearers such as foxes to more northerly islands was a convenient way to expand the lucrative fur trade (Towns et al. 2011b, Drake et al. 2011). Rodents stowed aboard ships and were accidentally, as well as intentionally, introduced to many islands. Some species, e.g., cats and mongooses, were even introduced to control previously introduced pest populations (Towns et al. 2011b, Drake et al. 2011). Though the rate of island invasions appears to be slowing worldwide, new introductions are still occurring, and intact island ecosystems are under constant threat (Atkinson and Atkinson 2000). The geography of invasions has typically been related to national wealth; exploration and industry-building (such as the fur trade) required capital. Even today, richer countries are allocating resources to removal of non-natives, as poor countries that lack these resources undergo further invasions (e.g., both cane toads and mongoose have reached Samoa within the last ten years and are now spreading; S. Boudjelas, personal communication). We consider solutions to this widespread problem later in the chapter.

Seabirds are especially vulnerable to introduced predators. Though many seabird species function as apex predators at sea, they are relatively defenseless on land (Towns et al. 2011b). Thus even the most aggressive seabird species avoid predators by nesting on remote islands or steep cliffs inaccessible to terrestrial mammals. Many species also exhibit philopatry, with such a strong affinity for their birth colony that they cannot relocate should the habitat become unsuitable (Smith et al. 2011). Because ideal habitat is limited, colonies can reach very high densities of breeding birds; for instance, in the late 1960s sooty shearwaters (*Puffinus griseus*) nested in densities up to 13, 800 burrow entrances ha^{-1} on 238-ha North East Island in the Snares Islands in sub-Antarctic New Zealand (Scott et al. 2008). The reproductive strategy of most species involves few eggs and long generation times, tradeoffs for a relatively long lifespan. All of these traits contribute to make an entire colony highly susceptible to only a few individual predators (Towns et al. 2011b).

The foremost threat to seabirds on islands is predation by invasive mammals. Of 80 introduced species on islands listed by Atkinson (1989), at least 40 are known to prey upon seabirds. We identified the most widespread and destructive of these mammals in Towns et al. 2011b. (For a complete list of predators present on our focal island systems, with their scientific names, see Mulder et al. 2011a) Introduced predators of seabirds have also been implicated in declines and/or extinctions of terrestrial invertebrates, herpetofauna, land birds, native mammals, and native plants on islands. Beyond causing species declines of their prey, introduced predators differ in their overall impacts on islands because of differences in their predatory behavior and their indirect effects on island ecosystems.

2.3.2 Hardwired as predators: cats and foxes

Carnivorous "superpredators" have similar impacts on seabird island ecosystems because their main effect is a decrease in almost all available prey populations, especially seabirds. Of the globally invasive superpredators, cats are the most destructive to seabird populations (Towns et al. 2011b), but they have also extirpated land birds, lizards, and native mammals (Drake et al. 2011). Foxes are similarly destructive to seabirds, other ground-nesting birds, marsupials, reptiles, and sea turtles, though fox distribution is more limited than that of cats (Drake et al. 2011). Carnivore invasion of an island, given enough time, will inevitably decrease animal species richness.

However, carnivores can persist longer on a seabird island when introduced herbivores or mesopredators are present as an alternative food source. For instance, rats, mice, and rabbits often function this way for invasive cats (Pontier et al. 2002). Both cats and foxes have been known to extirpate all food resources, including seabirds, until the predators starved themselves to extinction. Fur trappers released voles, mice, and Arctic ground squirrels to the Aleutians as an alternative food source for the introduced foxes, which regularly died off when they had depleted the seabird colonies (Bailey 1993, Ebbert and Byrd 2002). Because alternative prey can subsidize and increase carnivore populations, multiple-species introductions can cause hyperpredation on island natives, reducing seabird and other native prey populations severely.

Superpredators have also been implicated in a host of indirect ecosystem effects, mostly brought about by decreases in native prey and hence decreased functioning of that species in its ecosystem niche. For instance, cats have altered seed dispersal in the Canary Islands by preying on the lizards that carry seeds and re-depositing the seeds in their own feces (Nogales et al. 1996). Foxes may compete with native predators for ground-nesting birds in the Aleutians (Bailey 1993). Indirect effects are most dramatic, however, when bottom-up processes are interrupted. For example, Croll et al. (2005) showed foxes were responsible for entire vegetation community shifts in the Aleutians by cutting off the flow of seabird-mediated marine nutrients, allowing shrub-dominated tundra to replace nutrient-responsive grasses. Because foxes consume a variety of invertebrates in the intertidal zone, they may also interfere with the typical flow of nutrients at the marine-terrestrial interface (Carlton and Hodder 2003).

Prediction of these indirect effects depends upon predator-specific behavior. For example, cats will kill large numbers of seabirds without eating them, leaving their carcasses on the surface to rot. This behavior no doubt alters the soil invertebrate community and microbial decomposer guilds (though this effect has not been studied). In contrast, foxes hoard eggs and carcasses in preparation for a lean winter. In this way a seabird predator may indirectly add seabird nutrients to the soil, especially if the cache is abandoned. These different predatory behaviors may even affect what carrion becomes available to scavengers, including rodents.

2.3.3 Omnivores and seed dispersers: rats, pigs, and gulls

Omnivores also decrease seabird populations, but their direct effects on island ecosystems may be more complicated because of their herbivory. For example, they may pollinate plants or disperse seeds, enabling the spread of island natives or invasive weeds, but they may also drive plant species to local extinction (Drake et al. 2011). All of these effects alter the community composition of plants directly, in contrast to the carnivorous predators whose effects on island vegetation were mediated by animal prey populations.

Rodents are the most widespread introduced mesopredators on islands. There are three species of invasive rats among these, and all are generalist omnivores. Their diets change according to what is available, though they generally consume more plants than animals, and plant parts consist largely of seeds (Drake et al. 2011). The Norway rat or brown rat (*Rattus norvegicus*) is the largest and the strongest swimmer, allowing it to depredate larger seabirds (Towns et al. 2006) and to easily disperse to nearby islands in an archipelago (e.g., Russell et al. 2005). The ship rat or black rat (*Rattus rattus*) is an excellent climber, allowing it to prey upon seabirds of all life stages and from all nesting guilds: tree nesters, ground nesters, crevice and hole nesters, and burrow nesters (Jones et al. 2008). Finally, the Pacific rat or kiore (*Rattus exulans*) is comparatively small, but it has been known to attack Laysan albatross 30 times its own size (Jones et al. 2008).

Considering their distribution as well as their impacts on seabird populations, ship rats are currently the most widespread and destructive seabird mesopredators. However, the time passed since invasion may bias our understanding of predator impacts. Because the Pacific rat invasions began earliest on the islands where they occur, this small rodent may have already been responsible for a wave of extinctions prior to European exploration (Steadman 2006). Ship rats were firmly ensconsed in Mediterranean island ecosystems over 2,000 years ago, and their current effects on French islands, even with burrow-nesting seabirds, are far less severe than on Pacific islands (Ruffino et al. 2009). Rat species often co-occur on the same island, but interspecific interactions are poorly studied, although intraguild predation is known to occur (Russell 2011).

Pigs are important among globally introduced predators because of the tremendous physical disturbance that they create by rooting in the soil. Not only do pigs consume seabird eggs, chicks, and adult birds (thereby excluding some seabirds from islands entirely), they are highly omnivorous and will prey on any trophic level, from plants and invertebrates to small mammals and ground-nesting birds (Matisoo-Smith 2009, Drake et al. 2011). Soil disturbance by pigs may drastically alter the habitat for terrestrial invertebrates, and they also eat large numbers of earthworms and land snails, with potential consequences for ecosystem processes. They can swim between islands in an archipelago and will forage for intertidal invertebrates (Carlton and Hodder 2003) and freshwater eels (McIlroy 2005), though most of their diet consists of plant parts (Campbell and Long 2009).

Not all island predators are mammals. Native seabirds such as gulls can become pests because of human-assisted environmental conditions and can therefore threaten more fragile seabird populations. Gull populations are often subsidized by open access to landfills, and this has lead to rapid growth of gull populations in the eastern North America and around the Mediterranean (for reviews, see Vidal et al. 1998, Donehower et al. 2007). This negatively affects tern populations, and roseate tern colonies in particular are now actively managed to deter gull predation in the United States (Whittam and Leonard 1999). However, culling gull populations can become a politically charged management decision (J. Ellis, personal communication).

Rats, pigs, and gulls may have either positive or negative impacts on island plants. Rats can pollinate some plant species (e.g., Ecroyd 1996), and all omnivores are known to disperse seeds, though gulls are probably best at it because of the distances they can fly. Both pigs and gulls have been implicated in the dispersal of non-native plants (Drake et al. 2011, Ellis et al. 2011). All of these omnivores can also kill individual plants, though pigs appear to inflict the most damage on soil, tree trunks, and roots. However, rats also eat the seeds of some plants (e.g., *Streblus banksii*, a long-lived New Zealand tree) and sometimes will consume all of the aboveground parts, driving the plant to local extinction (e.g., several species of *Carmichaelia* [Fabaceae], E. Cameron, personal communication). Island plants in general appear to be weakly defended against herbivory, compared with their mainland counterparts, and rats prefer to eat island plants than introduced mainland species (Nuñez et al. 2008). Overall, invasive omnivores are likely to directly alter island vegetation dynamics, in addition to their impacts on animal prey.

2.3.4 Unexpected predators: mice and ants

Most difficult to predict are the effects of seabird predators that seem inconspicuous or unlikely to cause harm, and these have received little attention. In contrast to a carnivorous predator that can kill many individuals of its prey, or an omnivorous predator that directly affects populations of both animals and plants, some predators have relatively small individual impacts. However, when these predators are present in large numbers, they can significantly reduce seabird populations. The community- and ecosystem-level consequences of such predation remain understudied.

Mice, despite their small size, can have large effects on seabird populations *en masse*. Though mouse predation on seabirds has been mostly ignored, on Gough Island they were filmed killing birds over 300 times their size *via* many individual bites to the body cavity, nearly driving the Tristan albatross to extinction (Wanless et al. 2007). Mice eat mainly invertebrates (Marris 2000), but seabirds may subsidize their populations in some cases. At very high densities, mice may cause hyperpredation on island invertebrates, both terrestrial and intertidal, thus competing with local birds for prey (Angel and Cooper 2006). Changes in invertebrate communities could also potentially alter ecosystem processes such as decomposition. Rats, if present, usually suppress mouse populations (Russell 2011), but this makes mouse effects harder to evaluate, as well as elevating the risk of a mouse boom following rat eradication.

Despite extensive predation by invasive mammals, the biggest pending threat to seabird islands may be a tiny insect, albeit a colonial one. At least five species of ants are currently spreading throughout the tropics, with known negative consequences for native vertebrates: tropical fire ants (*Solenopsis geminata*), red imported fire ants (*S. invicta*), yellow crazy ant (*Anoplolepis gracilipes*), Argentine ant (*Linepithema humile*) and little fire ant (*Wasmannia auropunctata*; Plentovich et al. 2009). In Hawaiʻi, shearwater chicks displayed foot injuries from ants so severe that up to 20% did not fledge on islands invaded by tropical fire ants (Plentovich et al. 2009).

As invaders, ants are poised to greatly reduce global invertebrate biodiversity (Holway et al. 2002); they are probably a significant threat to land snails, which exhibit high levels of endemism, as well as to land crabs (Drake et al. 2011). Ants were implicated in the most dramatic incarnation of an "invasional meltdown": where multiple non-native species facilitate each other, moving the entire ecosystem toward an alternative state (Simberloff and Von Holle 1999). On tropical Christmas Island in the Indian Ocean, multi-queen "super-colonies" of crazy ants extirpated the local red land crab, which was a keystone species regulating seedling densities and decomposition of leaf litter (O'Dowd et al. 2003; Mulder et al. 2011a, Box 4.2). The ants also formed mutualisms with introduced honeydew-producing scale insects, whose populations exploded, leading to an outbreak of sooty mold that killed canopy trees. The forests of Christmas Island function very differently now, and it is questionable whether such an altered system can ever be restored. Without constant monitoring, increasing human traffic to islands will encourage unchecked invasions that interact in this way. This makes inconspicuous species like ants a particularly serious threat.

2.3.5 Susceptibility of island biota to introduced predators

Island isolation can be an advantage — isolated islands are rarely invaded — but their isolation becomes a disadvantage when they *are* invaded. Since such islands usually lack predatory mammals, other island animals usually lack evolved defenses against them, exhibiting "island naïveté" (Towns et al. 2011b, Drake et al. 2011). However, some groups are clearly more vulnerable than others. This depends mainly upon size, which influences the predator's choice of prey, plus a combination of motility and habitat use, which determines the predator's opportunity.

We have already discussed why seabirds in general are poorly defended against invasive predators, endangering the island ecosystems that depend upon seabird nutrient inputs and disturbance regimes. Smaller-bodied seabirds, e.g., storm petrels, tend to be most vulnerable to predation by invasive rodents, while larger-bodied birds, e.g., albatrosses, are generally less vulnerable (but see examples above; Jones et al. 2008). Ground nesters and burrow nesters also tend to be more vulnerable than tree nesters and crevice nesters to some superpredators, i.e., foxes (Byrd et al. 2005), but burrow nesters rebound most quickly when invasive predators are removed (Towns et al. 2011b). Land birds that nest or forage on the ground are similarly at risk, especially those that have evolved flightlessness (Drake et al. 2011). However, land birds in the tropics may be slightly less vulnerable, since they evolved with land crabs and so have not entirely lost their anti-predator defenses (Atkinson 1985).

Size and habitat use also determine the vulnerability of invertebrates to invasive mammals, with large-bodied, flightless adult insects and larvae at greater risk than small, mobile species or life stages (Drake et al. 2011). Those that spend more time on the ground or in the slow-moving larval stage provide predators with greater opportunity, while insects that use sheltered crevices may less at risk (e.g., New Zealand weta, Gibbs 2009). Land crabs and land snails are of particular concern because of their keystone species status and their endemism, respectively (Drake et al. 2011). On the one hand, large-bodied and slow-moving invertebrates may be easier to monitor and more likely to garner support for their protection. On the other hand, smaller, more inconspicuous invertebrates may be easily overlooked, yet crucial to ecosystem function in as-yet unforeseen ways.

Size appears to be slightly less important to the vulnerability of island herpetofauna and native mammals. Though some herpetofauna are more vulnerable as juveniles than adults (e.g., tuatara [*Sphenodon punctatus*], Towns et al. 2007) the most vulnerable are ground-dwelling, nocturnal species (qualities which increase predator opportunity) with low fecundity (Drake et al. 2011). Native mammals are a slightly different case, though size influences their susceptibility in some cases (Dickman 1996). Coastal islands are often home to relict or endemic species that are closely related to invasive mammals, making them susceptible to disease transmission, e.g., trypanosomes, bubonic plague, and *Salmonella* (Drake et al. 2011). Native mammals also may compete with invasive predators for prey, an indirect effect that is poorly understood.

2.3.6 Directions for future research

It is not always clear whether native plant and animal declines are due to direct effects (predation, herbivory, physical damage) or indirect effects (competition for prey, disruption of mutualisms such as pollination). Interactions between multiple invading species are poorly understood and deserve further research, especially those involving the three species of rat, which coexist but inhabit slightly different ecological niches. Predator impacts on amphibians and smaller invertebrates are largely unknown, and few studies have examined how insect community shifts may propagate indirect effects on island processes such as pollination and decomposition. Very little work has addressed island plant vulnerability to invasive herbivores. Finally, the effects of inconspicuous species like ants on seabird colonies and island ecosystem functioning deserve far more attention, considering the likelihood of further ant invasions and their potentially devastating consequences.

2.4 Restoration of Seabird Islands after Predator Invasion

Whole-ecosystem restoration is the "acid test" of ecology (Bradshaw 1987) and predator eradication is the obvious first step to restoration. However, eradication may have unintended consequences that must be actively addressed if recovery is to continue (e.g., population explosions by mesopredators, Russell 2011). Even removal of all the non-native species on an island does not necessarily lead to passive island recovery. Recreating island communities may depend upon the reintroduction of species extirpated by invasive species. If predators have caused a shift in vegetation communities, vegetation management may be needed to supply habitat for desirable "target" species (e.g., terns, Jones et al. 2011). In many cases, predator eradication is *necessary* but not *sufficient* for ecosystem recovery, and the island must be actively restored if the ecosystem is to function comparably to a reference site.

2.4.1 Constraints of predator identity on eradication projects

Different predators pose different cultural and technological challenges for the island manager. For example, many people have a cultural affinity for cats because of their history as human pets. Though feral cats are the most damaging seabird predators worldwide, it may be hard to gain societal acceptance for their eradication. Foxes, on the other hand, may make easier targets for eradication because of their use for centuries in the fur trade. Their distribution on islands is also limited to colder archipelagos (Towns et al. 2011b), in front of fewer public eyes. Eradicating any superpredator, however, carries the risk that mesopredator populations will rapidly increase in their absence, causing hyperpredation on seabird or other target populations. To address this risk, multiple-predator eradications are becoming more common, but these carry their own logistical challenges (Dunlevy et al. 2011). Because superpredators' main effects on islands are reductions in various prey populations, restoration of prey populations (if possible), especially keystone species such as seabirds, may be enough to restore island functioning.

Omnivorous predators present their own set of challenges. Rats are commonly seen as pests, though some animal rights groups do not agree (Dunlevy et al. 2011, Jones et al. 2011, and Towns et al. 2011a), and the Pacific rat holds important cultural significance for some Polynesian peoples (e.g., the Māori of New Zealand). Because of a long history of rat removal in urban and farm settings, the technology available for their eradication was available early (1950s) and has undergone many recent developments to improve specificity and cost-effectiveness at larger scales (Dunlevy et al. 2011). Pigs have mostly been introduced to islands as a food source, which has led to their inclusion in cultural traditions; many hunting groups advocate for their continued presence in coastal forests, even where they are known to be extremely destructive (Hawai'i; Atkinson and Atkinson 2000). Removing omnivores from islands can lead to unexpected effects because of their direct effects on vegetation (Drake et al. 2011). For example, pigs have been linked to the wide-range dispersal of invasive plants, which may be released from herbivory and thus proliferate in the pigs' absence.

Seemingly innocuous predators such as mice and ants may be the hardest to remove from islands, for two reasons. First, the threats from such animals are not well studied, and their removal may not become a priority until negative effects are very pronounced. Second, development of the technology for their removal has lagged behind that of larger, more conspicuous predators. Eradication of ants from islands is extremely difficult, although the big-headed ant (*Pheidole megacephala*) has been eliminated from several parks and offshore islets using hydramethylnon (Plentovich et al. 2009 and references therein). Because they have been largely overlooked and their effects may be unexpected, island monitoring in these cases may show the greatest potential for the discovery of surprising ecological mechanisms and unforeseen interactions among species.

Regardless of predator identity, once the predators are removed, post-eradication monitoring of islands is not a scientific luxury, but a management necessity. First, biosecurity is essential for successful restoration (Dunlevy et al. 2011): if the island is re-invaded but it goes unnoticed, predator populations will increase again and the project will fail. Second, if toxins are used in the eradication, non-target organisms must be monitored and the environmental fate of the poison tracked. This process can provide data for assessing risk in future projects, as well as reassuring stakeholders that the project was carried out safely and in compliance with environmental regulations (Dunlevy et al. 2011). Finally, target populations such as seabirds must be measured to evaluate the outcome of the project. Public support for such projects is largely based on the utilitarian premise that removing introduced predators will allow target pre-invasion biological communities to rebound (or to be actively restored). Reporting a project's benefits for island biodiversity is therefore an opportunity to strengthen public support. Failing to measure or to report positive outcomes may actually have negative consequences, by allowing those opposed to predator eradication in general to argue that the costs and risks of such projects outweigh their benefits (Dunlevy et al. 2011).

2.4.2 Restoration of island species: seabirds and more

We have described how island soils depend upon seabird nutrient additions and disturbance regimes, which affect plant nutrient balance and determine plant community composition. The hope for most island eradication projects is that seabird populations will naturally recover once the predator population is removed, and the island ecosystem will recover, unaided, in response to increased seabird presence. If seabird populations do not naturally recover, active restoration may be required, including chick translocation and social attraction (decoys, mirrors, and acoustic playback; Jones et al. 2011). However, while seabird population recovery is *necessary* to restore island functioning, just like seabird predator eradication, it may not be *sufficient*.

In many cases, the island species pool will have undergone deletions and additions that must be actively remedied with reintroductions or further eradications before island ecosystem function can recover (Fig. 2.1). For example, ornithogenic plant species may be lost from the island species pool in the absence of seabird nutrient inputs and disturbance. Predators, especially omnivores, can also act as filters influencing the island plant species pool—both directly, by consuming and potentially extirpating plant species or introducing new ones, and indirectly, by cutting off the seabird nutrient supply and disturbance, favoring species that might have been suppressed by seabirds. Higher trophic levels are likely to undergo similar selective pressure as an island transitions from seabird-dominated to predator-dominated (after invasion) and back again (during restoration).

Weed outbreaks are a likely, though often unexpected, outcome of restoration projects. New plant species can be introduced during seabird exclusion, and vegetation management may be needed during seabird recovery and reinstatement of their nutrient and disturbance regimes. This can include removal of non-native plants released from other pressures such as non-native herbivores. For example, eradication of non-native rabbits from Motunau Island in New Zealand required management of the non-native spiny tree *Lycium ferocissimum*, which can form thickets that exclude burrowing seabirds (Taylor 1968, Lawley et al. 2005).

2.4.3 The necessity of institutional leadership and collaborations

Globalization of conservation will increasingly require cooperation among government, non-profit, and for-profit institutions. On islands, the focus generally has been on restoring seabird populations rather than whole island ecosystems. Perhaps this is because islands, being terrestrial in nature, fall under the jurisdiction of one or more particular nations. However, island restoration must ultimately involve institutional leadership to help stakeholders arrive at measureable goals, and only relatively large institutions are capable of providing the long-term financial support to ensure island biosecurity and monitoring of island communities and ecosystems (Dunlevy et al. 2011). Institutional support is also necessary to aspire to the highest standard of ethics in eradication of invasive animals: specifically, that the most humane method available is used (short-term), that the humaneness of the available methods is actively improved (medium term), and that new, increasingly humane methods are actively developed (long term; Littin et al. 2004). Few local groups can mobilize the resources to develop new eradication methods and test new technology, which is important to ensure that introduced predators are removed from islands with as little suffering as possible.

There are caveats, of course, to this sort of international collaboration. Ecological knowledge and techniques tested in one system may not transfer to another. For example, the New Zealand method of rat eradication involves supplying poison bait at the time of year when other food supplies are diminished, making it more attractive and more effective. However, in the tropics, where resources are not allocated seasonally, this strategy may need rethinking (Dunlevy et al. 2011). Tropical islands face other difficulties, such as quicker decomposition of poison bait in the warm climate, which may require the pioneering of new, system-specific methods. Furthermore, not all seabird predators are widely distributed. This fact may actually impede collaboration on post-eradication restoration efforts, because eradication has been the main focus of international collaborations.

2.4.4 Setting goals and working with stakeholders

Setting manageable goals requires acknowledging human value systems and collaborating with stakeholders. The scope of the problem requires involving more local people in island restoration, from planning and financial support to active stakeholder participation. Ideally, stakeholders would initiate the project and seek institutional collaboration for planning assistance, (e.g., restoration of islands for traditional cultural use, such as subsistence harvest of seabirds by New Zealand Māori). In any case, planning personnel must begin discussions with local stakeholders early, or locals may become part of the problem rather than part of the solution, as when animal rights activists sabotage predator eradications (Towns et al. 2011a). All parties should clearly define project goals at the outset so success can be measured—both in biological and social terms. Some islands might be managed for particular species, some for preservation of open spaces and recreation, some for scientific research, and some for whole-ecosystem restoration (Jones et al. 2011). Some of these goals will require limited public access. In this case, education programs explaining the vulnerability of island biota may be critical to success. Most conservation volunteers want to make a difference or to feel a connection to nature (Miles et al. 1998); this goal may be enhanced with environmental education. Post-eradication monitoring is ideal work for local stakeholders, because it can motivate continued participation (Forgie et al. 2001) and increased ownership of the restoration outcomes (Towns et al. 2011a).

Regardless of institutional support, international collaborations and local participation, resources for conservation will always be finite, making some type of prioritization scheme necessary. With cost data (e.g., supplies, logistics, and labor costs) and a well-defined goal, cost-benefit analysis may be useful for conservation decision-making at many scales. Both terrestrial and marine biodiversity hotspots, as well as Important Bird Areas of the world, have already been prioritized at the global scale for the goal of stemming biodiversity loss (www.biodiversityhotspots.org, www.starfish.ch/reef/hotspots.html, www.birdlife.org/action/science/sites/). Island Conservation, an international non-profit specializing in island eradications and restoration, is currently using this approach at the global scale to prioritize potential new directions for their conservation efforts (E. McCreless, personal communication).

2.5 How Will Seabird Islands Respond to Global Change?

In this book we have explained how seabirds depend upon the islands on which they breed, how introduced predators disrupt this relationship and other aspects of the islands' ecology, and how seabird populations and whole island ecosystems may be restored. These lessons have been learned in a rather short period of geologic time, only about half a century. Over this time period, vast climatic, biological, and socio-political changes have taken place, and these will continue to influence the trends we have described. In fact, because seabird islands may be influenced not only by changes acting directly upon the terrestrial environment, but also by changes in seabird populations and changes in the ocean-based environments that support them, seabirds and seabird islands are important indicators of global change.

2.5.1 Defining global change

We define "global change" in the broadest possible sense. Climate change is included, but only as part of the collective ongoing changes wrought by human, animal, geologic, and chemical agents. These many influences can be organized as two nested sets of threats to seabird islands (Fig. 2.2). Invasive species and habitat loss act mainly upon the terrestrial environment of seabird islands. Pollution, overharvest and climate change also act directly on islands (e.g., ocean-borne plastic washes up on beaches), but on a much larger scale, they threaten global seabird populations where the birds spend most of their lives: at sea. Those seabird islands that escape the smaller set will still experience the larger set, because seabirds are the lynchpin connecting the marine and terrestrial systems.

Organizing the agents of global change in this way is admittedly artificial, because categories may overlap (e.g., habitat loss *via* sea level rise). Also, their effects on seabird populations as well as islands are likely to be synergistic. For example, seabirds in poor condition due to climate-related decreases in prey probably have lower contaminant tolerances; islands where seabird habitat has been converted for human use are more likely to undergo plant and animal invasions. We chose these categories for two reasons. First, they correspond somewhat to E. O. Wilson's five principal threats to all wildlife: habitat loss, invasive species, pollution, (human over-) population, and overharvest (2006). Second, the nature of the two nested sets points to possible strategies for risk mitigation. In some cases, island-based threats (invasive species and habitat loss) are easier to address because they are locally based; however, these local threats are globally distributed, and not all localities possess the will or resources to address them (Towns et al. 2011a). Despite this, the continuing globalization of island conservation, as well as the growing pool of data and success stories from predator eradications and island restorations, provide hope and guidance for the future (Dunlevy et al. 2011, Jones et al. 2011). In contrast, ocean-based threats to seabird populations (pollution, overharvest, climate change) require international solutions. Fortunately, due to their charisma, seabirds are well-suited to rallying international support, as demonstrated by the popularity of global pacts like the 2009 Agreement for the Conservation of Albatrosses and Petrels that protects 29 seabird species, with 13 member countries.

This book's focus is the terrestrial ecology of seabird islands. To that end, we have dedicated much of this book to evaluating the effects of invasive predators as the most important threat to seabirds and other island biota, as well as describing the habitat losses and changes in ecosystem function that result from predator invasions. Nevertheless, it is important to view our current knowledge through the lens of global change to evaluate what predictions can be made and what data stills need to be collected. Thus we will briefly examine the other important agents of global change we have identified, indicating where our conclusions allow us to predict community and ecosystem responses *on islands* and where future networks and collaborations may prove useful.

2.5.2 Ocean-based threats to global seabird populations

A full review of the myriad studies concerning direct effects of global change on seabird populations is outside the scope of this book, and this pursuit has been undertaken by seabird biologists elsewhere (Nettleship et al. 1994, Melvin and Parrish 2001). Because of their long life spans and low fecundity, survivorship of breeding-age adults is most important to the stability of seabird populations, and it is this life stage that is endangered at sea. In addition, many seabird species range extremely long distances to forage (Smith et al. 2011). These two facets of seabird biology make it difficult for population studies (usually based on breeding birds on islands) to relate a population decline to an oceanic threat, but they also emphasize the global nature of these birds and the potential of international cooperation to ameliorate such threats.

Humans and seabirds are both predators, competing for a share of the ocean's fish and invertebrates. This brings the two into close contact, sometimes turning humans into incidental predators of seabirds. High seas drift netting is no longer a significant threat due to an international moratorium (United Nations Resolution 46/215), but some previously affected species, like the sooty shearwater, are still recovering from decades-long declines (Towns et al. 2011b). Pelagic long lines disproportionately affect larger, longer-lived species such as albatrosses and petrels (Cooper et al. 2001), and some nations are actively addressing this risk (e.g., the United States National Bycatch Strategy). Furthermore, new tools such as bird-scaring lines and weighted hooks on longlines, have been proven to reduce bycatch (Melvin and Parrish 2001). Gillnets and setnets drown a large number of birds annually (reviewed in Zydelis et al. 2009), but the gear is set closer to shore than longlines, endangering a different and probably less vulnerable set of species. The trawling fisheries of both Northern and Southern hemispheres were once overlooked, but are now emerging as a major concern, especially because most birds killed by them cannot be counted under standard observer protocols (Moore and Zydelis 2008, Ryan and Watkins 2008). Species that routinely travel between the Northern and Southern hemispheres to forage may be susceptible to incidental take by more than one fishery (Towns et al. 2011b).

Observer data are key to modeling the population-level effects of bycatch, but rarely is observer coverage sufficient to account for the variability in this kind of data (Moore et al. 2009). Various indices can be computed to uncover potential seabird-fisheries conflicts (Duffy and Schneider 1994) and to decide whether the level of incidental take is sustainable (Dillingham and Fletcher 2008). However, poorly regulated or enforced fisheries, e.g., pirate fishers for Patagonian toothfish near the subantarctic Prince Edward Islands (Nel et al. 2002), may not observe national or international solutions.

A more insidious result of the fishing industry, for seabirds, may be the overwhelming global decline in fisheries harvests, indicating overharvest of the world's marine resources (Jackson et al. 2001). Indeed, development of pelagic fisheries in Peru and Namibia, with the subsequent decline of small prey fish, has been linked to seabird declines (Schaefer 1970, Crawford and Shelton 1978). "Fishing down the food web" (e.g., Pauly and Palomares 2005) means less prey for seabirds, greater energetic costs in finding it, and greater risk of competition with human fisheries.

Climate change has also taken its toll on the world's marine life, impacting the numerous prey species that support seabird populations worldwide. Climatic events such as the El Niño Southern Oscillation (ENSO) and the North Atlantic Oscillation (NAO) have both been correlated with decreases in seabird populations (Duffy 1993), though sea surface temperature (SST) is often the simplest covariate (e.g., Sandvik et al. 2005). A warmer overall climate may benefit those seabird species living in regions that are colder than optimal for their species, and less philopatric seabirds like auks and gulls may expand their range into areas where the new climate suits them (Hamer 2010). Of course, prey species will respond this way as well. This can lead to a temporal mismatch between prey availability and the bird's seasonal needs, causing prey-switching, e.g., from copepods to euphausiids (Hipfner 2009). Prey-switching and range-expanding competitors may alter the seabird community in as yet unforeseen ways. For example, Stempniewicz et al. (2007) put forth a hypothetical scenario in which subtle shifts in ocean hydrology between Arctic and Atlantic water masses could restructure the plankton community to favor small plankton, fed upon by small fish. In this scenario, piscivorous, cliff-nesting seabirds would gradually replace planktivorous burrow-nesters, decreasing the seabird nutrient additions to inland sites.

Finally, seabirds encounter a wide variety of contaminants at sea. Public attention has focused on plastic and oil because their direct effects are demonstrable and grotesque. In one observation, researchers witnessed Laysan albatross regurgitating plastic meals for their chicks (Young et al. 2009). Seabirds, especially Procellariids, ingest either whole plastic trash items (cigarette lighters, bottle caps), or else the raw plastic pellets ("nurdles") that remain when the item has physically weathered (Furness and Monaghan 1987). Plastic ingestion can block the digestive tract, or alternatively satisfy the bird's hunger, leading to less return for foraging effort. Unfortunately, the magnitude of this risk is poorly understood (http://marinedebris.noaa.gov).

Oil immediately destroys feather waterproofing and insulation, making birds susceptible to exposure, and when transferred to eggs, it may suffocate the embryo and keep the egg from hatching. Many seabirds have been oiled by catastrophic tanker spills like the Exxon Valdez in 1989, which killed an estimated 100,000 to 300,000 birds (Piatt and Lensink 1989). It is too early to tell how many seabirds may have been affected by the Deepwater Horizon disaster in 2010, wherein an offshore oil rig exploded, all equipment fail-safes subsequently malfunctioned, and over four million barrels of oil poured into the Gulf of Mexico over several months. However, despite the media attention given to large accidents, small, chronic inputs may be the greater ongoing hazard to seabird populations, especially during winter, when hydrocarbons degrade more slowly (Nisbet 1994). Fortunately, chronic oil discharges in some regions appear to be declining (Wilhelm et al. 2009).

Far less visible contaminants are an emerging concern. Organochlorines and heavy metals may bioaccumulate in individual animals because of slow excretion rates, then biomagnify up the food chain to become very elevated in marine predators like seabirds. Organochlorines like DDT and PCBs are stored in body lipids and become harmful when fat reserves are mobilized, causing eggshell thinning and impaired reproductive success, as in the California brown pelican. Heavy metals (Hg, Pb, Cd, and metalloid Se) are more easily excreted, except for toxic methyl-mercury (MeHg), which bioaccumulates in marine mammals and seabirds (Atwell et al. 1998; for seabirds as Hg bioindicators, see Monteiro and Furness 1995). While all of these contaminants significantly affect some seabird species, no species is currently known to be in decline solely due to these threats (for review, see Nisbet 1994). The effects of pollution are probably synergistic with other threats, including climate change (Miljeteig et al.

2009). Wide-ranging seabirds are likely to carry some of these chemical contaminants back to their breeding grounds, where their effects may be diluted or else accumulate in other island biota.

2.5.3 Island-based threats to communities and ecosystems

The island as a self-contained ecosystem makes an iconic cartoon, but all islands depend upon the oceans and the atmosphere, which are increasingly subject to anthropogenic change. While the above agents of global change act upon island ecosystems *indirectly, via* seabird populations, all agents of global change also act *directly* upon the islands themselves. Though the smaller set of agents (invasive species and land use change) may affect individual islands differently, these are threats faced by seabird islands worldwide.

Widespread biological invasions are a critical component of global change (Lubchenco 1998). Much of this book describes the introduced predators of seabirds, their consequences, and their eradication from islands. However, introduced herbivores and plants may also have deleterious effects on seabirds and seabird islands. For example, rabbits can graze island grasslands bare, causing erosion, and feral goats can minimize tree recruitment, changing forest to scrub within a single decade (Atkinson and Atkinson 2000). Exotic plants may eliminate seabird habitat or compete with other island vegetation for space, nutrients, and light. Introduced palms, widely distributed across the Pacific, create an environment unfavorable for seabirds and native forests, arresting succession and sustaining a low-nutrient alternative stable state (Young et al. 2010). However, non-native tree mallow (*Lavatera arborea*, Malvaceae) is an integral component of the plant community on petrel- and penguin-dominated Motunau Island, New Zealand (Hawke and Clark 2010), although the same plant severely degrades puffin habitat on Craigleith Island, Scotland (van der Wal et al. 2008). Therefore, the resilience of seabird islands to such invasions probably depends upon the nature of the invader(s), the climate and vegetation of the individual island system, and the identity of the seabirds present.

Islands often hold extractable resources. Seabird islands have been exploited for their stocks of guano for over 100 years in Peru, South Africa, Namibia, the Caribbean, and across the Pacific (Duffy 1994, Skaggs 1994, Safina 2002). Guano was used for fertilizer and explosives manufacturing before development of the Haber-Bosch process, and nations fought wars (e.g., the Chincha Islands War involving Spain, Peru, and Chile) and enacted legislation (e.g., the United States' Guano Islands Act of 1856; Skaggs 1994) to keep it cheap. Guano as a fertilizer is poised for a renaissance because of the increasing popularity of organically farmed foods. However, an unsustainable approach to guano extraction can destroy seabird habitat, as on Christmas Island (Reville and Stokes 1994) and the Xisha archipelago of China (Hsu and Melville 1994).

Past military uses still threaten island biota with radioactivity, chemical storage, and unexploded ordinance. Remote islands are often conveniently situated for military bases, e.g., the Aleutians; coastal islands often become training ranges, e.g., San Miguel of the Channel Islands (Mulder et al. 2011a). Many of these are now abandoned, and some have been returned to public ownership as nature reserves, e.g., Palmyra Atoll. Several Pacific islands used for nuclear tests, such as Bikini Atoll (Marshall Islands), are still unfit for human habitation due to high levels of radioactivity (Emery 2004), but seabirds nest on them anyway (Garrett and Schreiber 1988).

Compared to resource extraction, ecotourism seems a non-destructive use of seabird islands, but in some cases, it has caused seabird disturbance (e.g., the Gulf of California; Velarde and Anderson 1994). However, when undertaken carefully, tourism can be highly beneficial for islands. For example, Chumbe Island, Tanzania, was purposefully converted into a nature reserve for tourists, and the surrounding waters protected as a no-take marine reserve (Towns et al. 2011a). This project garnered "sustainable tourism" industry awards while eradicating invasive predators and hiring locals to work as rangers in the park.

Humans have long harvested seabird adults, chicks, and eggs for food, feathers, oil, and sometimes merely for sport (Safina 2002). This practice continues on a much smaller scale today as a cultural tradition of subsistence hunting, on islands from Alaska (gull egging by the Tlingit, N. Catterson, personal communication) to New Zealand ("muttonbirding" by local Māori, Wilson 2004). Historically, overharvest of some birds has led to extinction, but sustainable harvests are possible if the take coincides with a period of naturally high mortality for that life stage (Wilson 2004). Seabird populations are best ensured by close cooperation and trust between stakeholders and regulatory agencies (Moller et al. 2009), but the results of illegal harvest deserve further study (Baker et al. 2004).

In addition to its effects on ocean productivity and global seabird populations, climate change will directly affect islands and their inhabitants. Sea level rise is predicted to swamp many of the world's smaller islands, decreasing available seabird habitat. The Maldives, a low-elevation island nation, is already planning for such contingencies (Ramesh 2008). Even under less dire projections, climate will interact with seabird effects to alter ecosystem functioning. For example, seabirds tend to increase plant drought stress as measured by $\delta^{13}C$ (Mulder et al. 2011b), making island vegetation more vulnerable to increasingly warmer, drier conditions predicted with climate change. Increased frequency and severity of storm events will threaten larger plants already destabilized by seabirds (Fig. 2.3), opening light gaps and possibly affecting plant community composition. However, some trees, e.g., the widespread tropical species *Pisonia grandis*, are pre-adapted to these conditions and reproduce vegetatively when storm-damaged (Mulder et al. 2011a). Finally, because seabird nutrient runoff during storms probably exerts strong temporal control over nearshore aquatic productivity (Young et al. 2011), more frequent ENSO events may alter the timing of nutrient dispersal in nearshore marine waters, influencing the terrestrial-marine feedback loop.

2.5.4 Predicting island responses to global change

Unfortunately our current knowledge of seabird island ecology leads to few detailed predictions of island response in the face of global change. Although we compared island systems representing a significant range of latitudes, vegetation types, seabird taxa, and nesting guilds, data from our research network are not suited for this type of modeling. Further collaborations are clearly necessary to address research questions at this scale. For some aspects of global change, research can be effective by substituting space for time; for example, comparing seabird islands with and without predators has shown how ecosystems will be altered as predators continue to invade islands around the world. However, this approach only goes so far. For extrapolations of climate change to seabird islands, biologists will have to collaborate with meteorologists and oceanographers.

Seabird biologists already monitor and model regional seabird populations against the backdrop of changing sea temperatures, prey availability, etc. Ecosystem-level changes on islands are strongly controlled by changes to marine nutrient additions, which are driven by changes in seabird density. Thus, modeling changes in seabird nest density is a good place to start; it is relatively easy data to gather, and seabird biologists usually need it anyway. Uncovering how such changes are likely to propagate throughout the island ecosystem will require monitoring other island populations and communities at various seabird densities. Yet this approach still will not address the direct threats to islands that may or may not be mitigated by seabirds. Clearly, we need long-term data on seabird island ecology if we are to uncover trends over time.

In a perfect world, all variables on all islands could be monitored cheaply and remotely. In reality, monitoring can be expensive and is often considered a luxury rather than a necessity, even when biosecurity depends upon it (Dunlevy et al. 2011). We suggest prioritizing several geographic areas, then broadening this set as resources allow, or as need for the data expands. First, baseline data collection should be focused on archipelagos located in regions undergoing the most rapid climate changes: the Gulf of California (increasing ENSO cycling), the Aleutians (increasing ocean salinity), the French Mediterranean (increasing fire frequency with drought), and low-lying Pacific atolls (rising sea levels). Monitoring of subantarctic islands is also important because of the enormous distances commuted by the seabirds that nest there, so that changes in seabird densities may actually reflect climate change effects elsewhere. It is similarly important to monitor coastal islands (e.g., French Mediterranean islands near Marseilles, coastal North Atlantic islands), which may reflect terrestrial, anthropogenic influences such as gull expansions driven by food availability at landfills, rather than marine ones. Most importantly, data collection must be standardized to allow comparisons between systems, simultaneously maximizing the use of resources and broadening the scale of research.

2.6 Understanding and Protecting Seabird Islands: A Way Forward

Up until now, comparisons of multiple island systems have focused mainly on seabirds (e.g., Nettleship et al. 1994) or invasive predators (e.g., Veitch and Clout 2002), rather than on the islands themselves. By collecting data on soils and plants from island systems representing a wide range of climates and vegetation types, we were able to explore how seabirds influence island nutrient cycling and plant communities. We were unable to test statistically how these effects propagate to primary production, to higher trophic levels, or to marine feedbacks, because the data collected were either insufficient or incomparable across systems. We were able to point out areas where system-specific characteristics—climate, vegetation type, seabird identity, or location—might alter the general relationships between seabirds and the islands they inhabit, though we could only suggest (not test) the mechanisms at work. Through cross-system analysis we were also able to point to the most damaging and widespread invasive predators on islands, for seabirds as well as for other island biota, and case studies allowed us to suggest qualities that increase vulnerability for various island taxa. We have also identified areas where more research is needed: further data collection in specific areas, future collaborations with other areas of expertise (e.g., climate modeling), and monitoring islands over time.

Cross-system analyses have been invaluable to our efforts at uncovering emergent trends in seabird island ecology. We suggest that this approach could be even more useful with the standardization of data collection techniques and the willingness of researchers and conservation personnel to collect a "standard" dataset on each island they visit. These baseline data become more important when conservation actions are put into place, because outcomes can be measured over time. Usually, the effects of predators on island communities and ecosystems remain unknown because they can only be directly measured where data exist both *before* and *after* either invasion or eradication. These data would allow the cross-system comparisons that this book was unable to accomplish: those related to island conservation outcomes. Consistent monitoring is critical to evaluating and improving restoration techniques, thereby making conservation more cost-effective in the long run.

Our progress in understanding the ecology of seabird islands, eradication of introduced predators, and restoration of islands, together with recognition of the threats facing seabirds and seabird islands at the global scale, also informs the larger issue of how to remedy the global biodiversity crisis (reviews of the crisis and various solutions: Western 1992, Lubchenco 1998, Singh 2002, Wilson 2002, Kingsford et al. 2009). In order to protect biodiversity on seabird islands, protecting seabirds is essential, and the greatest threat to most wildlife is habitat loss (Wilson 2006). Because seabirds depend on both land and sea, we must look to the state of both their marine and terrestrial habitats. Unfortunately the majority of islands worldwide are located in regions where biodiversity is most at risk. Of the terrestrial diversity "hotspots" listed by Conservation International for their high endemism and high rates of habitat loss, 10 out of 34 are composed of archipelagos, including the Philippines with over 7,100 individual islands (www.biodiversityhotspots.org). Almost all of the coastal hotspots include offshore islands as well. Most are located in the tropics, where introduced predators are poised to wreak the most havoc (Towns et al. 2011b, Drake et al. 2011). Much of seabirds' habitat at sea is also at high risk of biodiversity loss, which could endanger its ability to support seabirds in the future. Marine hotspots of endemism and risk include coral reefs, especially in the tropics, coinciding with many of the terrestrial hotspots noted above (Roberts et al. 2002). However, some seabirds travel long distances to forage at productive cold-water seamounts or upwelling areas along underwater ridges or coasts (e.g., Duffy 1989, Louzao et al. 2006, Morato et al. 2008, Amorim et al. 2009), and these highly productive areas bring them into direct conflict with humans. Ideally seabirds would be protected by land and sea, and they would continue to function as nutrient transporters and disturbance agents for the islands they support, which in turn harbor them from predators.

In *The Future of Life*, Edward O. Wilson proposes a multi-pronged solution to stemming global biodiversity loss (2002), which takes place in three stages of habitat protection: 1) creation of nature reserves that are legally protected from human disturbance; 2) restoration of degraded land surrounding these protected areas, enlarging their footprints to further protect the core; and eventually 3) linking existing parks and reserves by protected corridors, thereby rebuilding wilderness. Islands, however, do not fit neatly into this terrestrial model of conservation. They are already isolated by their marine boundaries, which make it possible to remove some threats to biodiversity entirely (e.g. introduced predators, Dunlevy et al. 2011) and also make it likely that, with proper biosecurity, islands will remain free of land-based threats. In addition, seabirds remain unbounded by the terrestrial-marine interface, so in some cases, it is possible for an island to recover its main ecological drivers with little active management (Jones et al. 2011). It is also possible to enlarge the footprint of protection around the island, by protecting and restoring nearby islands, increasing biosecurity for all (Dunlevy et al. 2011).

Ideally, analogous to Wilson's third stage of "rebuilding wilderness," these island habitats would be linked by also protecting the surrounding marine environment. For species of seabirds that feed near their breeding grounds, marine reserves would decrease the potential for seabird-fisheries conflicts (Duffy and Schneider 1994). Ecotourism activities centered on such a marine reserve may have the additional benefit of providing unofficial patrols, if proprietors are educated in the need for biosecurity. Within an archipelago-scale marine reserve, islands could be managed for different levels of public access, with the innermost islands being the most restricted and the outermost islands available for recreation, tourism, or traditional seabird harvests. This approach could boost local economies through fisheries and tourism, create intrinsic rewards for local stakeholders, protect seabirds and other marine life, and preserve whole island ecosystems. In 2008, the small island nation of Kiribati, with many international collaborators, created the largest marine protected area in the world. The Phoenix Islands Protected Area, covering 408, 250 km^2—an area the size of California—includes extensive coral reefs with dense fish communities, large areas of deep-sea habitat, and eight islands, some hosting vast seabird colonies (www.phenonixislands.org). Ultimately, a network of these archipelago-based marine reserves, strategically placed across a range of latitudes and marine environments, could probably protect many seabird species and their island habitats from decline.

Collaboration between marine reserve planners, seabird biologists, and seabird island managers is the key to the "ideal" scenario above, as well as the involvement of national, international, and non-governmental institutions, as well as many local stakeholders. The growing number of actively managed seabird islands around the world is evidence that such collaborations are possible, and that more and more people consider the protection of seabirds and seabird islands a worthwhile conservation goal. This book is also evidence that our knowledge of seabird island ecology, introduced predators and their removal from islands, and how to restore island ecosystems is growing and will continue to grow.

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2.9 Tables

Table 2.1 Summary of the effects of removing seabirds from islands

Change	Pool or property
Decrease	Soil N and P
Decrease	Plant N
Decrease	Soil physical disturbance (compaction / tillage, depending on nesting guild)
Shift	Soil microbe and invertebrate community species composition
Shift	Plant community species composition
Increase	Island-scale plant species richness (plant invasion / dispersal from regional species pool)
Decrease	Regional plant species richness (lost ornithogenic plants)
Decrease	Abundance of some terrestrial consumers
Shift	Prey choice by seabird predators
Decrease	Runoff of nutrients into intertidal zones
Decrease	Marine algal N
Shift	Intertidal community species composition
End Result	Island-scale alternative state?

2.10 Figures

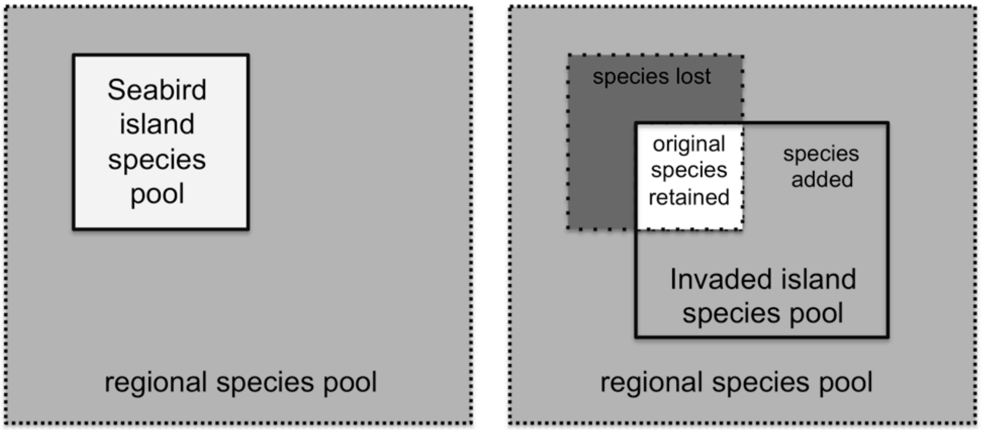

Fig. 2.1 Model of vegetation community on a seabird island before and after invasion (Before, left; after, right.) Seabirds filter out species that can not tolerate high-nutrient, high-disturbance conditions. Some of these species depend upon seabirds and will be lost after invasion. Other species from the regional pool will be added, either facilitated by the invasive predators or released from inhibition by seabirds. For the island community to be restored, some species may need to be actively removed, and other species actively restored to the island.

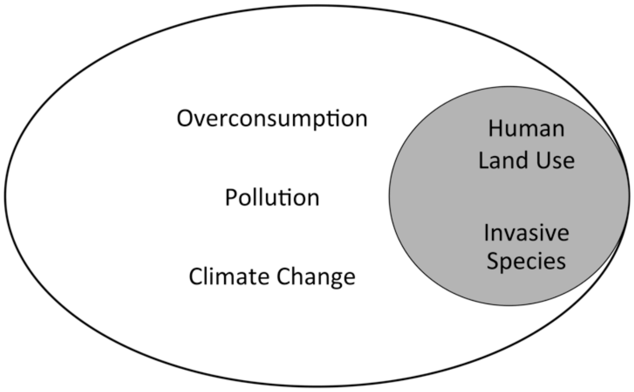

Fig. 2.2 Nested sets of global change threats facing seabird islands. The smaller set causes localized damage to some islands, but the larger set cannot be avoided, because these threats act both directly (on some islands) and indirectly, via regional or global changes in seabird populations.

Fig. 2.3 The roots of *Streblus banksii*, a rare New Zealand tree, are undermined by high densities of burrowing seabirds on Middle Island, New Zealand, threatening the tree's stability especially during high winds. Climate change may further threaten large trees on seabird islands. Photo: M. Durrett.

Chapter 3.

Seabirds as agents of spatial heterogeneity on New Zealand's offshore islands[1]

3.1 Abstract

Aims. This study investigates how burrow-nesting, colonial seabirds structure the spatial patterns of soil and plant properties (including soil and leaf N) and tests whether burrow density drives these spatial patterns within each of six individual islands that vary greatly in burrow density.

Methods. Within individual islands, we compared semivariograms (SVs) with and without burrows as a spatial trend. We also used SVs to describe and compare the spatial patterns among islands for each of 16 soil and plant variables.

Results. Burrow density within a single island was only important in determining spatial structuring in one-fifth of the island-variable combinations tested. Among islands, some variables (i.e, soil pH, δ^{15}N, and compaction; microbial biomass and activity) achieved peak spatial variance on intermediate-density islands, while others (i.e., net ammonification, net nitrification, NH_4^+, NO_3^-) became increasingly variable on densely burrowed islands.

Conclusions. Burrow density at the within-island scale was far less important than expected. Seabirds and other ecosystem engineers whose activities (e.g., nutrient subsidies, soil disturbance) influence multiple spatial scales can increase spatial heterogeneity even at high densities, contrary to current thinking that heterogeneity is greatest in low-resource environments.

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[1] Durrett MS, Wardle DA, Mulder CPH, and RP Barry (in review) Seabirds as agents of spatial heterogeneity on New Zealand's offshore islands. Submitted to *Plant and Soil.*

3.2 Introduction

It has been proposed that spatial heterogeneity is greatest where resources are low, creating new niches that contribute to species diversity (Huston and DeAngelis 1994). However, ecosystem engineers that create or modify the habitat of other organisms (Jones et al. 1994) may alter both resources and spatial heterogeneity. For example, rabbits, voles and marmots fertilize the soil near their mounds, which both increases patchiness and reduces the patch size of soil resources (Oloffson et al. 2008; Questad and Foster 2007; Yoshihara et al. 2010). Where such agents are excluded, the amounts and spatial heterogeneity of these resources both decrease (Bruckner et al. 1999). On the other hand, prairie dogs, pocket gophers and marmots that alter ecosystems via intense bioturbation and/or excessive nutrient additions can cause greater homogenization of soil resources and thereby decrease their spatial variability (Bangert and Slobodchikoff 2000; Sherrod and Seastedt 2001; Yoshihara et al. 2009), in a manner similar to the effects of plowing and fertilization of agricultural croplands (Li et al. 2010; Robertson et al. 1993). If both very low and very high densities of ecosystem engineers can cause increased homogenization of soil resources in an ecosystem, it follows that peak spatial heterogeneity and spatial dependency are likely to occur at some intermediate density of such agents, and this serves as our working hypothesis.

Seabird-dominated islands are ideal systems for testing this hypothesis, because seabirds are well-documented ecosystem engineers (Smith et al. 2011). For burrowing seabirds (order Procellariformes), nests consist of interconnected tunnels up to 3 m long in softened, tilled soil whose surface is scratched bare of seedlings and litter. These birds feed at sea, depositing acidic, mainly insoluble, N-rich guano during takeoff and landings, and annually plowing it under, along with detritus such as feathers, failed eggs and carcasses (Warham 1990). Most species reuse the same nest site each year and prefer to nest in dense colonies, along steep ridges with ledges or tall trees for easy takeoff (Warham 1990). These activities translate to considerable spatial patchiness at the within-island scale (Fig. 3.1), which could create similar spatial patterns in many seabird-engineered ecosystem properties, such as soil N and C, leaf N and C, microbial biomass and activity, and net ammonification and nitrification (Wait et al. 2005).

Despite their colonial lifestyle, seabirds are no longer primary ecological drivers throughout much of their historical range; introduced rats (*Rattus* spp.) in particular have reduced or extirpated seabird populations on islands throughout the world (Towns et al. 2011). Our study took place on offshore islands of northeastern New Zealand and included three islands invaded by European rats (*R. norvegicus* and *R. rattus*) and three that are rat-free seabird sanctuaries, which collectively represent a wide range of seabird densities. Previous investigations have documented numerous seabird effects on island soils: elevated soil δ^{15}N (indicative of marine N inputs), increased N, P, and C, decreased pH and soil compaction (Fukami et al. 2006) and increased microbial biomass, activity, and decomposition rates (Wardle et al. 2007; Wardle et al. 2009). However, no studies on these islands (and just a single study worldwide: Wait et al. 2005) have considered how the spatial patterning of ecosystem properties relates directly to spatial variation of seabird burrows and bird densities.

This study seeks to describe how seabird burrow density influences the spatial patterns of soil and plant properties both within and among islands, by testing the following predictions: 1. Soil and plant properties *within each island* will covary with burrow density over space, and density will be more important for predicting within-island spatial patterns in these variables than will the topography (e.g., slope, aspect, elevation) of the sites in which the where seabirds nest. 2. *Among islands*, we expect that islands with intermediate seabird densities will have the greatest heterogeneity (spatial variance, which includes both structured and unstructured variability) and patchiness (spatial structure or spatial dependency, the ability to predict spatial variance between two points from the distance between them) and the lowest spatial range (spatial grain, the patch size and distance between patches). If fully supported, our among-island hypothesis should hold true for all plant and soil variables that are directly impacted by seabirds at the whole island scale.

3.3 Methods

3.3.1 Study sites

The six islands used in this study are located within 20 km of the east coast of the North Island of New Zealand and have been previously described in detail elsewhere (Fukami et al. 2006; Mulder et al. 2009). They are Te Haupa (a.k.a. Saddle I.; TEH), Motuhoropapa (Noises group; MOP), Motueke (a.k.a. Pigeon I.; MOT), Ohinauiti (Ohinau group; OHI), Ruamahuanui

(Aldermen group; RNI) and Atiu (a.k.a Middle I., Mercury group; ATU). Island areas range from 6 to 32 ha, and the soils are volcanic or sedimentary; soil origin was homogenous over the extent sampled. The climate is temperate and humid; temperatures in 2005 averaged 13.0° C (June) to 18.4° C (January) with 83-91% relative humidity (peaking in June, the Austral winter). Precipitation averages 1250 mm per year, most falling as winter rain. Vegetation is composed of broadleaf evergreen secondary forest and coastal shrubs. Other than seabirds, storms and fire are the main ecological disturbances, but these islands have not burned for several decades, nor was there any sign of recent storm damage during sampling (P. Bellingham, pers. comm.). Canopy cover ranges from 75% to 90%, and both canopy and understory vegetation are less dense where seabirds are present (Mulder et al. 2009).

Seabird burrow densities within these islands range from 0 to > 3.5 burrows m^{-2}. Burrows are sometimes solitary, though they are usually found in small groups or large colonies on steep slopes and high ridges. Three islands in our study (OHI, RNI, ATU) have never been invaded by rats and support colonies of common diving petrels (*Pelecanoides urinatrix*), flesh-footed shearwaters (*Puffinus carneipes*), fluttering shearwaters (*Puffinus gavia*), grey-faced petrels (*Pterodroma macroptera gouldi*), little blue penguins (*Eudyptula minor*), and white-faced storm petrels (*Pelagodroma marina*). In contrast, only grey-faced petrels and little blue penguins are typically found on rat-invaded islands (at relatively low densities; TEH, MOK, MOP).

3.3.2 Data collection

We covered as much ground as possible considering the logistic and topographic constraints of each island (i.e., steep, unsafe slopes, rock faces, and unvegetated beaches were not sampled). The areal extent sampled on each island averaged approximately 1 ha, ranging from ~6800 m^2 on RNI to ~13000 m^2 on ATU. Sampling usually took three days per island, and all island visits took place between February 12 and April 19, 2005. On each island, we placed 35 points haphazardly at least 10 m apart in a rough grid within the forest. Sample points were not chosen on colonies only, but were chosen specifically to represent a range of burrow densities as well as different topographical features such as gullies, slopes, and ridges. At each point, we measured the distance to the nearest three burrows within 5 m in order to calculate burrow density at the plot scale (detailed in Appendix 3.A). For each point we collected soil from the top 15 cm using a 2-cm diameter soil corer. Soil compaction data and leaf collection were limited to fewer than six islands by logistic anomalies. On TEH, MOK, RNI and ATU, we measured soil compaction in the top 10 cm using a Dickey-John soil compaction tester (Auburn, Illinois, USA). On MOK, OHI and RNI, we also collected plant leaves from *Melicytus ramiflorus* (Violaceae), a common, weedy shrub species; at each sample point where it was present, we took the youngest fully expanded leaf from three branches.

Each soil sample (sieved, < 4 mm, and with large roots and debris removed) and leaf sample was oven-dried (60°C ~16 h), ball-milled for homogeneity and analyzed for total C and N, and $\delta^{13}C$ and $\delta^{15}N$, using a PDZ Europa GSL Elemental Analyzer attached to a PDZ Europa 20-20 CF-IRMS. Repeat analysis of the laboratory standard, referenced against Pee Dee Belemnite and IAEA N-1, yielded precision of +/- 0.2‰. We measured soil $\delta^{15}N$ because it is an indicator of marine N input to island soils, and plants reflect this isotopic signature, even years later (Mizutani et al. 1988). We measured leaf $\delta^{13}C$ as an indicator of leaf water stress (Ehleringer et al. 1993), which often increases with seabird burrowing activity, possibly due to root damage (Mulder et al. 2011).

To measure basal respiration (BR, an indicator of microbial activity; Anderson and Domsch 1978) on each soil sample, we weighed soil subsamples (sieved, < 4mm) of 10 g dry weight into glass jars fitted with septa lids, adjusted each sample to 50% water content by dry weight, and pre-incubated jars at 16° C overnight. To measure CO_2 production, we injected 1cc of gas from the headspace of each jar into an Infrared Gas Analyzer (Model ADC-225-MK3, Analytical Development Company, Hoddeson, UK) interfaced with a voltmeter, using CO_2 standard curves to calculate each unknown concentration. Basal respiration was calculated as the rate of CO_2 efflux from the soil over three hours (Wardle 1993). We measured substrate induced respiration (SIR, an indicator of microbial biomass; Anderson and Domsch 1978) in a similar manner, after mixing in an easily assimilated C substrate (powdered glucose; 3% by dry weight) and re-incubating samples for three hours (Anderson and Domsch 1978; Wardle 1993). We measured BR and SIR for one soil sample per sample point. We also measured the pH of a slurry of field-moist soil (< 2 mm) and distilled water (1:2.5 ratio), using a membrane pH meter (H18314, Hanna Instruments, Smithfield, Rhode Island, USA) in the laboratory.

For each soil sample, we calculated net N ammonification as the difference between ammonium (NH_4^+) content in incubated and un-incubated soil subsamples; net nitrification was determined similarly for nitrate (NO_3^-; Robertson et al. 1999). Two soil subsamples (10 g dry weight, sieved <2 mm) were adjusted to 50% water content by weight, and one was incubated in a closed jar at 16° C for 14 days, with the lid opened daily for gas exchange. We extracted both subsamples with 2*M* KCl. Concentrations of NH_4^+ and NO_3^- were determined colorimetrically on a dual-channel Technicon Autoanalyzer III (Robertson et al. 1999).

3.3.3 Data analysis

All variables were analyzed using geostatistics, the branch of statistics that deals explicitly with describing and predicting spatial patterns, and which allows for non-independence of data points (i.e., points located closer together may be more similar than those far apart; Clark 1979). Data analyses were performed in R 2.10.1 (R Development Core Team 2010, Vienna, Austria), using the geoR package (Ribeiro and Diggle 2001). Within each island, results were based on analysis of the semivariogram (SV), a model of spatial semivariance (γ) calculated between all possible pairs of sample points, dependent upon the *lag* distance between each pair of points (Fig. 3.2; Clark 1979). Spatial models can include a component based on random spatial directionality (i.e., anisotropy), so we investigated this possibility, but anisotropic models were uninformative (details in Appendix 3.B). Thus all SVs referred to hereafter are omnidirectional (i.e., isotropic). This is not unusual, as geospatial analyses usually assume isotropy (e.g., Baraloto and Couteron 2010).

The parameters of each SV describe the spatial patterns present in one response variable on one island (Fig. 3.2; Clark 1979); we compared these model parameters across islands with different seabird densities to evaluate support for our hypotheses. For example, the *sill* represents the maximum spatial variance, described here by the asymptote of an exponential model (Fig. 3.2); we compared the SV sills to evaluate patterns in spatial heterogeneity. Measures of spatial aggregation or “patchiness” can also be calculated from the SV as the proportion of structural variance to the total variance of the sill (*PSV*, ranging from 0 to 1; Fig. 3.2). At PSV=0, the nugget (representing variability at very short lags) is similar to the sill; all variation is randomly dispersed (i.e., “not patchy”) and the model poorly explains variation over space. At PSV=1, all variation is explained by the lag distance between points, aggregated into well-defined areas, and the data are thus “extremely patchy.” The final parameter of interest is the *range* of spatial variation (the lag at which the sill is nearly reached; specifically about 90% of the sill for exponential models; Fig. 3.2). A longer range indicates a coarser spatial grain, and if a variable is spatially independent (PSV=0), there will be no spatial range; in this particular study, ranges estimated at less than the minimum lag of 10 m probably represent functionally independent data points.

Spatial models may also include a *trend* variable, with which the response variable consistently varies over space. (In practice, the spatial model is applied to the residuals of a linear regression, removing the linear effect of the trend variable.) We compared the fit of each island’s SV models with and without a linear burrow density trend to determine whether seabirds are spatially linked to each response variable. Similarly, to ensure that the birds’ ecosystem engineering activities predicted spatial patterns, rather than their choice to nest on steep, high ridges, we compared spatial models including elevation, aspect, and slope (with and without burrow density). To compare model fits, we used the likelihood ratio test (LRT; Wilks 1938). The test statistic is calculated by doubling the absolute difference between two maximum likelihood estimates (MLEs): the MLE of the null model (no trend) and the MLE of the alternative model (with a spatial trend). To determine statistical significance of the spatial trend, the test statistic was compared to a χ^2 distribution with degrees of freedom equal to the difference in number of parameters between the models (in our case, df=1) to generate a p-value for each model fit comparison (Wilks 1938).

3.4 Results

Islands with higher densities of burrowing seabirds (i.e., RNI, ATU) had lower average pH and soil compaction, increased soil C, soil N, and leaf N, and increased soil and leaf $\delta^{15}N$ (Figs. 3.3 and 3.4). Relationships between mean response variables and island mean seabird density across the six islands often demonstrated a threshold above which the relationship changed direction or slope. For example, microbial activity and biomass (indicated by BR and SIR, respectively) peaked on intermediate-density islands, at values approximately double those of very high or very low-density islands (Figs. 3.4a, 3.4b). Generally, as burrow density and both forms of inorganic N increased, more NH_4^+ was immobilized (i.e., net ammonification rates became negative), while net nitrification rates increased (Figs. 3.4c-f).

3.4.1 Seabirds as spatial drivers at the within-island scale

Burrow density (used as an explanatory variable in the trend) significantly improved the fit of 21 out of 76 spatial models at p=0.05 (only about 4 would be expected by chance), but these seabird-dependent variables differed by island (Table 3.1). The fewest variables were structured by seabirds on TEH and ATU, which were the lowest- and highest-density islands (Table 3.1). On each of the other islands, four or five variables (about a third of those tested) spatially covaried with seabird density (Table 3.1). Variables most consistently influenced by burrow density were soil C:N (on four islands), soil pH (on three islands) and soil $\delta^{15}N$ (on three islands). Almost all variables tested were spatially linked to burrow density on at least one island; exceptions were for NO_3^-, leaf N and leaf $\delta^{15}N$ (Table 3.1).

To rule out the seabirds' choice of nesting sites on steep slopes and ridgelines as the actual driving force behind these spatial relationships, we re-tested SVs yielding significant results above, first including topographic trends (elevation, slope and aspect) in the model. Burrow density still significantly improved model fit over topography alone for 16 (i.e., 76%) of the 21 significant spatial relationships in Table 3.1. When the five topography-linked models (marked "T" in Table 3.1) were removed from the set of seabird-driven variables (all significant models in Table 3.1), a clear pattern emerged: burrows spatially structured more variables on intermediate–density islands (MOP, 5; MOK, 4; and OHI, 4) than those with very low or very high seabird densities (TEH, 0; RNI, 2; ATU, 1).

3.4.2 Patterns in spatial variability among islands

Two distinct patterns of spatial heterogeneity emerged from the SVs (Figs. 3.5, 3.6). In the first, total spatial variance (represented by SV sills) peaked on islands with intermediate seabird densities, notably MOK and OHI. Soil pH best exemplifies this pattern, as it became markedly less variable and more spatially homogeneous at very low and very high burrow densities (Fig. 3.5b). The same pattern held for soil compaction, soil $\delta^{15}N$, BR and SIR (Figs. 3.5d, 3.5g, 3.6a, 3.6b). The second pattern is best shown in seabird burrow density itself: as its value increased, so did its spatial variance, so that the highest-density island ATU attained the highest sill (Fig. 3.5a). Sills of NH_4^+ and NO_3^- closely followed this pattern (Figs. 3.6e, 3.6f), as did soil N, net ammonification and net nitrification though more weakly (Figs. 3.5e, 3.6c, 3.6d). Both these patterns involved low sills in conjunction with low burrow densities, and indeed the lowest-density island (TEH) displayed the lowest SV sill in 8 of the 13 SVs in which it was included (Figs. 3.5, 3.6).

The degree of spatial structure in these variables, as indicated by PSV, did not mirror patterns of spatial heterogeneity (Figs. 3.5, 3.6). One-third of these 85 models exhibited spatial independence ($PSV \approx 0$) and nearly another third exhibited low spatial dependence ($PSV < 0.4$). Variables demonstrating the most spatial structure (with $PSV > 0.7$ on 3 or more islands) were burrow density, soil $\delta^{15}N$, net nitrification, soil NH_4^+, and leaf $\delta^{15}N$ (Figs. 3.5i, 3.5o, 3.5p, 3.6l, 3.6m). Other variables attained this degree of spatial dependence on two or fewer islands, notably soil C, N, C:N, BR and SIR (Figs. 3.5k, 3.5m, 3.6i, 3.6j, 3.6o). Among the six islands, degree of spatial structure tended to increase with burrow density. The islands with the lowest burrow densities, TEH and MOP, did not often demonstrate spatial structure, but more spatially dependent variables were found on intermediate-density islands MOK and OHI, (Figs. 3.5, 3.6) despite low PSVs for burrow density (Fig. 3.5a). SVs from the most densely-burrowed island, ATU, attained a high degree of spatial structure much more often than the rest ($PSV > 0.7$ for 7 of 13 soil variables; Figs. 3.5, 3.6).

Overall, estimated SV ranges produced few discernible patterns among variables or islands. One-third of the 85 SVs had estimated spatial ranges close to 0 m (Figs. 3.5, 3.6), which is shorter than the shortest sampling lag of 10 m; this often corresponded to a lack of spatial dependence ($PSV=0$). An additional third indicated spatial ranges between 10 and 50 m, indicating that for many variables on these islands, sampling points become independent when separated by 50 m (Figs. 3.5, 3.6). The spatial grain associated with seabird burrow density was estimated at ~40 m on TEH, ~270 m on MOP, ~110 m on MOK, 0 on OHI (though this value is unreliable; see above), ~20 m on RNI, and ~40 m on ATU (Fig. 3.5q). The highest-density islands rarely produced ranges longer than 100 m, though the lowest-density islands often did (Figs. 3.5, 3.6).

3.5 Discussion

Seabird burrow density within each island spatially covaried with the modeled response variables in less than a third of cases (Table 3.1), contrary to expectations that density would strongly predict spatial patterns of ecosystem properties. The predicted relationship held true more often on intermediate-density islands than on those with low burrow densities (e.g., TEH, where other ecosystem processes likely structure properties) or high burrow densities (e.g., RNI, ATU, where "patches" created by seabirds were expected to coalesce). Seabirds have demonstrated their capacity for ecosystem engineering in many island systems around the world (Smith et al. 2011), and the high-density islands in this study had generally lower pH and soil compaction and increased soil C, N, and δ^{15}N, and leaf N and δ^{15}N (Figs. 3.3 and 3.4), consistent with previous work across islands in this temperate forested system (Fukami et al. 2006; Mulder et al. 2009; Wardle et al. 2009) and other comparable systems (Mulder and Keall 2001; Markwell and Daugherty 2003). Topography of seabird nesting sites (i.e., elevation, aspect, and slope) was not an adequate substitute for burrow density in most models (Table 3.1), affirming that seabird nesting activity, rather than the non-random choice of nesting sites by the seabirds, alters the ecosystem around them—albeit in spatially unpredictable ways.

In support of our hypothesis that those islands with intermediate seabird densities will have the greatest spatial heterogeneity, the spatial variance of pH, soil compaction, marine-based guano additions, and microbial activity and biomass all peaked on islands of intermediate density (even though average values of these variables did not). Our data reveals that seabirds begin to spatially homogenize these variables past a threshold of approximately 0.15-0.50 burrows m^{-2} (i.e., the upper burrow density for OHI and the lower density for RNI). Guano contains large quantities of uric acid and reflects high-trophic level, marine-derived seabird diets (Bird et al. 2008; Hobson et al. 1994), so soil in guano-fertilized patches should have lower pH and enriched δ^{15}N, which is consistent with our results (Figs. 3.3b, 3.3f, Table 3.1). The only previous study to use geostatistics on seabird islands found that, on an arid archipelago in the Gulf of California, seabirds reduced the soil pH far inland from their nesting cliffs and thus increased spatial heterogeneity relative to islands lacking seabirds (Wait et al. 2005). However, in the current study, pH was spatially linked to within-island burrow density only on MOP, MOK, and OHI (Table 3.1). Soil pH commonly influences soil microbial processes (Bardgett 2005; Wardle

2002), and the spatial variance of BR and SIR also peaked on intermediate-density islands (Figs. 3.5b, 3.6a, 3.6b). As seabird density increased, the values and spatial variances of BR and SIR all decreased (Figs. 3.4a, 3.4b) along with those of pH (Fig. 3.3b, 3.5b), which is consistent with microbial inhibition by low pH. Though soil respiration increased in the presence of seabirds (Wardle et al. 2009), this is the first indication of decreased microbial activity and biomass in very dense seabird colonies.

However, in our study seabirds did not homogenize all variables even at the highest burrow densities (i.e., to ~3.5 burrows m^{-2}). Instead, as burrow density increased among islands, heterogeneity in those variables related to soil inorganic N transformation (net ammonification, net nitrification, soil NH_4^+ and NO_3^-) continued to increase (Figs. 3.6c-f). Burrows were not consistently related to these variables within individual islands (Table 3.1). Net ammonification was consistently negative which indicates NH_4^+ immobilization by microbes (Fig. 3.4c). Meanwhile, net nitrification, a process that depends upon a steady supply of NH_4^+, was positive on most islands and greatest on intermediate- to high-density islands (Fig. 3.4d). Soil NO_3^- was one of the few variables that was not spatially linked to within-island seabird density on any island (Table 3.1) though it showed considerable within-island variation (Fig. 3.4f) as well as spatial dependence on some islands (Fig. 3.6n). This means that NO_3^- is neither homogenized nor spatially random, but there is no evidence that seabirds directly alter its spatial structure at any burrow density. Alternatively, individual plant canopies in tree-dominated systems may spatially structure the soil supply of dissolved organic N, microbial biomass N, and inorganic N (Gallardo 2003a, Rodríguez et al. 2009), especially NO_3^- (Gallardo et al. 2000), a possibility that merits investigation in our system. In addition, soil texture can mediate the spatial influence of individual trees, resulting in very small nutrient patches in loamy soil when water is scarce (Rodríguez et al. 2009), such as was the case during the sampling period in our study.

The greatest spatial dependency in our measured response variables was most often found on high-density islands (higher PSVs in Figs. 3.5, 3.6), rather than on intermediate-density islands as we predicted. This pattern contrasts with the result that seabirds more often spatially structure variables within intermediate-density islands: high-density islands are very patchy, yet seabird burrow entrances do not explain this patchiness over space. Burrows themselves demonstrated maximal spatial dependence on very low-density islands (which is expected for colonial birds; Smith et al. 2011) and on high-density islands, suggesting strong habitat preferences (Fig. 3.5i). These conflicting patterns indicate that, despite our original hypothesis, burrowing seabirds probably defecate at different spatial scales than they dig. Although other bird species obviously should show more dispersed spatial influence, e.g., grazing geese that leave white smears behind them, this is somewhat surprising for burrow-nesters that spend most of their brief island visits either inside their burrows or directly outside the entrances (Warham 1990). Even burrowing birds, however, may create patches that are not spatially related to their nests, such as those associated with "takeoff trees" where guano is voided as the birds ascend trees before flying from the island, or with thin spots in the forest canopy preferred as landing sites (pers. obs.). Spatial decoupling of guano from burrows would explain why, on several intermediate- to high-density islands, soil and leaf $\delta^{15}N$ were patchy (Fig. 3.5o-p), yet unrelated to within-island burrow density (Table 3.1). In contrast, a few birds in isolated colonies may dramatically raise the soil $\delta^{15}N$ near their nests (i.e., TEH and MOP; Table 3.1), suggesting that this property is a good indicator of seabird influence when burrow densities are low. This is consistent with use of this variable as a marker for ancient or deserted seabird colonies (Hawke 2001; Mizutani et al. 1988).

We found no evidence that intermediate-density islands have the smallest patches and distances between patches (spatial grain); instead this was the case on very low-density and very high-density islands (Figs. 3.5, 3.6). However, low-density islands also produced very long ranges for some variables. This means that in general, one can situate spatially independent plots 50-100 m apart on higher-density seabird islands, but on lower-density islands more distance is needed to avoid spatial autocorrelation. The "low" 50-100 m ranges found in this study are comparable to ranges estimated in temperate pine and hardwood forests (Worsham et al. 2010) as well as in fertilized cultivated agricultural fields, to which seabird colonies are sometimes compared (Gillham 1956). For example, ranges for soil C, net ammonification and nitrification potential were estimated at 48-108 m in an annually tilled Michigan field vs. 7-26 in an uncultivated control site (Robertson et al. 1993). Our finding that two-thirds of 85 spatial models exhibited low (or no detectable) spatial dependence in our study indicates great "nugget" variability at distances shorter than our shortest sampling lag, and this is reinforced by the result that one-third of the models estimated spatial ranges of at or near 0 m (Figs. 3.5, 3.6). Other tree-dominated ecosystems have demonstrated such fine scale spatial structuring with ranges from <1 to <10 m (Baraloto and Couteron 2010; Gallardo et al. 2000). Even without ecosystem engineers present, soil properties subject to biological processes display more spatial variability than those governed by geochemical processes alone (Gallardo 2003b), and ranges of even closely related variables (e.g., NO_3^- and NH_4^+) can vary by a factor of 4-5 (Gallardo et al. 2000). Such fine-scale spatial structuring in some variables, contrasted with the 50-100 m ranges of others, contradicts our underlying assumption that the engineering activities of seabirds would structure ecosystem properties at all spatial scales.

3.5.1 Conclusion

Ecosystem engineers modify the availability of resources to other organisms through their physical activities (Jones et al. 1994), and understanding how this influences the soil environment at different spatial scales may depend upon more complex measures than simply their presence or absence. Ecosystem properties clearly respond to seabird activity at different spatial scales, probably because of the dual roles of the birds in increasing both nutrient deposition and soil disturbance. Burrow density was far less important than expected as a continuous predictor of within-island spatial heterogeneity, but spatial variance in some ecosystem properties (soil pH, $\delta^{15}N$, and compaction; microbial biomass and activity) responded instead to *thresholds* of burrow density. Even at very high densities, seabirds increased spatial variability (particularly for variables related to inorganic N transformations), in a manner similar to that shown for other burrowing animals such as rabbits, voles and marmots in other ecosystems (Oloffson et al. 2008; Questad and Foster 2007; Yoshihara et al. 2010), but in contrast to some other animals that homogenize their spatial domains (Bangert and Slobodchikoff 2000; Sherrod and Seastedt 2001; Yoshihara et al. 2009). In soil, high patchiness is often associated with low-nutrient environments where nutrient depletion enhances heterogeneity (Huston and DeAngelis 1994), but our results suggest that ecosystem engineers can be an important exception especially when they cause resource availability and spatial heterogeneity to increase simultaneously.

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3.8 Tables

Table 3.1 Likelihood ratio tests comparing within-island SV fits with and without a seabird burrow density trend for each of six islands. Significant results (p-values from χ^2 distribution, df=1) were investigated further with a spatial model that first included topographic covariates (elevation, aspect, and slope), again comparing fits with and without burrow density. Where burrow density failed to improve model fit over topography alone, results are marked "T." Islands are arranged in order of increasing burrow density (c.f. Fig. 3.3)

Variable	TEH	MOP	MOK	OHI	RNI	ATU
Soil pH	0.6869	**0.0046** **	**0.0065** **	**0.0004** ***	0.1693	0.7613
Soil C	0.7977	0.0500	0.2302	0.6736	**0.0102** *T	0.6796
Soil comp.	0.1860	NA	**0.0309** *	NA	0.5194	0.2397
Soil N	0.6514	0.0856	0.4375	0.9936	**0.0044** **	0.8797
Leaf N	NA	NA	0.2382	0.1181	0.2212	NA
Soil δ^{15}N	**0.0000** ***	**0.0026** **	0.5140	**0.0035** **	0.8581	0.1951
Leaf δ^{15}N	NA	NA	0.3446	0.1632	0.8941	NA
BR	0.5982	**0.0300** *	0.2458	0.1888	0.0699	0.9383
SIR	0.3102	0.1433	0.2532	0.3729	**0.0193** *T	0.3147
Net nitrif.	0.2008	**0.0001** ***	0.9499	0.1309	**0.0149** ***	0.4792
NH_4^+	0.9902	0.9594	0.0536	**0.0136** *	0.0781	**0.0282** * T
NO_3^-	0.3240	0.9742	0.1214	0.8505	0.5248	0.7353
Soil C:N	0.3386	**0.0173** *	**0.0133** *	**0.0140** *	0.3849	**0.0132** * T

Islands: TEH, Te Haupa; MOP, Motuhoropapa; MOK, Motueke; OHI, Ohinauiti; RNI, Ruamahuanui; ATU, Atiu. Soil comp., soil compaction; BR, basal respiration; SIR, substrate-induced respiration; Net ammonif., net ammonification; Net nitrif., net nitrification. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

3.9 Figures

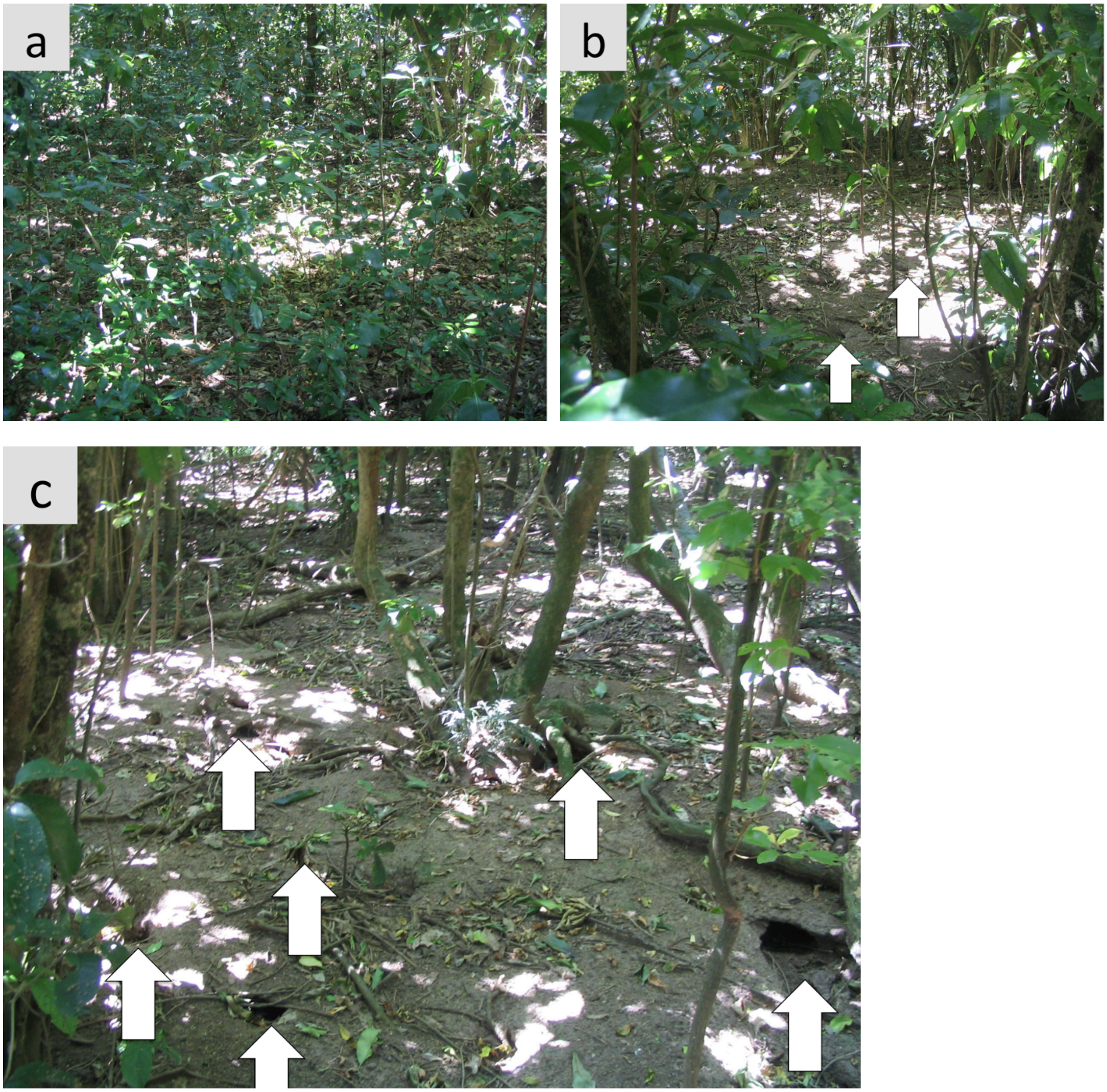

Fig 3.1 Within-island heterogeneity on Ohinauiti, an intermediate-density seabird island. Photographs were taken within 20 m of one another, and represent a range of burrow densities: a) off colony, ~0.0 burrows m^{-2}; b) colony edge, ~0.05 burrows m^{-2}; c) diving petrel colony, ~0.1 burrows m^{-2}

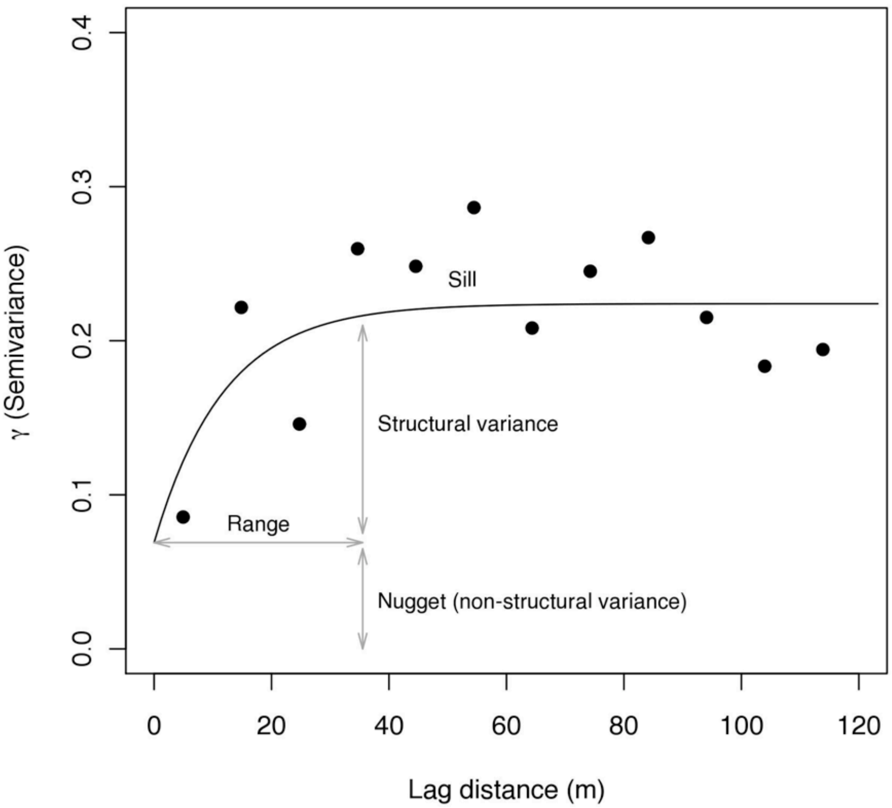

Fig 3.2 Example semivariogram (SV) of leaf N from Ruamahuanui, fitted with an exponential model. The semivariance γ is a unit-free measure of variance in a set of values measured at pairs of points separated by a particular lag distance. The nugget represents non-spatially structured variation, while the sill estimates the total semivariance. The ratio of spatially structured variance to the sill (Proportional Structural Variance, PSV) estimates the degree to which the variable is spatially structured, and the minimum lag between samples achieving the sill is the range of spatial variance. The parameters estimated from this empirical SV contribute to Figs. 3.5f, n, v

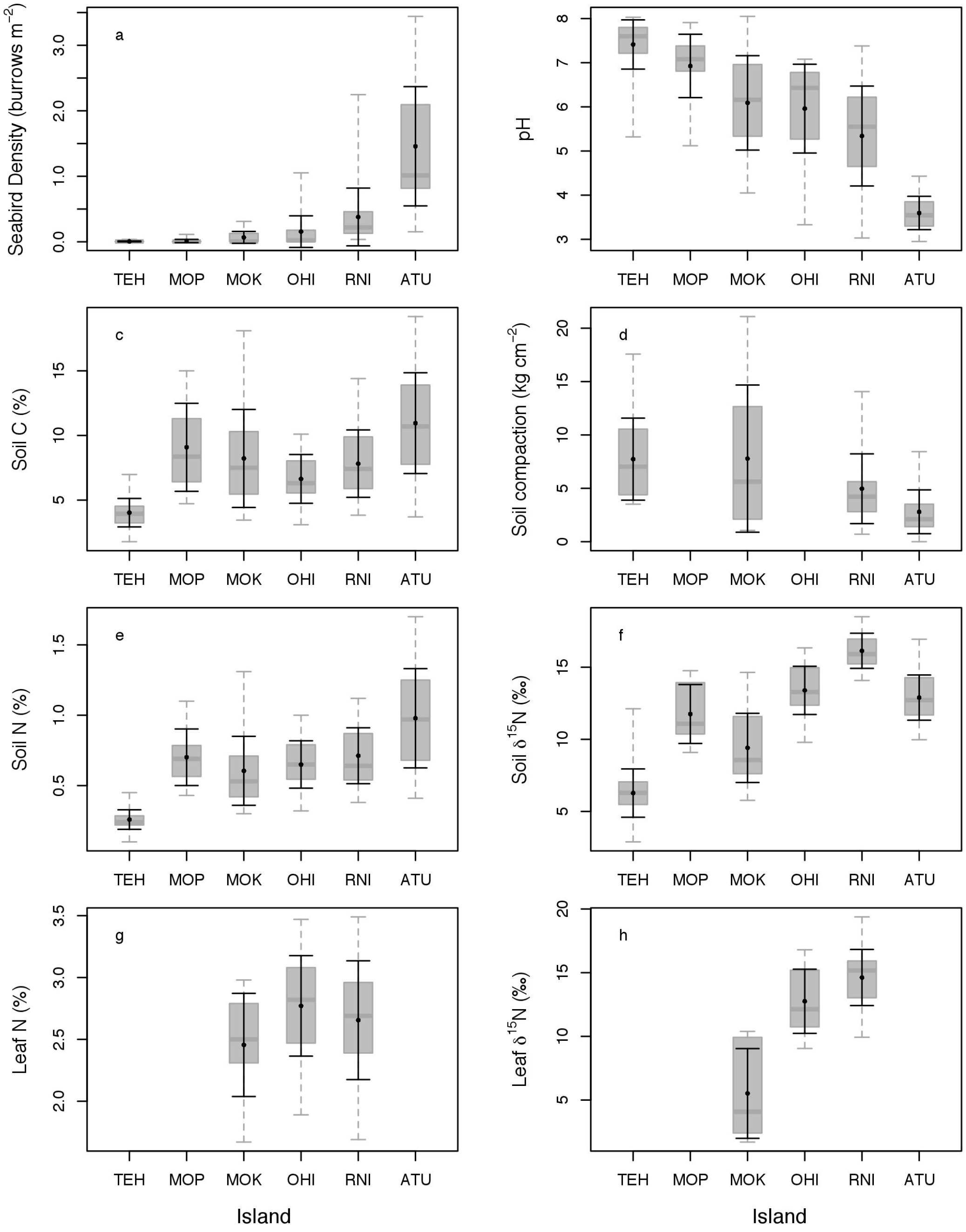

Fig 3.3 Means with standard deviations (in black) and boxplots (in gray) of seabird burrow density and various soil and leaf properties on six islands. Islands are arranged in order of increasing burrow density. Boxes are centered on the median and represent the first through third quartiles; whiskers represent the entire range. TEH, Te Haupa; MOP, Motuhoropapa; MOK, Motueke: OHI, Ohinauiti; RNI, Ruamahuanui; ATU, Atiu

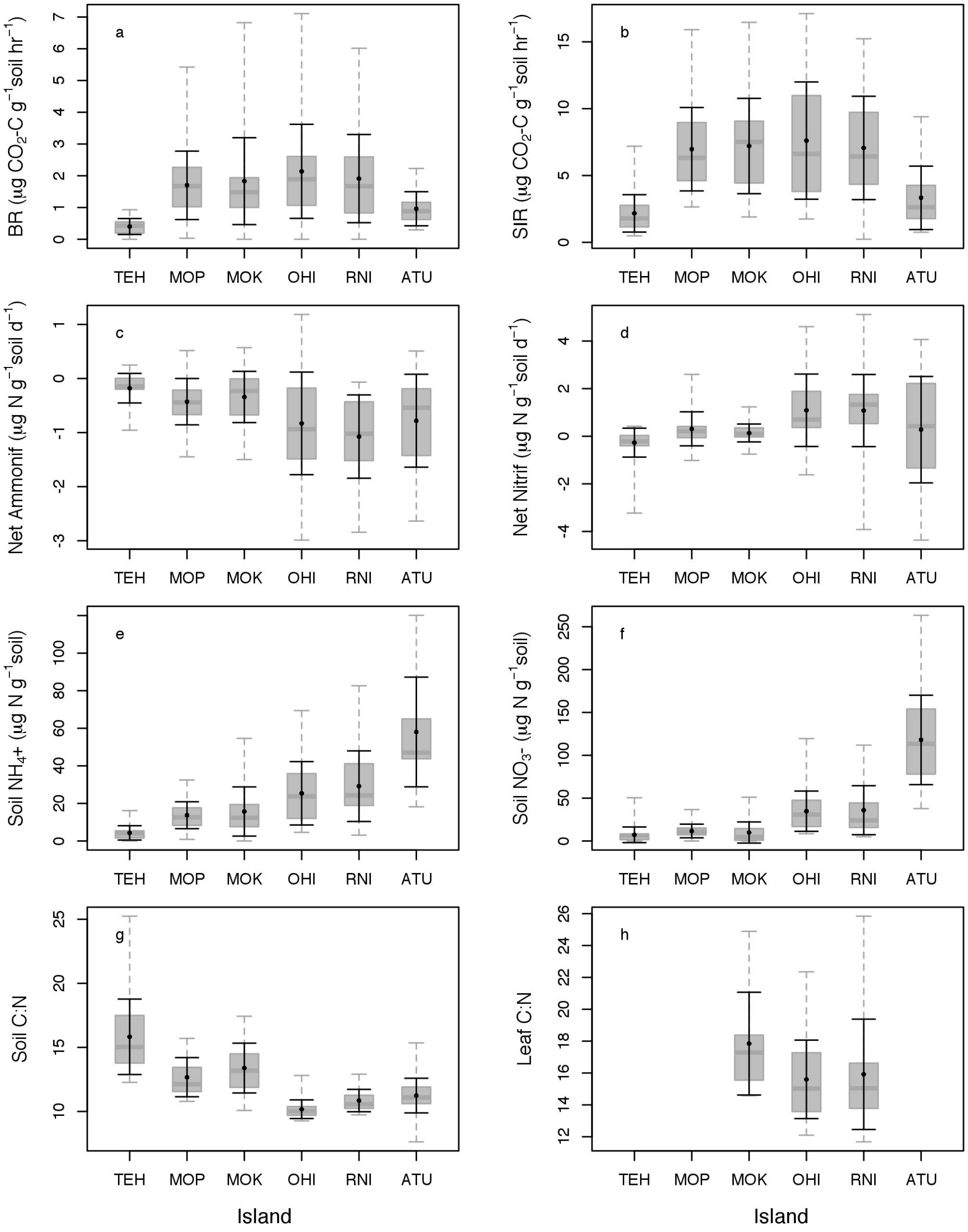

Fig 3.4 Means with standard deviations (in black) and boxplots (in gray) of soil properties and processes on six islands. Islands are arranged in order of increasing burrow density. Boxes are centered on the median and represent the first through third quartiles; whiskers represent the entire range. (For island codes, see Fig. 3.3). BR, basal respiration, a proxy for microbial activity; SIR, substrate-induced respiration, a proxy for microbial biomass

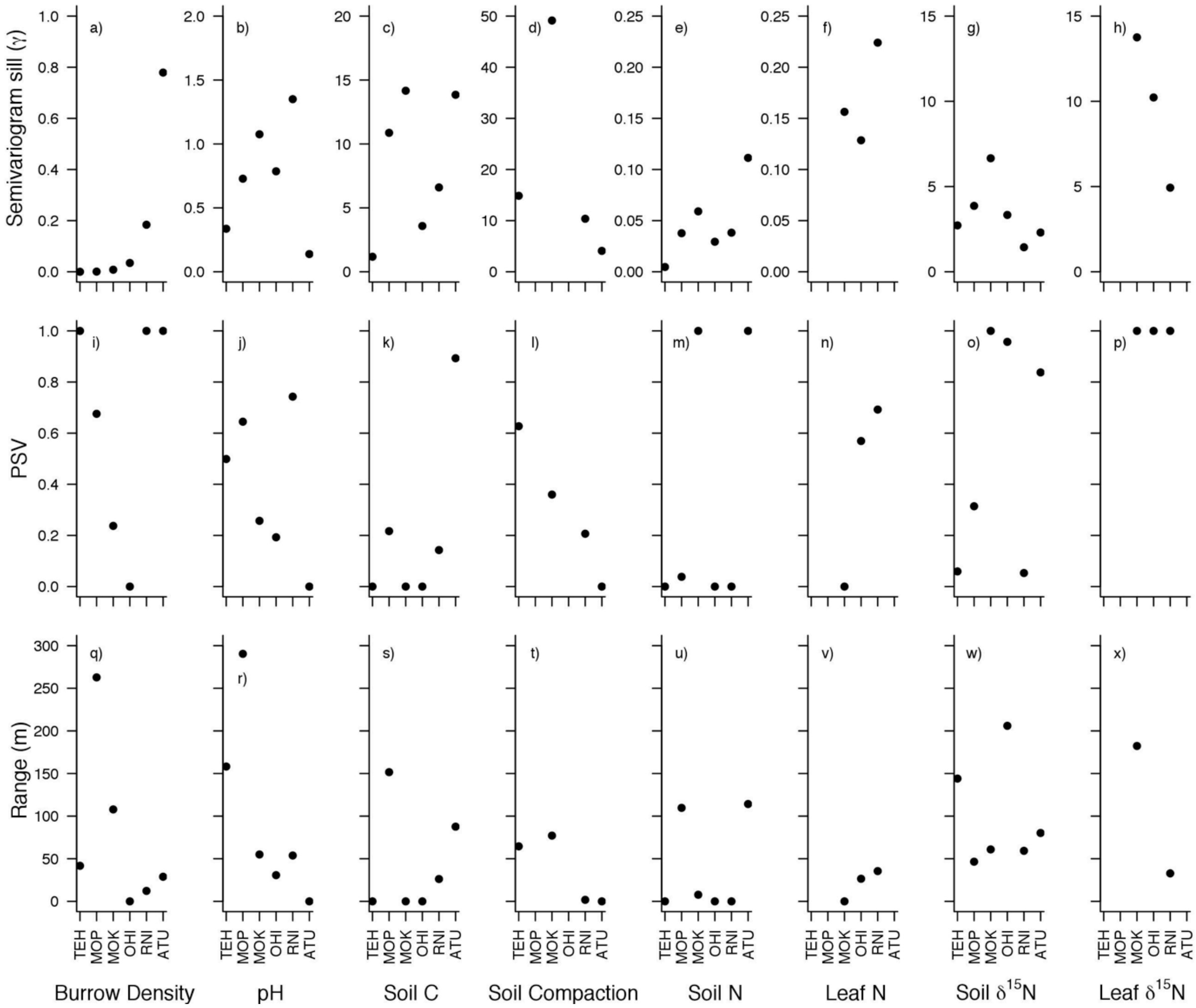

Fig 3.5 Semivariogram parameters (sill, PSV, and range) modeled for soil and leaf properties on six islands. Islands are arranged in order of increasing burrow density (see Fig. 3.3 for island codes). PSV, proportional structural variance

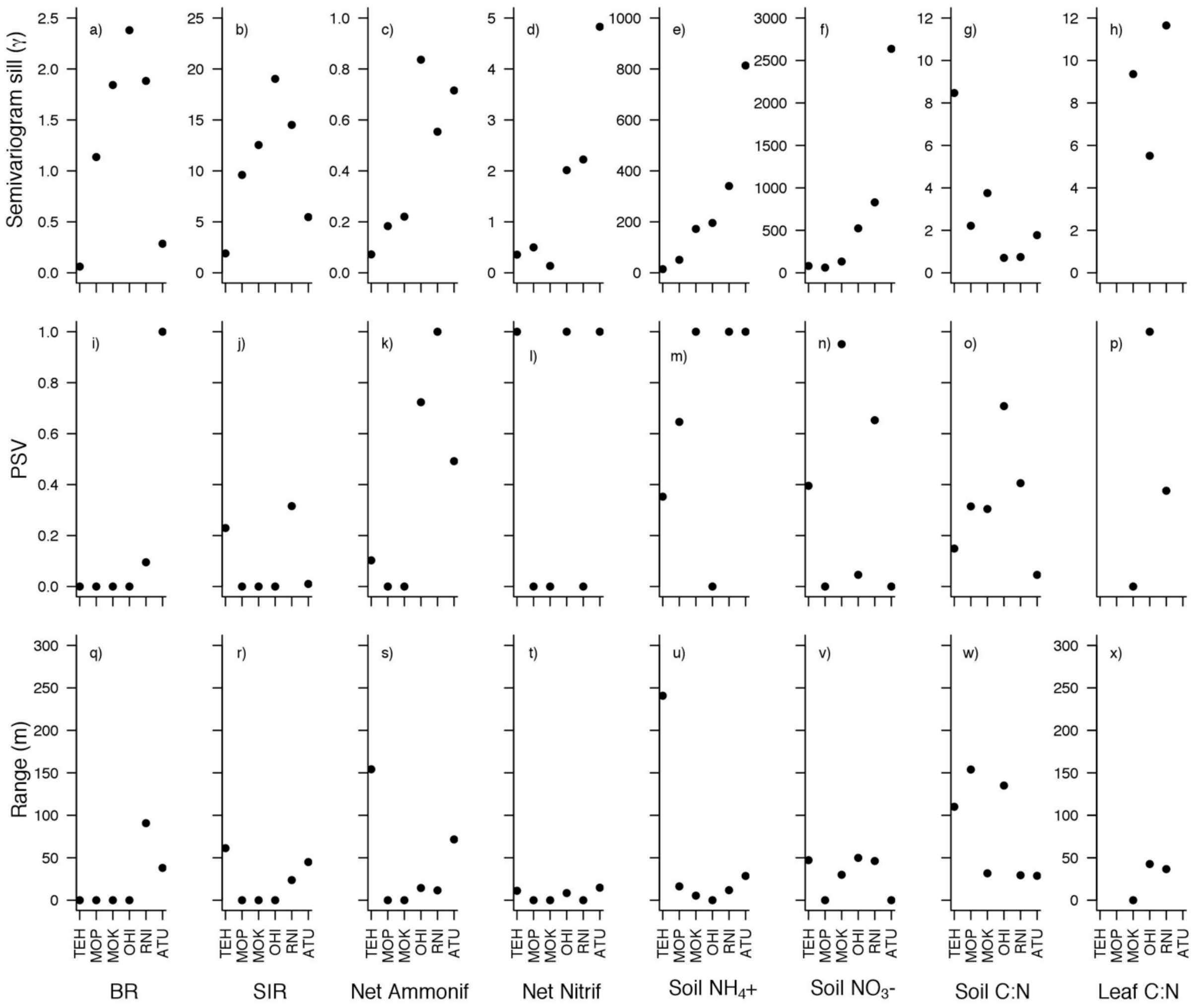

Fig 3.6 Semivariogram parameters (sill, PSV, and range) modeled for soil microbial processes and properties on six islands. Islands are arranged in order of increasing burrow density (see Fig. 3.3 for island codes). PSV, proportional structural variance; BR, basal respiration, a proxy for microbial activity; SIR, substrate-induced respiration, a proxy for microbial biomass; Net ammonif., net ammonification, net balance of NH_4^+ produced and assimilated by soil microbes; Net nitrif., net nitrification, a similar net balance of NO_3^- production and assimilation

Appendix 3.A

Seabird burrow density calculations and modeling

Counting all of the burrows in a reasonably sized area surrounding each sample point was impossible due to time constraints. High-density plots in particular would be subject to inaccuracies of counting, but a hidden or hard-to-find burrow would be even more important in low-density plots. Estimation of burrow density (BD), with acceptance of some random error, was the only realistic option. Our goal was to transform our field-measured index (distance-to-burrow, or DTBs, for the three closest burrows to the plot center) into a value representing burrows per area.

We used independently collected DTB data matched to burrow counts from multiple 100 m^2 plots established on a larger set of 21 islands (Mulder et al. 2009) to parameterize a model of burrow density. We assumed that BD was approximately homogeneous over the scale of 10 m x 10 m (100 m^2). We first calculated BD using three DTBs measured from the plot center, divided by the search area needed to find three burrows (Fig 3.A-1a, 3.A-1b). In our geospatial study, this methodology meant fixing the third DTB (the farthest distance measured) as the radius of a circle centered on the sample point and encompassing the search area. If three burrows could not be found within 5 m, then 5 m became the radius of the search area (Fig 3.A-1c). This method results in BDs calculated on a continuously varying scale from <1 m^2 to ~78 m^2, which are sensitive to small changes in DTB when burrow densities are high (because DTBs become short and search areas very small, e.g., Fig 3.A-1a).

We regressed these DTB-calculated BDs (equivalent to BDs from the 3-burrow search areas in Fig. 3.A-1) against the known densities counted in the plots from the larger study (equivalent to BDs from the square plots in Fig. 3.A-1). The resulting model, below, was log-transformed (ln[x+0.01]) to meet the assumptions of linear regression. On both sides of the equation, BD is counted or calculated in burrows m^{-2}.

[3.A-1] $$\text{Counted BD} = -0.01 + (0.010 + \text{DTB} - \text{Calculated BD})^{0.923}$$

The calculated value based on DTB could predict burrow counts well ($F_{(1, 286)} = 6421$, $p < 2.2\text{x}10^{-16}$, $R^2 = 95.7\%$) so we used it to convert all of our distance-based index (DTB) measurements into area-based seabird burrow densities (equivalent to BDs from the 5 m radius circle in Fig 3.A-1) for use in this geospatial study.

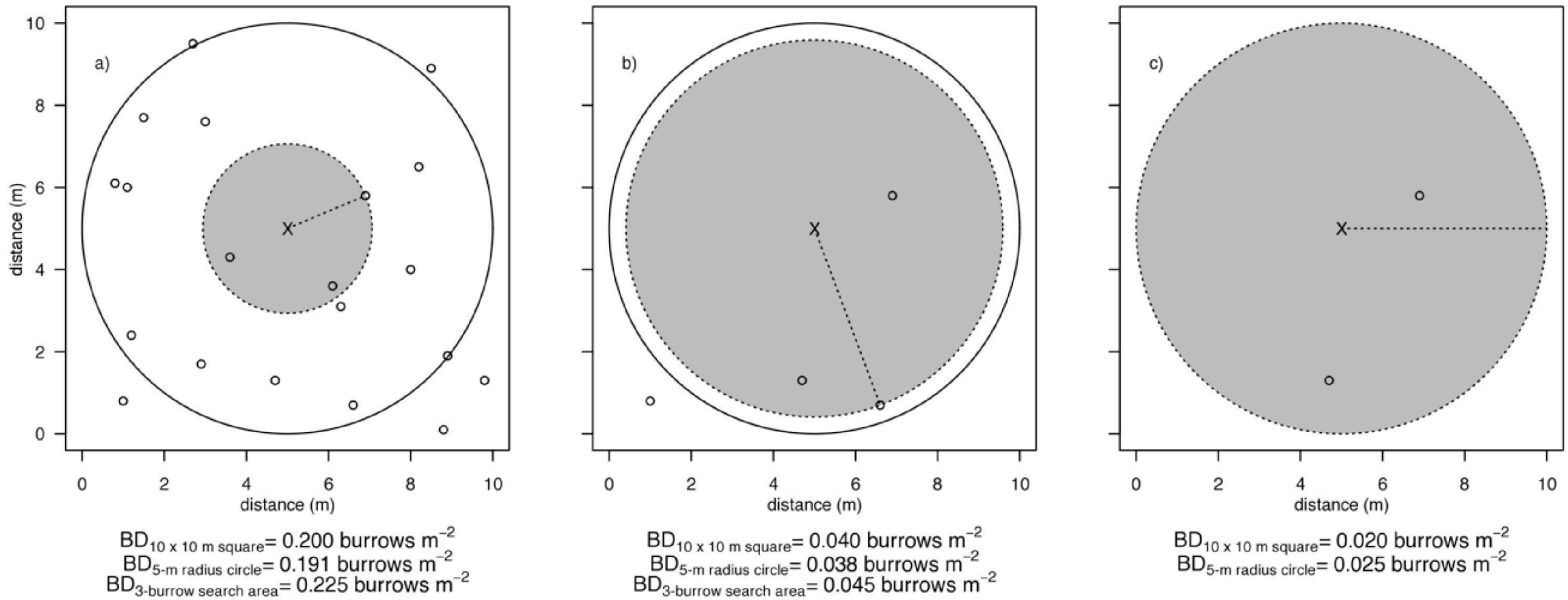

Fig 3.A-1 Examples of three burrow densities, each calculated three different ways. A square plot (10m x 10m), a circular plot (radius 5m, area (~78 m^2), and a circular plot with a radius equal to the distance to the third nearest burrow. X indicates the plot center; small circles represent burrow entrances. Shaded areas indicate the area searched to find three burrows (a, b) or else the maximum circular search area (c) while dotted lines drawn from the plot centers indicate the radius used to calculate the search area.

Appendix 3.B

Anisotropic modeling

Geostatistical studies such as this one commonly assume isotropy (the lack of unidirectional gradients in spatial data); however in some cases the researchers visually assess semivariograms (SVs) and spatial plots and deem their data isotropic (e.g., Gundale et al. 2011). An alternative approach is to geometrically adjust the spatial coordinates in order to improve precision when modeling and mapping (e.g., the aniso.coords() function in R). However, we expected anisotropy to be present throughout our dataset for two reasons. First, seabirds are colonial nesters, and a single patch of burrows may cause gradients in other variables depending upon their distance from seabird influence. This is a topic of investigation, rather than an obfuscating feature. Secondly, each island in our dataset is of a unique size, three-dimensional shape, and orientation with respect to wind and ocean currents. Most of these islands are considerably longer than they are wide, with a sharp ridgeline running the length of the island, and a saddle or steep-sloping gulley near the middle. If island geography were causing measurable gradients in the data, anisotropy would be detectable, either along the long axis of the island, or else in the perpendicular direction.

To examine the extent of anisotropy in our dataset, we modeled variance over space (using a SV) for each variable on each island and used the Likelihood Ratio Test (LRT; see Methods) to compare anisotropic models with the isotropic (omnidirectional) model. Anisotropic models included an initial estimate of the angle of anisotropy (either the long direction of the island or its perpendicular, visually estimated from island maps) and the ratio of anisotropy (the longest range of the data compared the shortest range, visually estimated from SVs along with the usual visual estimates of sill and range parameters). In one set of models, we fixed the initial psiA. In case these initial angles were too constricting, however, we re-ran the models allowing the psiA to be estimated by maximum likelihood.

Of the 340 spatial models tested (consisting of 16 variables, most modeled on 6 islands, with 2 initial angles, either fixed or estimated), only 38 (11.2%) were a significant improvement over the unidirectional model (defined as $p < 0.05$; Table 3.B-1). Overall, model sills were usually only very slightly affected by inclusion of anisotropy, with equal numbers showing slight increases and decreases, and the spatial range of most variables on most islands were considerably shortened compared to the range of the omnidirectional model (Table 3.B-1). The Proportional Structural Variance (PSV) was always greater when anisotropy was included, in most cases increasing to the maximum value of 1 (unless PSV=1 in the omnidirectional model, in which case there was no change). These changes in range and PSV are consistent with a "patchier" distribution of the variable when modeled in a single direction, whereas the omnidirectional model is an average of parameters estimated in all directions. If the spatial processes in question were truly isotropic, any individual directional model would align closely with an omnidirectional average; thus our models demonstrate that some degree of anisotropy is present, as expected, on all six of our islands.

Despite providing evidence of anisotropy, the significant directional models fail to point to any consistent island-wide directional patterns, with a couple of exceptions. On the island of Motuhoropapa, the estimated angle of isotropy for both burrow density (143°) and pH (136°) correspond well, though spatial ranges for each model differ greatly (Table 3.B-1). Conversely, on Motueke and Ruamahuanui, spatial ranges of many variables align well (around 9-10m, the smallest lag in this study) but the estimated angles of anisotropy span the compass. However, several variables measured on Ruamahuanui—soil total N, soil NO_3^-, soil NH_4^+, and leaf N—appear to covary along a similar directional gradient, estimated at approximately 60° (Table 3.B-1). Anisotropic parameters estimated from burrow density SVs, which we assumed would demonstrate the strongest and most consistent anisotropy, failed to align closely with other variables (except in the case of MOK, noted above) and did not significantly improve the omnidirectional model at all on the two most densely burrowed islands, Ruamahuanui and Atiu. Soil $\delta^{15}N$, a variable directly influenced by seabird guano additions, shows significant anisotropy only on Atiu, where burrow density was not found to be anisotropic, reinforcing the need to explain spatial patterns in this variable. Similarly, soil water content and leaf $\delta^{13}C$, expected to be spatially driven by seabird burrowing, were not found to be significantly anisotropic on any island, indicating that this proposed mechanism needs careful evaluation.

In all, this exploration of anisotropy on the six study islands did not support a clear anisotropic pattern for each island that could be used to systematically improve all the islands' SVs (i.e., parameters in Figs. 3.5 & 3.6). Including anisotropy in these models would only obscure rather than simplify parameter comparisons among islands. Instead, anisotropic modeling further reinforces the difficulty of comparisons among islands with different histories and seabird influences, especially the links between above- and belowground properties such as soil and plant leaf N.

Table 3.B-1 Anisotropic models. Listed are those with a significantly better fit than the omnidirectional model, according to the Likelihood Ratio Test, and the resulting changes to semivariogram model parameters (sill, range, and Proportional Structural Variance, PSV). Angles of anisotropy (psiA) were either fixed or estimated from two initial angles visually estimated from island maps: one corresponding to the island's length, and the other perpendicular to that.

Island	**Variable**	**Init. psiA**	**Est. psiA**	**Δ Sill**	**Δ Range**	**Range**	**Δ PSV**	**PSV**	***p***	
TEH	Net ammonification	15	37	~ inc.	dec.	10	inc.	0.82	0.013544	*
TEH	Net ammonification	105	37	~ inc.	dec.	10	inc.	0.82	0.013544	*
TEH	Net nitrification	105	135	~ inc.	inc.	20	none	1	0.011767	*
TEH	Soil NH_4^+	15	32	~ dec.	dec.	36	inc.	0.67	0.014045	*
TEH	Soil NH_4^+	105	32	~ dec.	dec.	36	inc.	0.67	0.014045	*
TEH	Soil pH	15	4	~ dec.	dec.	17	none	1	0.000259	***
TEH	Burrow density	15	62	~ dec.	dec.	36	none	1	0.000050	***
TEH	Burrow density	105	62	~ dec.	dec.	36	none	1	0.000050	***
TEH	Burrow density	105	fixed	~ inc.	inc.	49	none	1	0.014689	*
TEH	Soil compaction	15	14	inc.	inc.	167	inc.	0.97	0.001316	**
TEH	Soil compaction	15	fixed	dec.	dec.	17	inc.	1	0.000221	***
MOP	Soil pH	70	136	dec.	dec.	28	inc.	0.53	0.028548	*
MOP	Soil pH	160	136	~ dec.	dec.	108	inc.	0.69	0.031604	*
MOP	Burrow density	160	143	dec.	inc.	329	inc.	0.98	0.005770	**
MOP	Burrow density	70	323	~ inc.	dec.	69	inc.	0.93	0.002624	**
MOP	Burrow density	160	fixed	~ inc.	dec.	170	inc.	0.83	0.005107	**

Table continued on following page.

Table 3.B-1 continued

MOK	BR	75	82	~ inc.	~ dec.	12	none	1	0.017895	*
MOK	BR	165	262	~ inc.	~ dec.	12	none	1	0.017895	*
MOK	Leaf $\delta^{15}N$	75	24	~ dec.	dec.	11	none	1	0.017962	*
MOK	Leaf $\delta^{15}N$	165	204	~ dec.	dec.	10	none	1	0.017937	*
MOK	Net nitrification	75	47	~ inc.	none	9	inc.	0.67	0.041836	*
MOK	Soil compaction	75	52	dec.	dec.	9	inc.	1	0.002988	**
OHI	Leaf N	15	fixed	~ inc.	~ inc.	28	inc.	0.78	0.043227	*
OHI	Leaf $\delta^{15}N$	15	1	~ dec.	dec.	304	none	1	0.031809	*
OHI	Leaf $\delta^{15}N$	105	181	~ dec.	dec.	304	none	1	0.031809	*
OHI	Leaf $\delta^{15}N$	15	fixed	~ inc.	inc.	359	none	1	0.032001	*
OHI	Burrow density	105	70	~ inc.	none	49	inc.	1	0.007373	**
OHI	SIR	15	21	~ inc.	~ inc.	11	none	1	0.002439	**
RNI	Soil NH_4^+	30	59	~ dec.	~ dec.	9	none	1	0.015620	*
RNI	Soil NO_3^-	30	60	dec.	dec.	9	inc.	1	0.020008	*
RNI	Soil compaction	120	226	inc.	none	9	inc.	0.98	0.005049	**
RNI	Soil total N	30	64	~ inc.	none	9	inc.	1	0.020417	*
ATU	BR	10	fixed	~ dec.	dec.	20	none	1	0.025959	*
ATU	Net ammonification	10	18	~ inc.	dec.	19	inc.	1	0.011823	*
ATU	Net ammonification	10	fixed	~ inc.	dec.	10	inc.	1	0.026906	*
ATU	Net nitrification	10	112	~ dec.	dec.	9	none	1	0.041245	*
ATU	Net nitrification	100	112	~ dec.	dec.	9	none	1	0.041245	*
ATU	Soil $\delta^{15}N$	100	145	~ dec.	dec.	45	inc.	1	0.000050	***

~ very slight, probably inconsequential increases (“inc") or decreases (“dec”)

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

Chapter 4.

Rat invasion alters seabird control over island nitrogen cycles[1]

4.1 Abstract

Burrowing seabirds alter island ecosystem functions by marine nutrient subsidies and physical soil disturbance, changing the local soil environment and the availability of soil organic substrate to microbes. In this study we investigate the often-opposing mechanisms by which seabirds directly and indirectly control island N cycling at the within-island scale, and how these pathways are altered by rat invasion. We performed structural equation modeling on soil and plant data from six islands, three invaded by rats and three rat-free, to identify seabird-mediated effects on N cycling pathways. Seabirds reduced soil moisture, but within rat-invaded islands this was due to reduced soil compaction, whereas on uninvaded islands it was related to reduced soil C. Within rat-invaded islands, seabird burrows were hotspots of increased soil C and organic N, but on uninvaded islands, cumulative seabird impacts locally decreased these substrate pools. Net ammonification and net nitrification potentials were strongly related to microbial activity and biomass, but only on uninvaded islands. These differing mechanisms suggest that rats have established an alternative island state by altering the seabird-driven mechanisms the control island N cycles. However, some patterns held true across all islands: seabirds reduced pH and soil water; soil C increased soil NH_4^+-N and NO_3^--N; large NH_4^+-N pools resulted in high immobilization or nitrification by microbes. These similarities provide hope that invasion-linked shifts in N cycling are subtle and that seabird recovery can ultimately restore seabird island function.

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[1] Durrett, M.S., Mulder, C.P.H., in preparation. Rat invasion alters seabird control over island nitrogen cycles. Prepared for submission to Soil Biology and Biochemistry.

4.2 Introduction

Seabirds forage in the oceans but return to land to breed and roost on over 10,000 islands worldwide, where they serve as primary ecological drivers (Smith et al., 2011). Those that nest in burrows alter island nutrient cycles via two main mechanisms: 1) soil chemical changes caused by marine nutrient subsidies, i.e., guano, carcasses, failed eggs, molted feathers, spilled food, and stomach oil expelled in nest defense; and 2) physical disturbance caused by burrowing, which redistributes surface leaf litter and allochthonous nutrient inputs deeper into the soil profile and adds dead plant material via root breakage and trampling of small seedlings (Smith et al., 2011). Both activities increase the C, N, and P of soil organic matter, while potentially altering its quantity and quality for soil microbial use. Seabirds also alter the local soil environment in ways that regulate microbial activity, but some effects are in opposition to others. For example, guano and other seabird nutrient inputs are acidic, so these additions decrease soil pH (Mulder et al., 2011) which can reduce microbial activity (Bardgett 2005). In addition, cultivation during burrowing reduces soil compaction thereby encouraging oxygen penetration and soil drying, but seabirds may also increase soil water holding capacity through additions of soil C (Bancroft et al., 2005). Different mechanisms may also produce the same result: for example, microbes may respond positively to either favorable soil moisture conditions or to additions of organic substrate (Bardgett 2005). It is still unclear which seabird-related mechanisms are most important to island N cycling at the within-island scale, which hampers efforts to predict island ecosystem function under different disturbance regimes and conditions of nutrient limitation.

Introduced predators, especially rats (*Rattus* spp.), have transformed seabird islands around the world via predation of seabirds, eggs and chicks, altering their effects on plant and soil properties with consequences for island plant and animal communities, trophic webs, and adjacent aquatic systems (Durrett and Mulder, 2011). This makes islands with and without rat invasion the ideal “natural experiment” for investigating how seabird densities impact ecosystems. Rat-invaded islands can have either decreased or increased litter decomposition rates compared to islands with many seabirds (Fukami et al., 2006; Wardle et al., 2009), and rat invasion alters soil invertebrate and microbial community composition (Fukami et al., 2006;

Towns et al., 2009). However, the mechanisms by which rats alter island N cycling remain unexplored.

Further, island history may have an important role to play (Bellingham et al., 2010), especially the legacy effects of seabirds (e.g., persistant $\delta^{15}N$ and long-term P retention; Mizutani et al., 1986; Mizutani and Wada, 1988; Hawke, 2001). Soil N has been used to predict an island's recovery period after rat eradication (Jones, 2010), which assumes that the return of seabirds in the absence of rats can restore seabird island N cycles. However, if the dominant processes controlling soil N are fundamentally altered at low seabird densities, "reversing" rat invasions by eradication alone may be more complicated (Mulder et al., 2009). Rat-invaded islands with only a few seabirds may still function like seabird islands with temporarily reduced marine subsidies, or else the invaded ecosystem may shift to an alternate state where different ecosystem processes and drivers prevail.

Plant water and N uptake are both affected by direct seabird impacts and indirect impacts mediated by microbial processes (Durrett and Mulder, 2011), but again, some mechanisms may be in opposition to others. For instance, seabird burrow density may be related to canopy size because the birds choose large trees with woody roots that enhance burrow stability (Gillham, 1961). On the other hand, if digging undermines and topples these trees (Maesako, 1999) then the density of large, stable trees will be reduced, and burrows may co-occur with smaller, younger trees. Seabird colonies often increase leaf water stress, but it is unclear what mechanisms are most important: decreased soil water availability, increased root damage and death, or decreased soil compaction that increases the costs of root foraging (Mulder et al., 2011). Similarly, seabird colonies frequently increase leaf N in plant species of various taxonomic and functional groups (Mulder et al., 2011), but multiple mechanisms could alter plant N uptake on these islands, such as seabird-driven effects on available N pools, tree size, or water availability for nutrient uptake. Finally, plants are often enriched in ^{15}N on seabird islands due to uptake of soil N derived from marine sources (Bergstrom et al., 2002; Fukami et al., 2006, Mulder et al., 2011); however, other physiological mechanisms or non-soil N sources may alter this relationship (Fangmeier et al., 1994; Erskine et al., 1998; Harrow et al., 2006; Szpak et al., 2012). Soil $\delta^{15}N$ has been used to indicate ancient or deserted seabird colonies (Hawke 2001; Mizutani et al., 1988) but can also be interpreted as a current, integrative measure of N cycle "openness"

(Martinelli et al., 1999). Thus localized soil $\delta^{15}N$ can be seen as an index of cumulative seabird impacts over time, which may serve as a useful predictor—either alternative or complementary to current burrow density—in models of ecosystem functioning.

This study evaluates the often-opposing effects of these seabird-mediated mechanisms on island N cycling at the within-island scale, using six seabird islands, three uninvaded and three invaded by rats. Our overall objective was to examine how seabird nutrient additions and physical disturbance directly and indirectly control soil and plant properties, and how these mechanisms are altered by rat invasion. Our goals are to 1) identify dominant pathways through which seabirds affect components of soil N cycling, particularly net ammonification, net nitrification and the resultant inorganic pools, 2) explain how these differ between uninvaded and rat-invaded islands, and by depth in the soil profile, and 3) evaluate the main mechanisms affecting plant leaf N. We also 4) explore whether an indicator of cumulative seabird effects, soil $\delta^{15}N$, can be used interchangeably with seabird burrow density in predicting various seabird impacts on island ecosystem function.

4.3 Materials and methods

4.3.1 Study system

The six islands included in this study are located off the east coast of the North Island of New Zealand, and have been described previously in detail (Fukami et al., 2006; Mulder et al., 2009). Three had been invaded by rats at the time of this study (Te Haupa a.k.a. Saddle Island, Motuhoropapa of the Noises, and Motueke by Hahei) which reduced seabird populations to very low numbers, leaving mainly grey-faced petrels (*Pterodroma macroptera gouldi*) and little blue penguins (*Eudyptula minor*). The other three (Ohinauiti of the Ohinau group, Ruamahuanui of the Aldermen, and Atiu a.k.a. Middle Mercury) have remained rat-free and host large multi-species colonies including common diving petrels (*Pelecanoides urinatrix*), fleshfooted shearwaters (*Puffinus carneipes*), fluttering shearwaters (*Puffinus gavia*) and white-faced storm petrels (*Pelagodroma marina*), in addition to those above.

The islands range from 6 to 32 ha in area and are located less than 20 km offshore. Soils are shallow (< 3 m), homogenous over the extent sampled, and of basalt origin with the exception of Te Haupa and Motuhoropapa whose soils are sedimentary. Air temperatures in 2005 averaged 13.0° C in June and 18.4° C in January with 83-91% relative humidity that peaks in winter (Mulder et al. 2009). Precipitation averages 1250 mm per year, most falling as winter rain. Vegetation is broadleaf evergreen secondary forest with 75-90% canopy cover (Mulder et al. 2009), ringed by shoreline shrubs, and both canopy and understory vegetation are less dense where seabirds are present (Mulder et al. 2009). The main ecological disturbances (besides seabirds) are storms and fire, but there was no sign of recent storm damage during sampling, and the last significant burns were estimated to be several decades ago (P. Bellingham, pers. comm.).

4.3.2 Data collection

The areal extent sampled on each island averaged approximately 1 ha, ranging from ~6800 m^2 on RNI to ~13000 m^2 on ATU. We distributed 35 sampling points in a haphazard grid, in similar forest, across a range of seabird densities (the highest and lowest encountered within ~1 ha). We purposefully sampled ridges, slopes, and gullies as we encountered them, but avoided unsafe slopes, rock faces, and un-vegetated beaches. Sampling usually took three days per island, and all island visits took place between February 12 and April 19, 2005 (summer to early fall). At each point, we measured the distance to the nearest 3 burrows within 5 m in order to estimate within-island burrow density (which ranged from 0 on the rat-invaded islands, up to ~3.5 burrows m^{-2} on Atiu; Table 4.1, Chapter 3). We also sampled soil from two depths, 0-15 cm ("surface") and 15-30 cm ("subsurface"). Where the common coastal species *Melicytus ramiflorus* occurred within 5 m, we measured diameter at breast height and picked 3 new leaves for isotope analysis. We used a Dickey-John soil penetrometer (Auburn, Illinois, USA) to measure soil compaction at each point.

We refrigerated the individually bagged soil samples for less than six weeks before analysis at the Soil Ecology Laboratory, Landcare Research Manaaki Whenua, Lincoln, New Zealand. We measured the pH of field-moist soil in a distilled water slurry (1:2.5 ratio) with a membrane pH meter (H18314, Hanna Instruments, Smithfield, Rhode Island, USA), and calculated soil moisture as gravimetric water content after over-drying at 60°C for 48 hours. For microbial activity and biomass, we adjusted 10 g soil subsamples (sieved to < 2 mm) to 50%

gravimetric moisture content and incubated individual jars in the dark at 16°C for three hours (after pre-incubation overnight at 16° C). To measure CO_2 production, we sampled 1cc of headspace at the beginning and end of the incubation, injecting it into an infrared gas analyzer (ADC-225-MK3, Analytical Development Company, Hoddeson, UK) interfaced with a voltmeter. Daily CO_2 standard curves were used to calculate each unknown concentration, and microbial basal respiration was expressed as $\mu g\ CO_2\text{-}C\ g^{-1}$ soil hr^{-1}. We measured substrate-induced respiration (SIR; an index of microbial biomass) by the same method, adding an easily assimilated C substrate (0.3 g powdered glucose) before incubation.

We used paired soil subsamples from each point to measure inorganic N, extracting each with 2*M* KCl before or after incubation of 10 g soil (50% water content) in the dark at 16°C for 14 days. Extracts were refrigerated for approximately four months before analysis for ammonium (NH_4^+) and nitrate (NO_3^-) on an autoanalyzer (Technicon, SEAL Analytical) in the Forest Soils Lab, University of Alaska Fairbanks, USA. Net ammonification was calculated as the difference in NH_4^+ content of post- and pre-incubation extracts. Net nitrification is calculated as the difference in NO_3^- content of post- and pre-incubation extracts. We also dried and ground soil and leaf subsamples, which were analyzed for nutrient contents (N, C, $\delta^{15}N$, and $\delta^{13}C$) using a PDZ Europa GSL Elemental Analyzer attached to a PDZ Europa 20-20 CF-IRMS (Lincoln University, Lincoln, New Zealand). Repeat analysis of the laboratory standard, referenced against Pee Dee Belemnite and IAEA N-1, yielded precision of +/- 0.2‰. Soil organic N was calculated by subtracting both inorganic N species from total soil N (more detail below).

4.3.3 Data analysis

The total number of sampled points (n=210) enabled structural equation modeling (SEM), a statistical approach accounting for the correlations between so many simultaneously sampled variables, rather than a multitude of simple linear models. This SEM approach, including “path analysis” of the type performed here, requires specification of multiple interacting mechanisms and their direct and indirect effects on other variables, allowing comparison of each path’s efficiency in explaining the data (Grace 2006). We performed all path analyses in the sem package (Fox, 2002, 2006) of R version 2.15.1 (R Development Core Team, 2012). Each path analysis was treated as an SEM containing only measured (manifest) variables, based upon a covariance matrix. To identify and compare the main soil N cycling mechanisms on rat-invaded and uninvaded islands, we ran a separate SEM for each group of islands. Plant data were only available from three islands (Motueke, Ohinauiti, Ruamahuanui) with intermediate seabird densities, so we could not model these data in the presence and absence of rats. To explore the importance of soil depth, we ran separate SEMs using surface and subsurface soil data. Covariance matrices for all models are presented in Appendix 4.A.

Before path analysis, data were *ln*-transformed where necessary to meet the assumptions of linearity, and island means were subtracted from each value to use the residuals for modeling. This adjustment effectively corrects for pseudoreplication and is analogous to including an "island" factor in a mixed linear model. It also limits the analysis to the within-island scale, making it preferable to adding "island" as an exogenous factor into the SEM. Because we knew that absolute values of many variables (including seabird density) differ by island and are related log-linearly (Mulder et al., 2009), using island residuals allowed for a more conservative analysis. Without this adjustment, models produce strong relationships because there are strong island-to-island differences, but the range of seabird densities (and other values) is much greater than would be found on any one island in this system. The simpler approach (with pseudoreplication) also conflates the island-to-island scale with the within-island scale, complicating interpretation. Limiting our analysis to the within-island scale also serves to constrain temporal variability in the data; some variables that we measured (e.g., soil moisture) may vary a great deal over several weeks or months, but there are no significant differences when measured within a few days within the same island (data not shown). Models using residuals reduce the island-to-island variability due to different sampling dates, allowing us to compare dry areas to wet areas within a single island (we assumed that areas measured as extremes (highest or lowest) in most variables would not change over a few weeks' time). Finally, our approach using residuals also retained a reasonable sample size for SEMs (~100 points), where the rule of thumb is 10 sample points per variable (Grace, 2006). Per-island mean values of each variable are included in Table 4.1.

Initial models included the variables and hypothesized relationships listed in Tables 4.2 and 4.3. Each model was re-run after eliminating weak paths (path coefficients < 0.10) in order to improve model fit, with the goal of presenting a data-fitted model indistinguishable from the null ($p > 0.05$; the null SEM perfectly fits the data, so larger p-values in this analysis indicate greater agreement between the data and the proposed model). Path coefficients were standardized for easy comparison, and in order to calculate total effect size of a path among multiple variables as the product of its path coefficients, which allowed us to compare the importance of various indirect paths within the same SEM. We began with the same model for each comparison pair (rat-invaded vs. rat-free; depth 1 vs. 2) and produced a best-fit model that differed from the null in each case; thus we can compare generally (though not statistically) the relative importance of the same pathway (e.g., seabirds → soil C), as well as patterns concerning multiple paths, in different SEMs. There is no statistical test to compare SEMs fitted to different data. However, we compared the AICs of model pairs by fitting the best model for one group of islands (e.g., invaded) to the other group (e.g., uninvaded), to increase our confidence that different models best fit the data for each pair (Appendix 4.B).

We did not investigate every possible path between every variable. Some paths were not included due to the specifics of data collection, rather than to an unsuspected mechanism. For example, soil water content likely contributes to net ammonification in the field (Booth et al., 2005), but in the lab, we adjusted all soil samples to common moisture before incubation. Other paths were not included because they would have created circular causation, and a SEM must be recursive (i.e., unidirectional causality) for parameters to be estimated. For example, paths between inorganic N species and total C are clearly bidirectional, but we specified such paths as unidirectional to investigate the mechanisms resulting in these inorganic N concentrations. Additional analyses posing the opposite directionality were not informative, the model fits were unacceptable, and they are not presented here. Finally, soil organic N was used in these models, rather than soil total N, because 1) total N is so closely correlated with soil total C ($r > 0.9$ for each island) that very little new information was added, decreasing model fit, whereas organic N was less strongly correlated; 2) both NH_4^+-N and NO_3^--N are included in total N, so that models using total N to predict its constituents became non-recursive; and 3) organic N is the substrate used for ammonification.

To probe the relationship between microbial activity and biomass in general (indicated by basal respiration, BR, and substrate-induced respiration, SIR) and microbial N cycling in particular (ammonification, nitrification), we used the residuals calculated above to run simple linear regressions among these variables on rat-invaded and rat-free islands. We also ran regressions using soil C:N, and BR adjusted per g soil C, as predictors for each of these variables.

4.4 Results

Seabirds altered the local soil environment, with direct impacts on soil compaction and pH in every model (Fig. 4.1). Seabird impacts (measured both as burrow density and integrated soil $\delta^{15}N$) indirectly decreased soil moisture on both invaded and uninvaded islands, but fitted SEMs strongly suggest that mechanisms at the within-island scale differed between these two sets (Table 4.4; Fig. 4.1). Soil C was the more important determinant of soil moisture within uninvaded seabird islands, while soil compaction became important on rat-invaded islands, opposing seabird-related increases in soil C (Table 4.4; Fig. 4.1). However, the indirect effects of these combined mechanisms were small (summed products of path coefficients were all <0.07; Table 4.4) and the most consistent effect of soil moisture, i.e., to slightly increase pH, was far outweighed by the strong, direct effects of seabirds acidifying the soil (Fig. 4.1a). Soil pH is clearly a strong control on soil N cycling within islands: acidic hotspots decreased organic N and increased NH_4^+-N on uninvaded seabird islands (Fig. 4.1a, 4.1c), whereas on rat-invaded islands, lower soil pH strongly decreased NO_3^--N and net ammonification potential (except in the 15-30 cm depth layer; Fig. 4.1b, 4.1d). Net nitrification potential was also affected by pH, though the direction of this relationship differed with rat invasion (Fig. 4.1a, 4.1b).

Seabirds directly affect the local organic matter substrate as well. Soil total C and organic N were positively correlated in all models (path coefficients ranged from 0.31 to 0.64), and local burrow density increased these variables on rat-invaded islands (Fig. 4.1b, 4.1d). In contrast, on uninvaded islands, the only (negative) relationship between burrow density and soil C is weak, and cumulative seabird impacts (local soil $\delta^{15}N$) drove decreases in both soil total C and organic N (Fig. 4.1a, 4.1c). Soil C:N ratio (calculated with total soil N) varied little either within or among islands, and did not predict net ammonification, net nitrification, basal respiration, or substrate-induced respiration ($p<0.05$ for only 5 out of 48 regressions), thus C:N was not included in the SEM analyses. Neither did soil respiration (BR) per unit soil C, another index of soil organic matter quality, predict net ammonification or net nitrification ($p<0.05$ for only 1 out of 24 regressions); therefore, this variable was not included in the SEM analyses.

Localized seabird impacts (soil $\delta^{15}N$ and burrow density) rarely predicted soil NH_4^+-N directly (i.e., only one model; Fig. 4.1d); however, they had notable indirect effects via pH (discussed above). Either soil total C or organic N was related to decreasing net ammonification potential in each model, which was in turn negatively related to NH_4^+-N in every model (Fig. 4.1). That is, the more NH_4^+-N was available, the more was used (either immobilized or nitrified, under standardized laboratory conditions). Net ammonification potential was almost always negative, indicating greater NH_4^+ utilization than production, and was negatively related to microbial activity (measured as BR) both on uninvaded seabird islands and in the subsurface on rat-invaded islands (Fig. 4.2). Similarly, net nitrification was positively related to microbial activity and biomass (BR and SIR) near the soil surface on uninvaded seabird islands (Fig. 4.2). Net ammonification and nitrification potential were inversely related on the surface of uninvaded islands and the subsurface of rat-invaded islands, coinciding with positive relationships between NH_4^+-N and NO_3^--N (Fig. 4.1a, 4.1d).

Within the islands of intermediate seabird densities, where plant leaves were sampled, both local burrow density and cumulative seabird impacts were positively related to bigger trees (though the $\delta^{15}N$-basal area relationship breaks down in deeper soils; Fig. 4.3). Seabird burrows were always associated with looser soil, though large trees tended to stabilize the surface (increasing surface compaction; Fig. 4.3a), and soil C was inversely correlated with compaction. Soil water content at both depths were inversely correlated with leaf $\delta^{13}C$ (depth 1, $p=0.003$; depth 2, $p=0.036$; $n=58$), supporting our use of leaf $\delta^{13}C$ as an integrated measure of plant water stress. Seabirds indirectly decreased leaf $\delta^{13}C$ via their impacts on soil C and compaction (Table 4.5; Fig. 4.3). However, the direct relationships of burrows and soil $\delta^{15}N$ to leaf $\delta^{13}C$ were positive and outweighed the indirect effects (Table 4.5). Large trees had higher $\delta^{13}C$ values, but tree size was also the most important driver of leaf N concentrations, and seabirds contributed to greater leaf N via various indirect pathways (Fig. 4.3). Leaf $\delta^{15}N$ signatures were strongly related to soil $\delta^{15}N$, which increased with local burrow density. Both NH_4^+-N and NO_3^--N were positively related to leaf N (surface soils) and leaf δ^{15}N (subsurface soils). Local soil water content, on the other hand, reduced leaf N and δ^{15}N (Fig. 4.3).

Cumulative seabird impacts (soil δ^{15}N) were strongly correlated with seabird burrow density only within rat-invaded islands (Fig. 4.1b, 4.1d). Within all islands, soil δ^{15}N was related to a different set of response variables from burrow density (though these sometimes overlapped; Fig. 4.1), and on uninvaded islands soil δ^{15}N predicted more variables than burrow density itself (Fig. 4.1a, 4.1c). However, not all variables could be predicted by this index, and some were better, and quite strongly, predicted by burrow density itself (Fig. 4.1).

4.5 Discussion

4.5.1 Seabird-mediated mechanisms controlling island N cycles

Different models from rat-invaded and uninvaded islands suggest that rats alter the mechanisms by which seabirds physically and chemically engineer the soil environment. On rat-invaded islands where seabird densities have been reduced, the negative impacts of burrowing (decreasing soil compaction and water retention) outweighed its positive impacts on summer soil moisture (increasing soil C, thus water holding capacity; Table 4.4). Within uninvaded seabird islands, seabirds unexpectedly *decreased* soil C, producing an overall negative effect on soil moisture (Fig. 4.1). Burrows were positively correlated with soil C among islands (Mulder et al., 2009), raising the question of how this pattern was reversed at very dense seabird hotspots. Extreme soil tillage may allow C to be lost via soil respiration; soil trenching experiments have shown ecosystem C losses where root damage is high (e.g., Díaz-Pinés et al., 2010).

The strong, direct effects of seabirds on pH outweighed the indirect effects of soil drying on pH (Fig. 4.1). Within rat-invaded islands with soil pH values close to neutral (Table 4.1), lower soil pH strongly decreased NO_3^--N, consistent with acid inhibition of nitrification (Booth et al., 2005; Fig. 4.1). Within uninvaded seabird islands, where soil can be quite acidic (Mulder et al., 2011), the negative relationship between pH and NH_4^+-N may be explained by two complementary mechanisms: 1) nitrification removes H^+ ions from NH_4^+, acidifying the soil, and 2) acidic soils trap alkaline NH_3 gas in solution as NH_4^+ (Ward, 1961; Hobara et al., 2005).

Despite the important role of NH_4^+ as a constituent of guano and an early product of its decomposition (Lindeboom, 1984), dense seabird hotspots at the within-island scale were not directly associated with increased NH_4^+-N pools (Fig. 4.1).

Burrow density was positively correlated with soil total C and organic N on rat-invaded islands (Fig. 4.1), as expected where seabirds till leaf litter beneath the soil surface (in contrast to decreased soil C at high seabird densities, explained above). This is consistent with findings that rats decrease overall soil C and N on these islands (Fukami et al., 2006; Wardle et al., 2007). Soil C was positively correlated with NH_4^+-N and NO_3^--N on both sets of islands, demonstrating that the extra organic substrate at seabird burrows promoted NH_4^+ and NO_3^- production under field conditions, similar to that on prairie dog mounds (Holland and Detling, 1990). Utilization of NH_4^+ usually outpaced production under lab conditions, driving a negative relationship between net ammonification potential and NH_4^+-N (Fig. 4.1), and between net ammonification potential and BR (Fig. 4.2). This suggests that on both sets of islands, organic substrate availability increases NH_4^+ production while also stimulating microbes to either immobilize or nitrify NH_4^+. Other seabird island studies have reported negative net ammonification (Hobara et al., 2005) and very high microbial activity stimulated by guano and other allochthonous nutrient inputs (Orchard and Corderoy, 1983; Wright et al., 2010). Microbial biomass also increases with guano fertilization (Lindeboom, 1984) and may be particularly high near seabird nests (Cocks et al., 1999).

Controls on nitrification varied by invasion status and depth. In the surface soils of rat-invaded islands, net nitrification potential was positively correlated with soil NH_4^+-N (Fig. 4.1), suggesting that available substrate limits nitrification rates. In contrast, on uninvaded islands, smaller pools of NH_4^+-N and greater utilization of NH_4^+ in laboratory incubations was linked to increased net nitrification potential in surface soils (Fig. 4.1a). This in turn was strongly and positively correlated with microbial activity and biomass (Fig. 4.2). Therefore, availability of NH_4^+ was not directly limiting the nitrifying bacteria on uninvaded islands. At least in the laboratory, NO_3^- accumulated while NH_4^+ was depleted. The relative abundance of inorganic N species in this system is thus similar to that of seabird dominated coral cays, where most NH_4^+ is nitrified to NO_3^- and the rest volatilizes to NH_3 gas (Schmidt et al., 2004).

4.5.2 Plant leaf N and $\delta^{13}C$

On the intermediate-density seabird islands that we visited, seabirds increased leaf N by various indirect pathways, involving both chemical (inorganic N) and physical (compaction and soil water) mechanisms (Fig. 4.3). However, tree size was the best predictor of leaf N concentrations, rather than inorganic N pools (Fig. 4.3). Individual trees with large root systems may be able to afford more luxury N consumption where soil N concentrations are high (Chapin, 1980), as they are in the presence of seabirds. Large trees on seabird colonies may also be widely spaced, and thus endure relatively little competition for soil resources; studies of aboveground C storage indicate fewer, but larger, trees on seabird colonies (Wardle et al., 2007). Soil NH_4^+-N and NO_3^- -N were both positively correlated to leaf N at the soil surface and to marine N use (leaf $\delta^{15}N$) in the subsurface (Fig. 4.3). Leaf $\delta^{15}N$ in our study was strongly dependent upon soil $\delta^{15}N$ as demonstrated on seabird islands around the world (Mulder et al., 2011).

Soil water content was negatively correlated with leaf N and $\delta^{15}N$ (Fig. 4.3), suggesting that plant N uptake over the life of the leaf is not limited by summer water availability. The same was true of subsurface soil compaction (Fig. 4.3), suggesting that seabird digging may improve plant N uptake by facilitating water percolation and root foraging (Nawaz et al., 2012). It is possible, however, that the leaves of broadleaf evergreens more closely reflect N uptake during the productive winter rainy season, rather than the drier summer period, when we sampled. Harrison (2006) suggested that plants probably have access to guano-derived N year-round, but that winter rains are necessary to mobilize surface deposits into the soil for plant uptake.

Seabirds burrow most densely under larger trees, which stabilize the soil surface (Fig. 4.3) and partially compensate for the birds' tendency to cause erosion (Furness, 1991). Though seabirds had some indirect effects decreasing leaf $\delta^{13}C$, these were offset by direct increases of $\delta^{13}C$ (Table 4.5), suggesting that dense seabird hotspots exacerbate leaf water stress, especially in larger trees (Fig. 4.3). Such "direct" effects of the birds include mechanisms we could not measure, like salt stress from seabird marine inputs (Bancroft et al., 2005; Hobara et al., 2005), or physical damage to twigs and branches (Ellis, 2005).

4.5.3 Soil $\delta^{15}N$ as an index of seabird impacts

Soil $\delta^{15}N$ and burrow density were not interchangeable in their predictive relationships at the within-island scale (Fig. 4.1 and 4.3; Tables 4.3 and 4.4); thus soil $\delta^{15}N$ is not a reliable alternative measure of seabird impacts within islands. Further, though burrows correlate well with high $\delta^{15}N$ values on rat-invaded islands, this was not true on rat-free islands with higher seabird densities. Across 18 islands in this archipelago and across nine archipelagos around the world, soil $\delta^{15}N$ is strongly related to seabird density (Fukami et al., 2006; Mulder et al. 2011); because soil isotope signatures persist for decades, $\delta^{15}N$ can be used to designate deserted or ancient seabird colonies (e.g., Mizutani et al., 1988; Hawke, 2001). However, a geospatial study on the same six islands investigated here found that burrow density did not spatially covary with soil $\delta^{15}N$ within individual islands, suggesting that guano input (responsible for the marine isotope signature) and soil disturbance due to nest construction are spatially decoupled (Chapter 3). In the current study, response variables were sometimes related to soil $\delta^{15}N$ and to burrow density in opposite directions, e.g., soil $\delta^{15}N$ tended to increase soil compaction while burrows decreased it (Fig. 4.1; Table 4.4). This measure therefore should be used carefully, in conjunction with current burrow densities, to indicate continuing seabird legacy effects such as relatively open N cycling (Martinelli et al., 1999), increased ammonification (Vervaet et al., 2002), NH_3 volatilization or NO_3^- leaching (Szpak et al., 2012).

4.5.4 Conclusion

Seabird-mediated controls on N cycling differ in many cases between rat-invaded and uninvaded seabird islands, reinforcing the view that predators provide important indirect controls on ecosystem nutrient dynamics (Schmitz et al., 2010). Sometimes ecosystem properties respond to different drivers, or to the same drivers in opposite directions. For instance, at the within-island scale, seabirds inevitably reduce summer soil moisture, but they do this via reduced soil compaction on rat-invaded islands and via reduced soil C on uninvaded islands. Where pH is reduced, net NO_3^- production is inhibited, but on rat-invaded islands only; soil acidification increases net NH_4^+ production/retention, but on uninvaded islands only. Seabird burrows on rat-invaded islands mean increased soil C and organic N for microbes, but cumulative seabird impacts on uninvaded islands are linked to decreased soil C and organic N. Net ammonification and net nitrification potentials were strongly related to microbial activity and biomass, but only on uninvaded islands. All these examples suggest that rats, by reducing populations of such powerful ecosystem engineers, have altered the mechanisms by which seabirds control island N cycling, thereby establishing an alternative state which may or may not be reversible (Mulder et al., 2009). Restoration may depend upon the extent to which these effects are indirect, via reductions in seabird populations, and the extent to which rats directly affect other ecosystem properties such as plant species composition.

Some patterns hold true regardless of rat invasion history: seabirds reduce pH and soil water; soil C increases soil NH_4^+-N and NO_3^--N; high NH_4^+-N results in much of it being immobilized or nitrified by microbes. Such cases provide hope that invasion-linked shifts in N cycling are ultimately subtle ones, rather than systemic changes likely to permanently alter ecosystem function. Further research is needed to explain the importance of these N cycling shifts to other island ecosystem processes, especially those resulting in plant productivity.

4.6 Acknowledgments

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Table 4.1 Means and standard deviations of variables included in the SEM analyses, by island.

Islands are arranged in order of burrow density. Data from surface soils only.

Variable	**TEH**	**MOP**	**MOK**	**OHI**	**RNI**	**ATU**
Burrow density (burrows m^{-2})	0.006±0.006	0.012±0.025	0.068±0.091	0.155±0.241	0.379±0.441	1.459±0.910
$\delta^{15}N$ (‰)	6.27±1.67	11.75±2.04	9.49±2.39	13.39±1.67	16.14±1.22	12.89±1.57
pH	7.41±0.56	6.93±0.71	6.09±1.07	5.96±1.01	3.60±1.13	3.60±0.38
Compaction (kg cm^{-2})	7.73±3.84	NA	7.78±6.90	NA	4.96±3.27	2.80±2.05
C (%)	4.03±1.10	9.08±3.40	8.22±3.79	6.63±1.88	7.82±2.61	10.95±3.90
N (%)	0.26±0.07	0.70±0.20	0.61±0.25	0.65±0.17	0.71±0.20	0.98±0.35
NH_4^+-N (μg g^{-1} soil)	4.31±3.81	13.71±7.15	15.70±13.09	25.39±16.87	29.17±18.80	58.03±29.20
NO_3^--N (μg g^{-1} soil)	7.22±9.14	11.66±7.97	9.90±12.34	34.76±23.49	35.92±28.59	117.94±52.17
Net ammonification (μg NH_4^+-N g^{-1} soil d^{-1})	-0.18±0.27	-0.43±0.43	-0.34±0.47	-0.83±0.95	-1.07±0.77	-0.78±0.86
Net nitrification (μg NO_3^--N g^{-1} soil d^{-1})	-0.27±0.61	0.31±0.71	0.14±0.38	1.09±1.52	1.08±1.51	0.28±2.24
BR (g CO_2-C g^{-1} soil hr^{-1})	0.40±0.25	1.70±1.08	1.83±1.37	2.14±1.48	1.91±1.39	0.96±0.54
SIR (g CO_2-C g^{-1} soil hr^{-1})	2.17±1.40	6.97±3.12	7.21±3.56	7.61±4.39	7.06±3.87	3.33±2.37
Basal area (cm^2)	13.9±16.6	79.4±147.9	128.8±309.0	85.0±123.5	309.4-311.4	131.3±287.2
leaf N (%)	NA	NA	2.45±0.42	2.77±0.41	2.65±0.48	NA
leaf $\delta^{15}N$ (‰)	NA	NA	5.5±3.5	12.8±2.5	14.6±2.2	NA
leaf $\delta^{13}C$ (‰)	NA	NA	-31.2±1.3	-30.6±1.7	-30.8±1.3	NA

TEH, Te Haupa; MOP, Motuhoropapa; MOK, Motueke; OHI, Ohinauiti; RNI, Ruamahuanui; ATU, Atiu

Table 4.2 Paths included in Fig. 4.1, with justification and predictions where appropriate.

Path	Reason
Seabird legacy (soil $\delta^{15}N$) ←→ burrow density	Addition of marine-based guano with high $\delta^{15}N$
Seabird legacy → soil $[NH_4^+]$ Burrow density → soil $[NH_4^+]$	Ammonia is a component of guano and its decomposition
Seabird legacy → soil total C, organic N Burrow density → soil total C, organic N	Seabird burrow excavation and tillage moves leaf litter underground and increases root breakage
Seabird legacy → soil compaction Burrow density → soil compaction	Seabird burrow excavation and tillage changes soil texture and may increase erosion
Seabird legacy → soil pH Burrow density → soil pH	Guano is mainly composed of uric and phosphoric acid; Acidic stomach contents are regurgitated for chick feeding and nest defense; NH_4^+ releases H^+ to soil during NH_3 volatilization
Organic N ←→ soil C	Organic matter composition
Soil C ←→ soil compaction Organic N ←→ soil compaction	Seabird burrow excavation & tillage of organic matter into the ground
Soil compaction → soil water (H_2O)	Friable soil allows water loss; Excess compaction allows runoff
Soil C → soil water	Soil C increases water holding capacity
Soil water → soil pH	Rain inputs may be neutral (increasing pH) or acidic (decreasing pH)
Soil pH → net ammonification, net nitrification Soil pH → $[NH_4^+]$, $[NO_3^-]$ Soil pH → Organic N	Acidic pH inhibits microbial processes, as measured both in lab (as potential flux rates) and field (as soil pools). Organic matter may then accumulate.
Soil C → net ammonification, $[NH_4^+]$ Organic N → net ammonification, $[NH_4^+]$	Substrates for N ammonification
Soil C → net nitrification, $[NO_3^-]$ $[NH_4^+]$ → net nitrification, $[NO_3^-]$	Substrates for nitrification
Soil water → $[NH_4^+]$, $[NO_3^-]$	Soil moisture controls rates of microbial activity (Moisture was controlled during in-lab fluxes)
Soil compaction → $[NO_3^-]$	Friable soil allows mineral N loss NO_3^- leaching; Excess compaction allows runoff. (Compaction eliminated in lab-measured net fluxes)
Net ammonification → $[NH_4^+]$ Net nitrification → $[NO_3^-]$	Lab-measured potential flux should relate to actual field flux resulting in end-product pool (Net = production – immobilization and loss)
Net ammonification → net nitrification	Ammonification supplies substrate for nitrification; Measured on same soil samples incubated in lab.

Table 4.3 Additional paths (beyond those presented in Table 4.1) included in Fig. 4.3, with justification and predictions where appropriate.

Path	Reason
Seabird legacy (soil $\delta^{15}N$) ←→ Tree basal area Burrow density ←→ Tree basal area	Seabirds often prefer to burrow under the roots of large trees where roots stabilize their burrows.
Tree basal area → soil C	Trees add leaf and root litter, increasing soil C; Large trees or those with high turnover add more C.
Tree basal area → soil compaction	Tree roots stabilize soil (large trees more so); Large trees also invite seabirds that destabilize soil.
Tree basal area → soil [NH_4^+], [NO_3^-]	Leaf and root litter provides organic N substrates for decomposition (large trees more so); Trees also use mineral N, removing it from soil into organic reservoirs (large trees more so).
Tree basal area → soil water (H_2O)	Large trees use more water, removing it from soil; Large trees also shade soil, decreasing evaporation.
Soil water → leaf water stress	Leaf water balance depends directly upon soil water reserves, especially in hot, windy conditions.
Soil water → leaf N Soil water → leaf marine N use ($\delta^{15}N$)	Plant uptake of marine-derived N is mediated by soil water available for N absorption and transport.
Soil C → leaf water stress ($\delta^{13}C$)	Soil C may reflect fine root death, which will increase soil C and leaf water stress concurrently, or fine root growth, which would alleviate leaf water stress by increasing water uptake.
Soil compaction → leaf water stress Soil compaction → leaf N	Excess compaction will interfere with root growth, but excessive permeability may decrease soil water cohesion interfering with water and N absorption.
Soil [NH_4^+], [NO_3^-] → leaf water stress	High ion concentrations around roots can disrupt osmotic balance, interfering with water uptake.
Soil [NH_4^+], [NO_3^-] → leaf N Soil [NH_4^+], [NO_3^-] → leaf marine N use	Plant uptake of marine-derived N Note: No data for mineral N preference of *Melicytus ramiflorus*, a common coastal tree species.
Tree basal area → leaf water stress	Large trees with many leaves suffer increased evaporation and water stress, but may also invest in larger root systems to accommodate water needs, ultimately decreasing leaf water stress.
Seabird legacy → leaf water stress Burrow density → leaf water stress	Seabirds break and damage tree canopies during takeoff and landing.
Tree basal area → leaf N Tree basal area → leaf marine N use	Trees differ in N allocation patterns according to age and size; a larger tree that has coexisted with a seabird colony for a long time may incorporate more marine-derived N into its tissues.
Seabird legacy → leaf N Seabird legacy → leaf marine N use	Higher soil $\delta^{15}N$ is consistent with more recent seabird-derived N sources, which are highly labile for easy plant uptake.
Burrow density → leaf N Burrow density → leaf marine N use	Seabirds may impact leaf N and marine N use *via* some other, indirect mechanism such as ammonia volatilization.

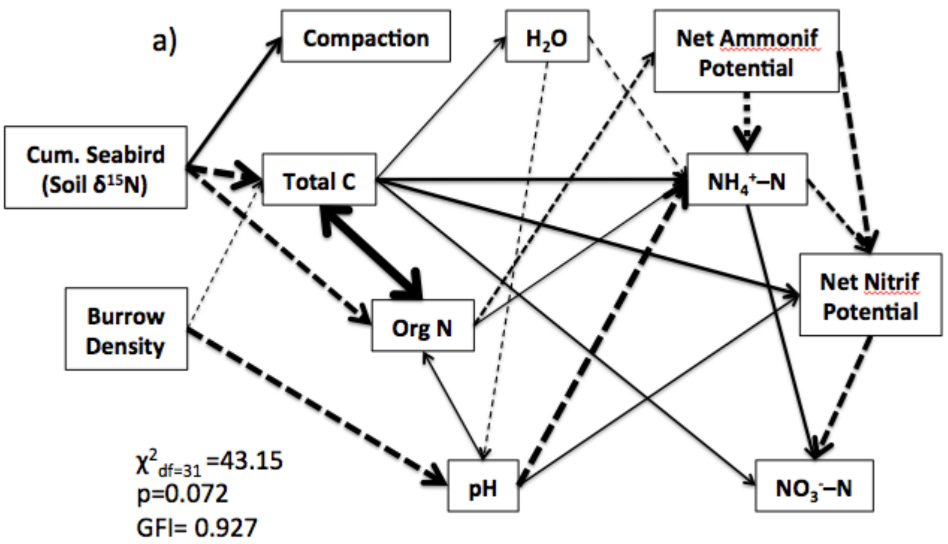
Table 4.4 Indirect effects of seabirds on soil moisture on uninvaded and rat-invaded islands. Path 1 represents the path from seabirds (measured as soil $\delta^{15}N$ or burrow density, BD) to the intermediate variable (soil C or soil compaction), and path 2 the intermediate variable to soil moisture (Fig. 4.1). The product of these path coefficients represents the total indirect effect of seabirds on soil moisture.

Island set	Depth (cm)	Sea-birds	Indirect effect via soil C			Indirect effect via soil compaction			Sum	Overall effect
			path 1	path 2	Product	path 1	path 2	Product		
Un-invaded	0-15	$\delta^{15}N$	-0.49	0.12	-0.059	NA	NA	NA	-0.059	negative
		BD	-0.10		-0.012	NA		NA	-0.012	
	15-30	$\delta^{15}N$	-0.39	0.17	-0.066	NA	-0.18	NA	-0.066	negative
		BD	NA		NA	-0.18		0.0324	0.032	
Rat-invaded	0-15	$\delta^{15}N$	-0.14	0.64	-0.090	0.10	0.41	0.0410	-0.049	negative
		BD	0.35		0.224	-0.55		-0.2255	-0.002	
	15-30	$\delta^{15}N$	NA	0.23	NA	0.15	0.21	0.0315	0.032	negative
		BD	0.20		0.046	-0.40		-0.0840	-0.038	

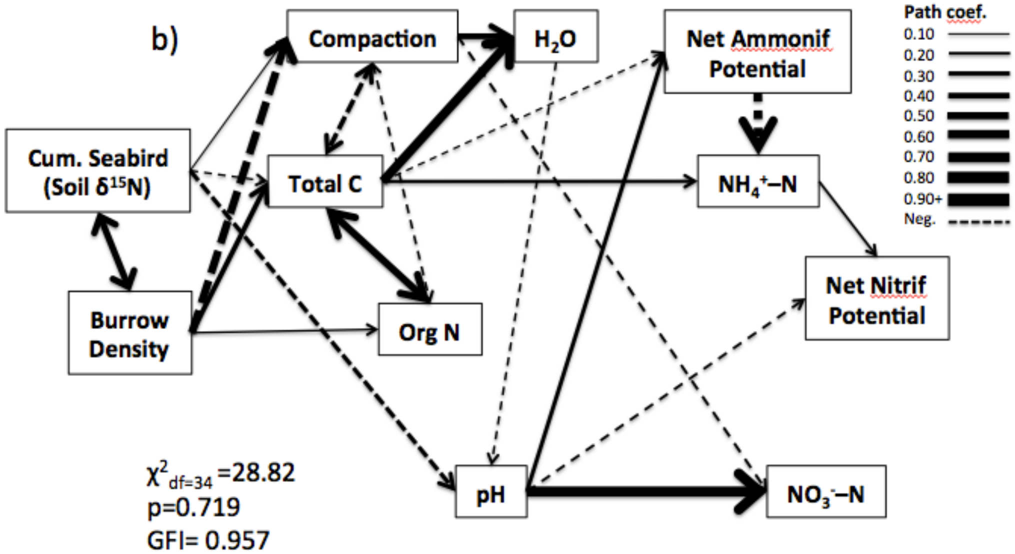
Table 4.5 Indirect effects of seabirds on leaf $\delta^{13}C$, indicative of plant water stress (Fig. 4.3). Seabird presence was measured as legacy impacts (soil $\delta^{15}N$) or burrow density, BD. The product of multiple path coefficients represents the total indirect of seabirds on this variable.

Depth (cm)	Seabirds	Path variables	Path coefficients			Product	Overall effect
0-15	$\delta^{15}N$	direct	0.32	NA	NA	0.320	positive
		soil C	-0.19	0.6	NA	-0.114	
		soil C, H_2O	-0.19	0.27	-0.5	0.026	
		soil comp	NA	NA	NA	NA	
		soil comp, H_2O	NA	NA	NA	NA	
	BD	direct	0.16	NA	NA	0.160	positive
		soil C	NA	NA	NA	NA	
		soil C, H_2O	NA	NA	NA	NA	
		soil comp	-0.38	0.34	NA	-0.129	
		soil comp, H_2O	-0.38	0.13	-0.5	0.025	
15-30	$\delta^{15}N$	direct	NA	NA	NA	NA	positive
		soil C	-0.11	0.32	NA	-0.035	
		soil C, H_2O	NA	NA	NA	NA	
		soil comp	0.24	0.37	NA	0.089	
		soil comp, H_2O	NA	NA	NA	NA	
	BD	direct	0.22	NA	NA	0.220	positive
		soil C	NA	NA	NA	NA	
		soil C, H_2O	NA	NA	NA	NA	
		soil comp	-0.23	0.37	NA	-0.085	
		soil comp, H_2O	NA	NA	NA	NA	

4.9 Figures

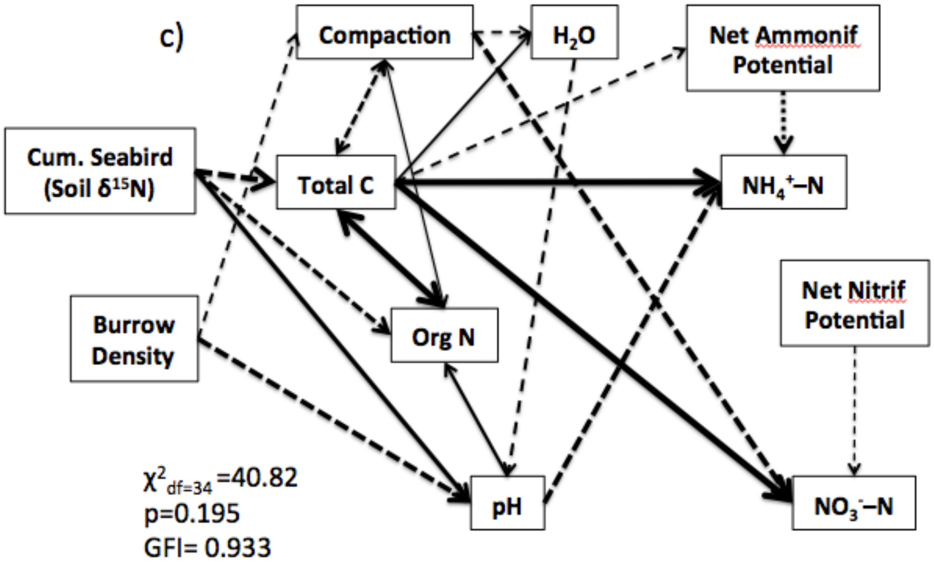


Uninvaded Seabird Islands, depth 0-15 cm

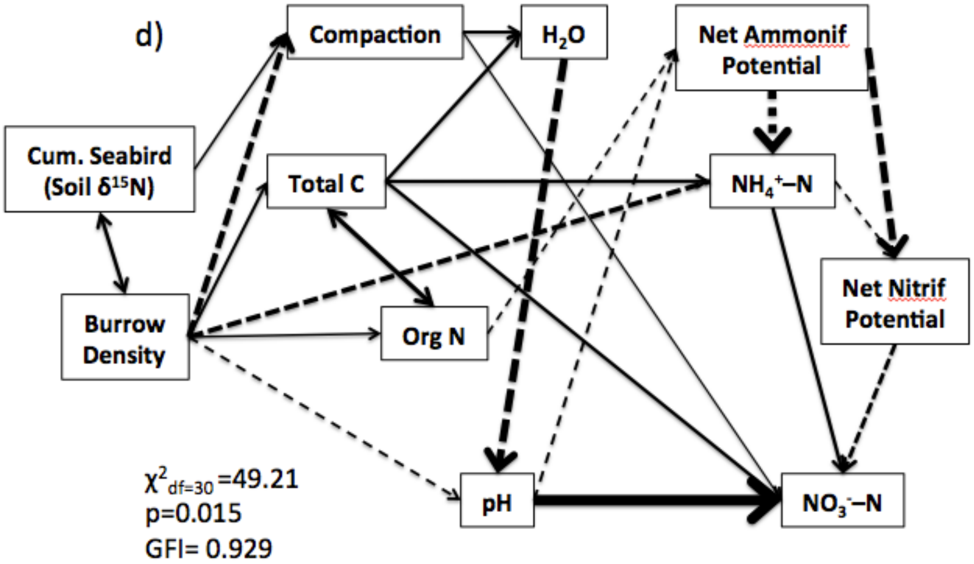


Rat-Invaded Seabird Islands, depth 0-15 cm

Fig. 4.1 Soil N cycling mechanisms on uninvaded and rat-invaded seabird islands at two soil depths. Line thicknesses correspond to path coefficients and dashed lines represent negative correlations. Paths with coefficients <0.10 were removed to improve model fit and are left out for clarity. Final fitted models were significantly different from that of a null model perfectly matching the data (p>0.05), except for d, and goodness-of-fit indices (GFI) were similar. Net Ammonif, net ammonification; Net Nitrif, net nitrification. Figure continued on following page.



Uninvaded Seabird Islands, depth 15-30 cm



Rat-Invaded Seabird Islands, depth 15-30 cm

Fig. 4.1 continued.

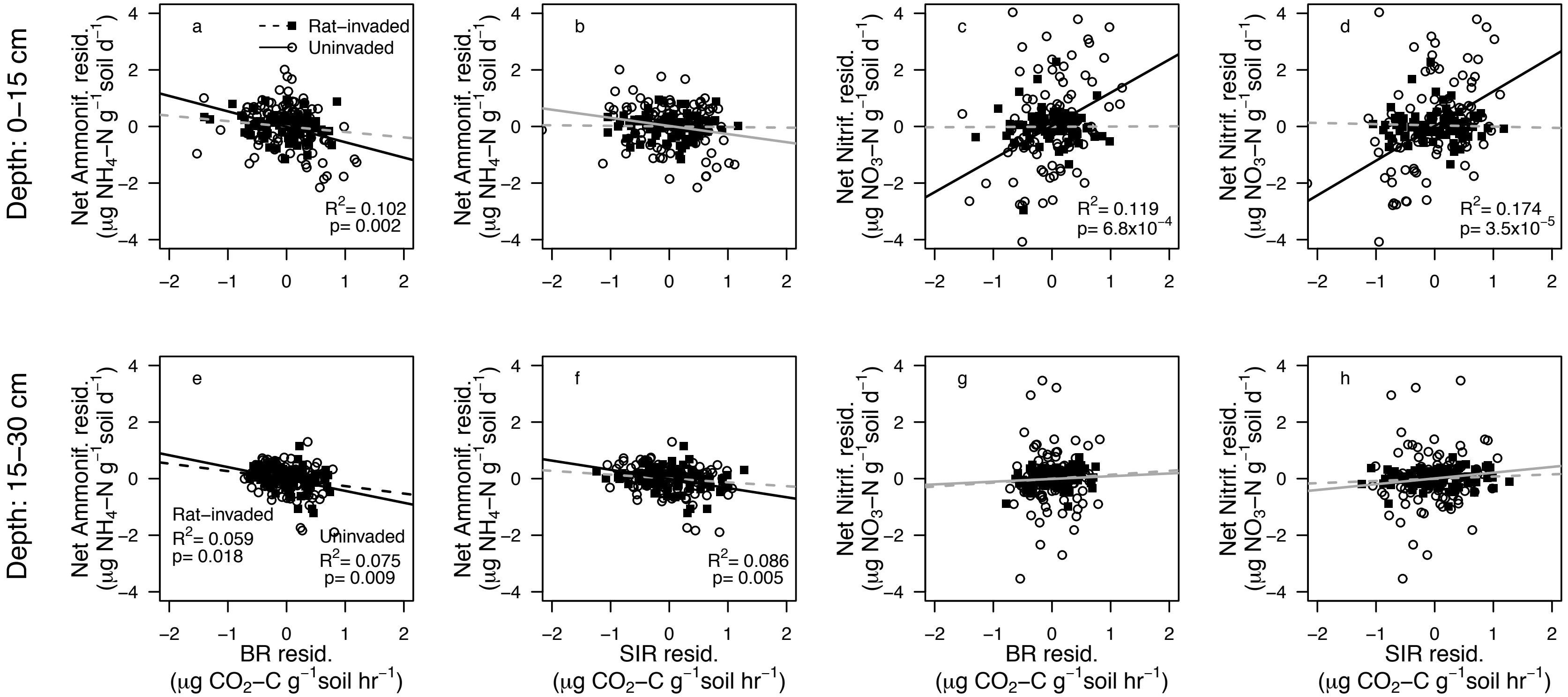


Fig. 4.2 Relationship of net ammonification and net nitrification to microbial activity (basal respiration) and biomass (substrate-induced respiration). Island means have been subtracted from the data so that residuals represent within-island variability. Uninvaded islands are indicated by solid lines, and invaded islands by dashed lines. Black lines represent significance at $p<0.05$; gray lines, $p>0.05$. BR, basal respiration; SIR, substrate-induced respiration; Ammonif., ammonification; Nitrif., nitrification.

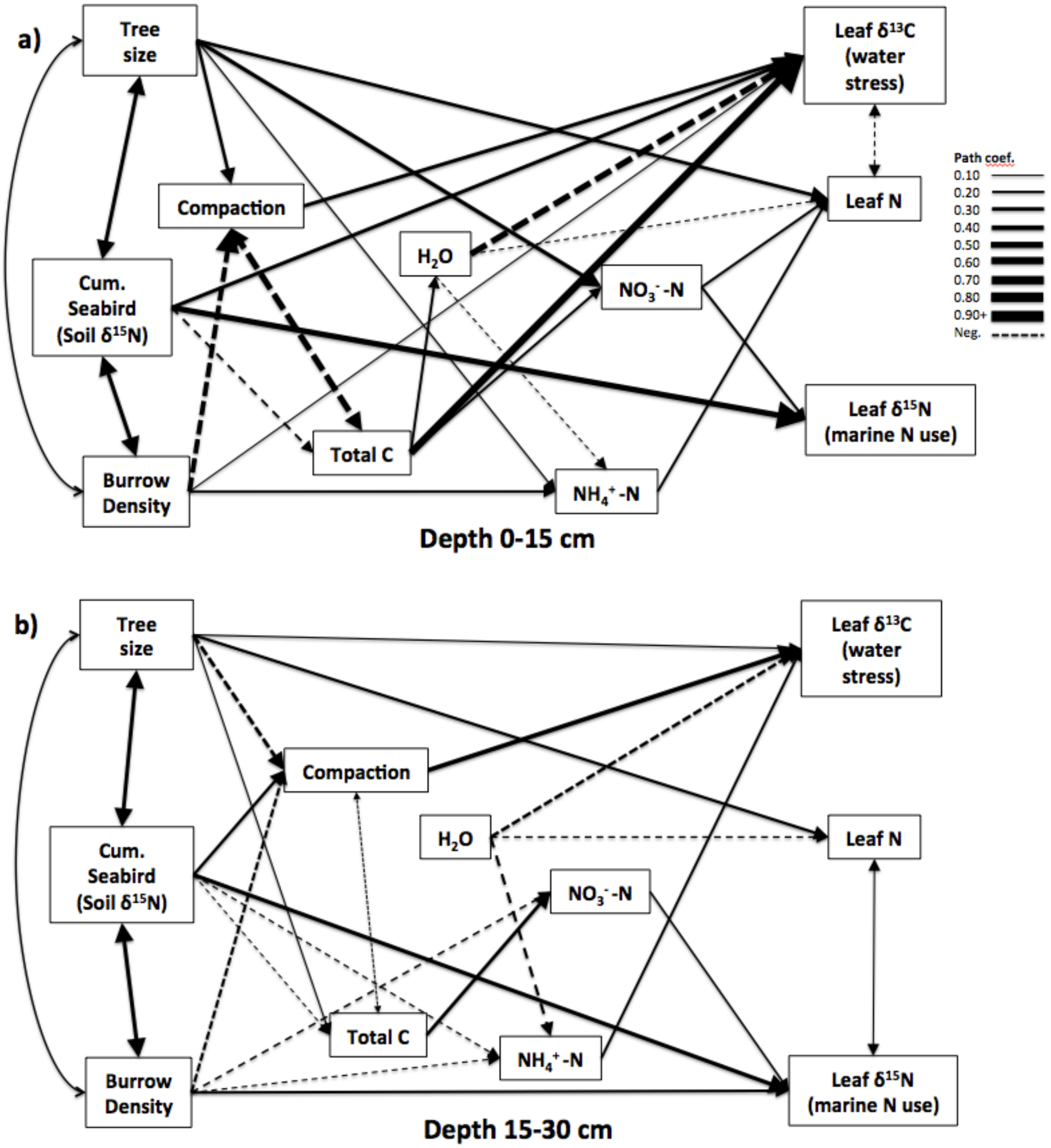


Fig. 4.3 Mechanisms related to leaf N and δ^{13}C on intermediate-density seabird islands. SEMs use soil variables measured at two depths: a) 0-15 cm and b) 15-30 cm from the surface. Tree data were taken from a common coastal species, *Melicytus ramiflorus*. Line thickness increases with strength of the relationship, and dashed lines represent negative relationships. Very weak paths (in gray) were removed to improve model fit. Both fitted models are indistinguishable from the null (a: $\chi^2_{df=24} = 29.29$, p= 0.21; b: $\chi^2_{df=23} = 12.31$, p= 0.97), though the first has a better fit (a: Goodness-of-fit index= 0.96, AIC= 113.29; b: Goodness-of-fit index= 0.98, AIC= 98.31).

Appendix 4.A

Covariance matrices used in SEMs

The data underlying the following matrices were used to construct the previous figures. With these data and the paths outlined in Table 4.2 and 4.3, one can reconstruct the path diagrams in Figs 4.1 and 4.3.

Table 4.A-1 Covariance matrix for N cycling on uninvaded seabird islands, soil depth 0-15 cm.

Corresponds to Figure 4.1a.

	pH	SON	C	comp	H_2O	Net nit	NH_4^+	NO_3^-	Net amm	$\delta^{15}N$	BD
pH	0.802	0.037	0.009	0.180	-0.747	0.443	-0.219	-0.147	-0.054	-0.101	-0.415
SON	0.037	0.096	0.079	-0.110	0.197	0.101	0.068	0.038	-0.057	-0.173	-0.031
C	0.009	0.079	0.093	-0.194	0.332	0.120	0.076	0.033	-0.048	-0.221	-0.039
comp	0.180	-0.110	-0.194	7.333	0.567	0.491	-0.156	-0.105	-0.158	1.076	-0.101
H_2O	-0.747	0.197	0.332	0.567	84.387	-1.345	-0.984	0.410	1.608	-0.598	-1.343
Net nit	0.443	0.101	0.120	0.491	-1.345	3.066	-0.041	-0.375	-0.431	-0.582	-0.422
NH_4^+	-0.219	0.068	0.076	-0.156	-0.984	-0.041	0.416	0.126	-0.285	-0.085	0.179
NO_3^-	-0.147	0.038	0.033	-0.105	0.410	-0.375	0.126	0.396	0.072	-0.128	-0.033
Net amm	-0.054	-0.057	-0.048	-0.158	1.608	-0.431	-0.285	0.072	0.731	-0.119	-0.142
$\delta^{15}N$	-0.101	-0.173	-0.221	1.076	-0.598	-0.582	-0.085	-0.128	-0.119	2.211	0.366
BD	-0.415	-0.031	-0.039	-0.101	-1.343	-0.422	0.179	-0.033	-0.142	0.366	1.245

SON, soil organic nitrogen; comp, compaction; Net nit, net nitrification; Net amm, net ammonification; BD, burrow density

Table 4.A-2 Covariance matrix for N cycling on rat-invaded seabird islands, soil depth 0-15 cm.

Corresponds to Figure 4.1b.

	pH	SON	C	comp	NH_4^+	$\delta^{15}N$	BD	H_2O	Net nit	NO_3^-	Net amm
pH	0.646	0.000	-0.018	-0.004	-0.081	-0.454	-0.122	-0.471	-0.094	0.590	0.092
SON	0.000	0.186	0.075	-0.548	0.059	0.029	0.053	0.604	0.016	0.008	-0.010
C	-0.018	0.075	0.098	-0.851	0.077	0.003	0.080	0.720	0.011	0.010	-0.019
comp	-0.004	-0.548	-0.851	30.698	-0.249	-1.690	-2.539	2.808	0.232	-1.075	0.053
NH_4^+	-0.081	0.059	0.077	-0.249	0.573	0.129	0.060	0.747	0.088	-0.109	-0.194
$\delta^{15}N$	-0.454	0.029	0.003	-1.690	0.129	4.139	0.853	-1.390	0.222	-0.192	-0.140
BD	-0.122	0.053	0.080	-2.539	0.060	0.853	0.817	-0.223	0.097	0.109	-0.063
H_2O	-0.471	0.604	0.720	2.808	0.747	-1.390	-0.223	26.867	-0.121	-0.803	-0.176
Net nit	-0.094	0.016	0.011	0.232	0.088	0.222	0.097	-0.121	0.347	-0.139	-0.046
NO_3^-	0.590	0.008	0.010	-1.075	-0.109	-0.192	0.109	-0.803	-0.139	1.056	0.103
Net amm	0.092	-0.010	-0.019	0.053	-0.194	-0.140	-0.063	-0.176	-0.046	0.103	0.159

SON, soil organic nitrogen; comp, compaction; Net nit, net nitrification; Net amm, net ammonification; BD, burrow density

Table 4.A-3 Covariance matrix for N cycling on uninvaded seabird islands, soil depth 15-30 cm.

Corresponds to Figure 4.1c.

	pH	SON	C	comp	H_2O	Net nit	NH_4^+	NO_3^-	Net amm	$\delta^{15}N$	BD
pH	0.848	0.026	-0.110	1.518	-1.803	0.090	-0.369	-0.204	0.003	0.507	-0.336
SON	0.026	0.096	0.056	0.348	-0.019	-0.027	0.055	0.032	-0.016	-0.127	-0.031
C	-0.110	0.056	0.153	-0.498	0.654	-0.034	0.195	0.179	-0.043	-0.268	-0.006
comp	1.518	0.348	-0.498	31.566	-9.685	-0.040	-1.647	-2.189	-0.088	-0.364	-0.738
H_2O	-1.803	-0.019	0.654	-9.685	62.564	-2.341	0.423	1.136	0.659	-1.972	-0.602
Net nit	0.090	-0.027	-0.034	-0.040	-2.341	1.109	-0.057	-0.149	-0.030	0.342	0.015
NH_4^+	-0.369	0.055	0.195	-1.647	0.423	-0.057	0.742	0.324	-0.182	-0.366	0.116
NO_3^-	-0.204	0.032	0.179	-2.189	1.136	-0.149	0.324	0.705	-0.051	-0.268	-0.053
Net amm	0.003	-0.016	-0.043	-0.088	0.659	-0.030	-0.182	-0.051	0.319	-0.042	-0.029
$\delta^{15}N$	0.507	-0.127	-0.268	-0.364	-1.972	0.342	-0.366	-0.268	-0.042	3.266	0.232
BD	-0.336	-0.031	-0.006	-0.738	-0.602	0.015	0.116	-0.053	-0.029	0.232	1.245

SON, soil organic nitrogen; comp, compaction; Net nit, net nitrification; Net amm, net ammonification; BD, burrow density

Table 4.A-4 Covariance matrix for N cycling on rat-invaded seabird islands, soil depth 15-30 cm.

Corresponds to Figure 4.1d.

	pH	SON	C	comp	H_2O	Net nit	NH_4^+	NO_3^-	Net amm	$\delta^{15}N$	BD
pH	0.883	0.000	-0.130	-0.161	-2.761	0.010	0.048	0.508	-0.064	-0.154	-0.148
SON	0.000	0.186	0.042	0.020	0.323	0.017	0.015	0.010	-0.024	0.106	0.053
C	-0.130	0.042	0.086	0.001	0.587	0.009	0.048	-0.025	-0.008	0.053	0.068
comp	-0.161	0.020	0.001	24.093	5.182	-0.030	-0.098	0.404	-0.449	0.514	-1.605
H_2O	-2.761	0.323	0.587	5.182	26.547	-0.083	0.168	-1.031	0.269	1.078	-0.084
Net nit	0.010	0.017	0.009	-0.030	-0.083	0.085	0.029	-0.049	-0.042	-0.050	0.062
NH_4^+	0.048	0.015	0.048	-0.098	0.168	0.029	0.717	0.212	-0.165	-0.091	-0.156
NO_3^-	0.508	0.010	-0.025	0.404	-1.031	-0.049	0.212	0.767	-0.087	0.030	-0.059
Net amm	-0.064	-0.024	-0.008	-0.449	0.269	-0.042	-0.165	-0.087	0.124	-0.049	0.013
$\delta^{15}N$	-0.154	0.106	0.053	0.514	1.078	-0.050	-0.091	0.030	-0.049	3.883	0.450
BD	-0.148	0.053	0.068	-1.605	-0.084	0.062	-0.156	-0.059	0.013	0.450	0.817

SON, soil organic nitrogen; comp, compaction; Net nit, net nitrification; Net amm, net ammonification; BD, burrow density

Table 4.A-5 Covariance matrix for leaf N and $\delta^{13}C$ on intermediate-density seabird islands, soil depth 0-15 cm.

Corresponds to Figure 4.3a.

	BD	$\delta^{15}N$	BA	NH_4^+	NO_3^-	comp	H_2O	Leaf N	Leaf $\delta^{15}N$	Leaf $\delta^{13}C$	C
BD	1.730	0.765	0.596	0.205	0.064	-2.305	-0.209	0.114	0.866	0.269	0.001
$\delta^{15}N$	0.765	3.290	0.388	0.034	-0.107	-1.045	0.280	0.036	2.057	0.550	-0.101
BA	0.596	0.388	2.109	0.224	0.405	1.297	-0.453	0.256	1.020	0.304	-0.038
NH_4^+	0.205	0.034	0.224	0.554	0.114	-0.609	-0.346	0.128	0.349	0.193	0.103
NO_3^-	0.064	-0.107	0.405	0.114	0.828	-0.261	0.163	0.145	0.575	0.035	0.054
comp	-2.305	-1.045	1.297	-0.609	-0.261	28.687	-0.377	0.031	-1.058	-0.507	-0.948
H_2O	-0.209	0.280	-0.453	-0.346	0.163	-0.377	33.858	-0.320	-7.252	-3.119	0.344
Leaf N	0.114	0.036	0.256	0.128	0.145	0.031	-0.320	0.191	0.310	-0.080	-0.014
Leaf $\delta^{15}N$	0.866	2.057	1.020	0.349	0.575	-1.058	-7.252	0.310	6.348	1.250	-0.047
Leaf $\delta^{13}C$	0.269	0.550	0.304	0.193	0.035	-0.507	-3.119	-0.080	1.250	2.055	0.115
C	0.001	-0.101	-0.038	0.103	0.054	-0.948	0.344	-0.014	-0.047	0.115	0.099

BD, burrow density; BA, basal area; comp, compaction

Table 4.A-6 Covariance matrix for leaf N and δ^{13}C on intermediate-density seabird islands, soil depth 15-30 cm.

Corresponds to Figure 4.3b.

	BD	δ^{15}N	BA	NH_4^+	NO_3^-	comp	H_2O	Leaf N	Leaf δ^{15}N	Leaf δ^{13}C	C
BD	1.730	0.515	0.596	-0.080	-0.057	-1.895	0.025	0.114	0.866	0.269	-0.010
δ^{15}N	0.515	3.107	0.000	-0.248	-0.104	1.878	-0.654	-0.065	1.438	0.303	-0.066
BA	0.596	0.000	2.109	0.297	0.400	-2.914	0.086	0.256	1.020	0.304	0.061
NH_4^+	-0.080	-0.248	0.297	0.657	0.211	-0.535	-0.826	0.054	0.819	0.386	0.099
NO_3^-	-0.057	-0.104	0.400	0.211	0.801	-1.261	-1.441	0.098	0.732	0.255	0.100
comp	-1.895	1.878	-2.914	-0.535	-1.261	31.000	1.526	-1.310	-1.772	1.489	-0.299
H_2O	0.025	-0.654	0.086	-0.826	-1.441	1.526	26.072	-0.352	-5.351	-1.929	0.099
Leaf N	0.114	-0.065	0.256	0.054	0.098	-1.310	-0.352	0.191	0.310	-0.080	-0.004
Leaf δ^{15}N	0.866	1.438	1.020	0.819	0.732	-1.772	-5.351	0.310	6.348	1.250	0.071
Leaf δ^{13}C	0.269	0.303	0.304	0.386	0.255	1.489	-1.929	-0.080	1.250	2.055	0.166
C	-0.010	-0.066	0.061	0.099	0.100	-0.299	0.099	-0.004	0.071	0.166	0.123

BD, burrow density; BA, basal area; comp, compaction

Appendix 4.B

AIC comparisons of SEMs fitted to different data

There is no hypothesis test for comparing two SEMs containing different paths and fit to different datasets. We briefly explored the extent to which an SEM fitted to a particular dataset differed from other SEMs fitted to other datasets. The results, below, confirm that each best-fit SEM is not only a better model, but a *far* better model, for the data that produced it, than is any model obtained from a different dataset. This demonstrates that patterns of N cycling, as modeled by SEMs, differ greatly among these different island sets and soil depths (despite the impossibility of testing for “significant differences”), and we are therefore justified in comparing patterns in N cycling among them.

Table 4.B-1 Akaike information criteria (AICs) obtained by fitting a SEM to one dataset, then applying that SEM to a different dataset. An increase of 2 AIC points indicates decreased model fit. Lowest AICs, and thus the best model fits for each dataset, are highlighted in bold.

Data used to obtain the best-fit SEM	Data to which SEM was applied			
	Uninvaded, 0-15 cm	Rat-invaded, 0-15 cm	Uninvaded, 15-30 cm	Rat-invaded, 15-30 cm
Uninvaded, 0-15 cm	**107.15**	236.01	142.47	233.38
Rat-invaded, 0-15 cm	209.77	**87.25**	178.50	190.34
Uninvaded, 15-30 cm	138.30	181.21	**98.83**	251.06
Rat-invaded, 15-30 cm	178.25	122.60	154.71	**115.21**

Chapter 5.

Foliar uptake of seabird-derived ammonia on New Zealand's offshore islands[1]

5.1 Abstract

Ammonia (NH_3 gas) volatilization from seabird colonies may be an important but overlooked plant N source dependent on NH_3 availability and plant N demand. We measured NH_3 gas concentrations and $\delta^{15}N$ values both on- and off-colony on ten seabird islands of northeastern New Zealand, including several where invasive rats have reduced local seabird densities. We used a stable isotope mixing model to quantify foliar uptake of NH_3 gas in a nine-month-long field experiment with plants grown in control, added N, added P, and seabird colony soils. Mean NH_3 gas concentrations across ten islands were 11.52 ± 2.68 μg NH_3-N m^{-3} and the mean $\delta^{15}N$ value of NH_3 was -26.70 ± 2.93‰. Though burrow densities did not predict NH_3 concentrations across or within islands, both NH_3 gas and its $\delta^{15}N$ value responded seasonally to occupancy by breeding seabirds. *Melicytus ramiflorus* and *Coprosma macrocarpa* demonstrated foliar uptake of NH_3 gas, which contributed up to 20% and 30% of their leaf N, respectively. Plants grown in control soil assimilated more NH_3 gas than those in seabird colony soil, which is high in both N and P. Addition of P also stimulated NH_3 foliar uptake, while N-fertilization decreased it. Because N demand stimulates NH_3 uptake and NH_3 availability is highly variable in time and space, maximal plant use of this resource may occur not on seabird colonies themselves, but at off-colony sites nearby. Plant assimilation of NH_3 gas should be included as a component of seabird island nutrient cycles, with implications for any system where marine-derived N deposition allows for NH_3 gas volatilization.

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[1] Durrett, MS, Ruess RW, Wooller MJ (in preparation) Foliar uptake of seabird-derived ammonia on New Zealand's offshore islands. Prepared for submission to Oecologia.

5.2 Introduction

Though discussions of plant mineral nutrition primarily focus on the plant-soil interface (e.g., Aerts and Chapin 1999; Chapin 1980), plants may derive up to 50% of their N from gaseous forms of reactive N, such as ammonia (NH_3; Sparks 2009). Climatic factors (temperature, relative humidity) and soil chemistry (pH, buffering capacity) may alter rates of both NH_3 volatilization (Cameron et al. 2013) and leaf uptake (Geβler and Rennenberg 1998). Additionally, plant physiological conditions, especially stomatal conductance and nutrient limitations, play an important role (Geβler and Rennenberg 1998; Sparks 2009). For instance, N-denied plants may grow exclusively on NH_3 gas (Krupa 2003), while N-saturated plants may become a source of NH_3 emissions at low background NH_3 levels (Farquhar et al. 1980). In addition, P-limited plants may assimilate more NH_3 gas due to inadequate root systems, limiting N uptake (Fogel et al. 2008), or P additions may alter plant stoichiometry, stimulating plants to assimilate more N by any route possible, and thus increase NH_3 uptake.

The process of plant NH_3 gas uptake via the leaf cuticle or stomata is usually addressed in the context of anthropogenic N additions: crop fertilization (e.g., Loubet et al. 2011), livestock emissions (van der Eerden et al. 1998) and industrial pollution (Harrison et al. 2000) all create NH_3 emission hotspots (Fangmeier et al. 1994). However, some localized ecosystems relatively unaltered by humans may also emit large quantities of NH_3 gas; seabird colonies are the most important point sources of NH_3 worldwide, releasing an estimated 6,000 kg NH_3-N per colony annually (Sapek 2013). Emissions from a single colony of burrow-nesting puffins on the Isle of May, Scotland, were compared to that of "a medium-sized chicken farm," and those of cliff-nesters were even greater (Blackall et al. 2007). Far higher uncertainties are associated with natural sources of NH_3 than with anthropogenic ones (Sutton et al. 2008), and there are few estimates of ambient NH_3 concentrations, rather than emissions, from seabird colonies (Table 5.1). Researchers on subantarctic Marion Island noted both the distinctive aroma of guano (Smith 1978) and the "ammonia shadow" of lush vegetation surrounding the otherwise denuded ground where birds were nesting, speculating that foliar uptake of NH_3 was especially important to plants downwind (Lindeboom 1984). Stable isotope analysis of plant leaves on Macquarie Island revealed that plants downwind of penguin rookeries were using NH_3 gas volatilized from seabird guano, although they were too far away to make use of seabird-derived soil sources (Erskine et al. 1998).

Stable isotope mixing models can be used to distinguish plant N sources when source (end-member) $\delta^{15}N$ values are distinct (e.g., Houlton et al. 2007). This method is ideal for tracking NH_3 uptake because its $\delta^{15}N$ value is often relatively low (e.g., -6 to -13‰; Erskine et al. 1998) compared with that of other N sources (e.g., +8 to +20‰ for soil NH_4^+; Erskine et al. 1998). Upon volatilization, NH_4^+ molecules containing ^{14}N diffuse more readily into gas than those with ^{15}N, resulting in a fractionation of up to -60‰ (Högberg 1997; Robinson 2001). However, more information is needed on the $\delta^{15}N$ value of NH_3 gas in natural systems (Gebauer 2000). Assimilation of isotopically depleted NH_3 gas will decrease the $\delta^{15}N$ value of autotrophs using this gas as an N source. For example, the $\delta^{15}N$ value of epiphytic lichens, normally ~0‰ (reflecting N_2 fixation), has been shown to decrease to -8‰ with NH_3 exposure at geothermal sites (Tozer et al. 2005). Plants on seabird islands often have $\delta^{15}N$ values of 10‰ or higher, reflecting soil N sources with high $\delta^{15}N$ values due to trophic enrichment in seabird diets (Mulder et al. 2011). Volatilization of NH_3 concurrently raises the $\delta^{15}N$ of the soil pool, which explains why the $\delta^{15}N$ of the NH_4^+ pool can sometimes exceed that of the guano or bulk soil from which it was mineralized (Mizota 2009a; Mizutani et al. 1991; Mizutani et al. 1986; Mizutani et al. 1985; Schmidt et al. 2010). Therefore, if a plant were to assimilate both NH_4^+ (a high $\delta^{15}N$ source) via its roots and NH_3 (a very low $\delta^{15}N$ source) via its leaves, the plant's leaf $\delta^{15}N$ values might remain relatively high, causing NH_3 to be overlooked as a plant N source.

This study investigates the importance of seabird-derived NH_3 gas as a plant N source on ten offshore islands of New Zealand, five with invasive rats that have reduced seabird populations, and five rat-free. Previous studies on these islands have shown that the overall soil and leaf $\delta^{15}N$ values reflect enriched marine-derived N (Fukami et al. 2006); however, seabird-derived N inputs within islands and across islands within the same archipelago can be spatially and temporally variable (Chapters 3, 4). We therefore measured the concentrations and $\delta^{15}N$ values of NH_3 gas both on- and off-colony wherever possible, across multiple islands. We predicted that if seabirds control NH_3 emissions, then concentrations of NH_3 gas on rat-free islands would exceed those on rat-invaded islands with few seabirds, and a similar pattern would hold true for seabird colonies compared to non-colony sites within islands. We also conducted a field experiment by planting cuttings of a native shrub in identical soils at a seabird colony and a control site; we manipulated these soils to assess NH_3 uptake under different nutrient regimes. We expected plants at the seabird colony to use more NH_3 gas (due to its availability), but that soil treatments would alter NH_3 uptake within a site. Specifically, we predicted that P addition would increase plant NH_3 uptake, while N addition would decrease it. Similarly, plants grown in soil from a control site should use more NH_3 than those grown in nutrient-rich seabird colony soil.

5.3 Materials and methods

5.3.1 Study system

The 18 seabird islands included in this study have been described in detail elsewhere (Fukami et al. 2006; Mulder et al. 2009). All lie within 50 km of the North Island of New Zealand and are characterized by warm temperate coastal forest. Most of their soils are shallow and volcanic, though several are sedimentary, and none except Goat I. benefit from a permanent fresh water source. Temperatures are moderate year-round (2004 daily means: 17.1-19.5 ˚C in Jan, 11.4-13.8 ˚C in July). The most abundant burrowing seabirds across all the islands are common diving petrels (*Pelecanoides urinatrix*), flesh-footed shearwaters (*Puffinus carneipes*), fluttering shearwaters (*Puffinus gavia*), grey-faced petrels (*Pterodroma macroptera gouldi*), little blue penguins (*Eudyptula minor*) and white-faced storm petrels (*Pelagodroma marina*). Burrow densities range from 0 to 3.5 burrows m^{-2} (Chapter 3) and depend strongly on the presence or absence of invasive European rats (*Rattus rattus* and *Rattus norvegicus*). Islands with extensive seabird colonies are noticeably more odiferous than those with only a few burrows (M. Durrett, pers. obs.).

In 2004, we collected soil (sieved to 4 mm) and plant leaves from 18 of these islands for stable nitrogen isotope analysis. Other samples such as guano, broken eggshells, and lichens were collected opportunistically from 2004 to 2006 and also analyzed. Stable nitrogen isotope compositions of samples are expressed in delta notation ($\delta^{15}N$ values) relative to an international standard of atmospheric nitrogen (IAEA-1). These were measured at Lincoln University, Lincoln, Canterbury, New Zealand, using a PDZ Europa GSL Elemental Analyzer attached to a PDZ Europa 20-20 continuous flow isotope ratio mass spectrometer (CF-IRMS) with a precision of ±0.2‰ (reported as 1 standard deviation calculated from at least 15 replicate measurements of a laboratory standard). Differences between rat-invaded and rat-free islands in soil and leaf $\delta^{15}N$ values of this dataset have been reported elsewhere (Fukami et al. 2006), but we used these values in comparison with other N sources to identify broad trends in $\delta^{15}N$ values across multiple islands.

5.3.2 NH_3 gas sampling

We sampled NH_3 gas on ten islands, at both high and low seabird densities (i.e., on- and off-colony sites), between January and March 2006. We used passive uptake samplers based on an Ogawa-style device (Roadman et al. 2003). The reactive surface was a 31.7 mm^2 disc punched from Whatman No. 1 filter paper, saturated with 5% (w/v) citric acid and secured in a plastic housing with a semi-permeable polytetrafluoroethylene membrane (i.e., PTFE or thread seal tape). On each island, we deployed 3 samplers per site for 2-24 hours. Samples were refrigerated until analysis to limit re-volatilization of NH_3. We performed stable nitrogen isotope analysis on the entire acid-treated disc, using a Costech Elemental Analyzer (ECS 4010) attached to a CF-IRMS (ThermoScientific Delta V) at the Alaska Stable Isotope Facility (AIF) of the University of Alaska Fairbanks (UAF) Water and Environmental Research Center (WERC), Fairbanks, Alaska, USA, where analytical precision was <0.2‰ (as tracked with a laboratory standard of peptone, No. P-7750 from Sigma Chemical Company, Lot #76f-0300). We used the N captured by each disc (as measured by the IRMS), disc surface area, and time deployed to calculate ambient NH_3 concentrations, according to the method of Roadman et al. (2003).

5.3.3 Experimental design

To test whether island plants use NH_3 gas as a N source, we established a nine-month-long experiment on Motuhoropapa, a privately owned island of ~10 ha which lies ~2.2 km offshore in the Noises group of the Hauraki Gulf, New Zealand. Norway rats (*Rattus norvegicus*) first invaded this island in the 1950s and have re-invaded at least six times between periodic eradication efforts (Clout and Russell 2006; Russell et al. 2005). However, Motuhoropapa was rat-free at the time of this study (March-November 2006), with the exception of one research subject, an intentionally released male Norway rat. Grey-faced petrels are large and relatively aggressive seabirds, and have continued to breed on Motuhoropapa despite rat invasion, though island seabird populations in general have declined (Cunningham and Moors 1985; MacKay et al. 2007). We used the two areas of highest petrel burrow density (the southernmost tip of the island and the southeastern peninsula known as Petrel Point), assuming these sites would provide concentrated NH_3 gas freshly volatilized from seabird guano. At both colonies, we counted 10 burrow entrances in a 100-m^2 plot; occupancy was estimated at 26% at the southern colony and 54% at Petrel Point. (We left wooden craft sticks upright in burrow entrances and subsequently counted sticks knocked down by visiting petrels. However, our method was not robust due to timing and lack of replication; it is best considered a qualitative estimate.) For each seabird colony we chose an off-colony control site 50 m away with similar slope, aspect, and canopy cover.

At each of these four sites, we placed 80 cuttings of a common native shrub, *Coprosma macrocarpa* subsp. *minor* R.O.Gardner et Heads ex A.Druce (Rubiaceae), in hanging baskets for maximum exposure to seabird-derived NH_3 gas (Fig. 5.1). Cuttings were collected from individuals distributed widely within the island. We stripped each 10-cm cutting of all but four leaves and cut each remaining leaf in half to reduce transpiration, decrease fungal spread and roughly standardize leaf area (~8 cm^2). We dipped each cutting in beta-Indolylbutric acid (a root-forming hormone powder with negligible N content; less than 1 mg was used) and planted it in a separate 0.5-L black plastic planting bag. To explore the effects of nutrient availability on plant NH_3 gas uptake, we randomly assigned plants to one of four soil types: seabird soil (dug from the colony site), control soil (dug from the control site), control soil with added N (urea pellets), and control soil with added P (superphosphate powder). Fertilization rates of N and P (0.200 kg N m^{-2} and 0.020 kg P m^{-2}, respectively) mimicked annual nutrient inputs by burrowing petrels (Furness 1991). To autonomously water plants throughout the year, we employed two water-catchment buckets at each site with gravity-feed irrigation to one hanging basket of each soil treatment (10 plants each). Soil treatments were kept in separate baskets so nutrients could not migrate via the water supply, and the watering system was duplicated at each site in case one failed.

We visited the island four times over nine months. We set up the experiment in early March 2006, about a month before the petrels begin to arrive for egg-laying. Some birds arrived earlier to prospect for new breeding sites or to scrape out their nests before the breeding season, and we saw evidence of this activity. When we returned in early May, petrels were clearly using burrows on site. On our September visit, we heard many chicks in their burrows, especially at Petrel Point (MacKay et al. 2007). By mid-November, chicks were large and 4-6 weeks away from fledging. On each visit, we collected NH_3 gas at each seabird colony and control site and refilled water buckets for the experimental plants.

We harvested all surviving plants in November, removing new leaves and sampling soil from the bags. Many seedlings also "volunteered" in the experimental soils, and we collected all of those that were large enough to positively identify to species (*Coprosma macrocarpa, Melicope ternata* A.Cunn (Rutaceae) a.k.a. wharangi*, Melicytus novae-zelandiae* (A.Cunn.) P.S.Green (Violaceae)*, Dysoxylum spectabile* (G.Forst.) Hook.f. (Meliaceae) a.k.a. kohekohe*,* and *Tetragonia tetragonoides* (Pall.) Kuntze (Aizoaceae) a.k.a. kohike. Sample sizes from the southern colony were too low to provide statistical power (no cuttings survived on the colony, and only 4 at the control site), so we proceeded with laboratory analysis using only the Petrel Point site. All leaves and soil from Petrel Point were oven-dried at 60˚ C for two days and ground on a rolling mill for stable nitrogen isotope analysis (as described above).

5.3.4 Data analysis

To test whether the presence of seabirds was associated with higher NH_3 concentrations across the ten islands, we performed a two-way ANOVA on the independent variables rat status (rat-invaded vs. rat-free) and site (on- or off-colony). A paired t-test would have been a more appropriate test for site effects, but several rat-invaded islands had no seabird colonies and some rat-free islands had no off-colony sites, so our paired samples were too few for the necessary degrees of freedom. We also used linear regression to test whether burrow density could explain variation in NH_3 gas concentrations and $\delta^{15}N$ values. By assuming that the $\delta^{15}N$ values of NH_3 stay similar from year to year, which allowed us to combine soil and plant $\delta^{15}N$ data from 2004 with NH_3 $\delta^{15}N$ data from 2006, we performed a one-isotope ratio, two end-member (NH_3 gas and soil N) mixing model (Fry 2006)

[5.1] $$f_{NH_3} = (\delta^{15}N_{leaf} - \delta^{15}N_{soil\,N})/(\delta^{15}N_{NH_3} - \delta^{15}N_{soil\,N})$$

where f_{NH_3} represents the proportional contribution of NH_3 gas to plant leaf N. This analysis also assumes that plants are using soil resources with a similar $\delta^{15}N$ value to that of the bulk soil. Combining the lowest and highest estimates of NH_3 and soil $\delta^{15}N$ values for each island in each possible variation, we calculated the minimum and maximum proportional contribution of a plant's N from NH_3 gas. We used a similar analysis on our experimental plants from Motuhoropapa, using the highest and lowest mean $\delta^{15}N$ values for NH_3 gas across sampling periods (the variability among seasons dwarfed the variability within a single sampling period, and we assumed that plants use NH_3 gas year-round). To test whether experimental cuttings and seedlings used NH_3 gas as a source of N, we performed a multi-way ANOVA on leaf $\delta^{15}N$ values, including seabird presence, soil treatment and plant species as factors. All statistical analyses were performed in R 2.15.1 (R Development Core Team 2012, Vienna, Austria).

5.4 Results

5.4.1 Across multiple islands

We measured NH_3 gas concentrations and $\delta^{15}N$ values on ten offshore islands of northeastern New Zealand (Table 5.2). Both of these variables were characterized by a significant interaction between rat invasion status (and thus whole-island seabird populations) and location within an island (thus plot-level burrow density; p_{int}=0.0228 for NH_3 and p_{int}=0.0132 for $\delta^{15}N$ values; Fig. 5.2). Rat invasion was not a significant factor controlling NH_3 gas concentration (ANOVA; p=0.756). However, location within an island (seabird colony or comparatively burrow-free control site) had a marginally significant effect (p=0.0704): within rat-invaded islands only, seabird colonies had lower NH_3 gas concentrations (p=0.0167; Fig. 5.2c). Ammonia on rat-free islands (large seabird populations) had higher $\delta^{15}N$ values than that of rat-invaded islands overall (p=0.0226), but within rat-free islands only, NH_3 from seabird colonies had lower $\delta^{15}N$ values than off-colony sites (marginally; p=0.0547; Fig. 5.2b). Across ten islands, burrow density itself (measured in a random island plot) did not significantly affect either NH_3 gas concentration or $\delta^{15}N$ values when on- and off-colony sites were considered together. When seabird colonies were considered separately, however, higher burrow densities were correlated with lower δ^{15}N values in NH_3 gas (R^2=0.273, p=0.0127), while at off-colony control sites considered separately, this relationship was reversed (R^2=0.242, p=0.0058).

The δ^{15}N values of seabird eggshells, guano, and bulk soil from 18 islands were at least 10‰ on rat-free islands, and the δ^{15}N of NH_3 gas ranged from -15 to -35‰ (Fig. 5.3a). Soil, NH_3 gas, lichen thalli, and leaves from two tree species (*Coprosma* sp. and *Melicytus* sp.) all had higher δ^{15}N values on rat-free islands than on rat-invaded ones (Fig. 5.3a). Soil δ^{15}N values increased with depth in the soil profile, and the δ^{15}N values of soil inside seabird burrows (from any island) were comparable to those of the soil on rat-free islands (Fig. 5.3a), which host many seabirds. The δ^{15}N values of lichens, including *Ramolina* spp., *Usnea* spp., and unidentified foliose species, ranged from -19 to +9‰ (Fig. 5.3a), which brackets 0‰, the δ^{15}N value of another potential N source for lichen, N_2 gas. Two coastal broadleaf trees, *Coprosma macrocarpa* and *Melicytus ramiflorus*, exhibited leaf δ^{15}N values from -3 to +17‰, which were in many cases lower than the δ^{15}N value of soil (at any depth; Fig. 5.3a).

The estimated contribution of NH_3-N gas for *Coprosma macrocarpa* was 10-18% (median of the minimum estimate, median of the maximum estimate) and did not significantly differ between rat-free and rat-invaded islands (Fig. 5.4). For *Melicytus ramiflorus*, NH_3-N contributed 4-6% to leaf N on rat-free islands, and 4-13% on rat-invaded islands; these maximums differed significantly (p=0.0133; Fig. 5.4d).

5.4.2 Experiment on Motuhoropapa

Ammonia concentrations and δ^{15}N values varied significantly from season to season on Motuhoropapa (ANOVA; p<0.0001; Fig. 5.5), but not between the southern and southeastern sites (p=0.847), and not between each seabird colony and its control site (p=0.536). Concentrations of NH_3 gas increased throughout the year from March, when seabirds were just starting to prospect for breeding sites, to November, when chicks were nearly ready to fledge (Fig. 5.5e, f; M. Durrett, pers. obs.). In May, the southern colony and its control exceeded the southeastern colony and its control in NH_3 (p=0.0235; Fig. 5.5f), and in September, control sites exceeded the seabird colonies in NH_3 (p=0.0223; Fig. 5.5g). Within any particular sampling event, the highest variability in the NH_3 gas samples collected was always found at one of the seabird colony sites (Fig. 5.5e, f). Even at their highest, NH_3 gas concentrations from this island were the lowest found on any of the ten islands sampled (compare Figs. 5.2 and 5.5). However, the $\delta^{15}N$ values of soil and NH_3 gas from Motuhoropapa were comparable to combined values across 18 islands (Fig. 5.3b), validating these end-members for use in the stable isotope mixing model related to our field experiment. Ammonia gas $\delta^{15}N$ values on Motuhoropapa ranged from -15 to -42‰ with the highest in May and the lowest in November (Fig. 5.5a-d). Within a single visit, there were no significant differences driven by site or seabird presence ($p > 0.1$ in 4 two-way ANOVAs).

We harvested only 28 of our 320 original *Coprosma macrocarpa* cuttings (mortality exceeded 91%), and 24 of the survivors were from Petrel Point or its control site. The *Coprosma macrocarpa* cuttings from our experiment had higher leaf $\delta^{15}N$ values (approximately 7-17‰) than those from other islands (Fig. 5.3b). Cuttings placed at the seabird colony had higher $\delta^{15}N$ values (effect of seabird presence, $p=0.0233$), except for in control soils (effect of soil type, $p<0.0001$; Fig. 5.6a). No cuttings planted in control soil with added N survived.

We also harvested seedlings of several species (see methods) that volunteered in the experimental pots. For all seedlings combined, there was a significant effect of species ($p<0.0001$) and soil type ($p=0.0054$) on leaf $\delta^{15}N$ value, as well as a marginal difference between plants at colony and control sites ($p=0.0558$). There were not enough seedlings to perform similar tests for individual species. However, *Melicope* seedlings that germinated in control soil had higher $\delta^{15}N$ values at the seabird colony, and so did *Dysoxylum* seedlings that germinated in seabird soil (Fig. 5.6b, c). This pattern was reversed for *Dysoxylum* seedlings that germinated in soils with added N (Fig. 5.6c), and all seedlings that germinated in this soil treatment had highly elevated $\delta^{15}N$ values (Fig. 5.6).

A one-isotope mixing model estimated the average contribution of NH_3 gas to plant leaf N at 0-10% for *Coprosma* cuttings and volunteer seedlings alike (Fig. 5.7b, e). Many estimates of NH_3 uptake were negative, because leaf $\delta^{15}N$ values were more positive than soil $\delta^{15}N$ values (compare Fig. 5.6, Table 5.3), and the $\delta^{15}N$ values of the NH_3 gas available to the plants were not negative enough to offset this. There was a significant effect of soil type (ANOVA; $p=0.0169$), explaining 34.7% of the variability in mean estimates for *Coprosma* cuttings. There were significant effects of both soil type ($p=5.83 \times 10^{-4}$) and seabird presence ($p=6.62 \times 10^{-4}$) for seedlings, together explaining 60.1% of the variability in mean estimates (estimates were higher on the seabird colony). Both cuttings and seedlings grown with added P relied most heavily on NH_3 gas; over half of cuttings in this group used at least some NH_3 gas (Fig. 5.7a), many getting up to 15% of their leaf N from it (Fig. 5.7c). Seedlings grown with added N, however, appeared to use no NH_3 gas (Fig. 5.7). Neither did *Coprosma* cuttings grown in seabird colony soil (Fig. 5.7a-c), but almost half of seedlings used NH_3 gas for up to 10% of plant N, on average (Fig. 5.7e). For plants grown in control soil, estimated contributions were on average small, but positive, for both cuttings and seedlings (5.7b, e); however, the same plants had the highest potential for NH_3 use (5.7c, f). Maximum estimated contributions of NH_3 gas approached 20% for both cuttings and seedlings (Fig. 5.7c, f).

5.5 Discussion

5.5.1 Availability of NH_3 gas on seabird islands

Across all islands, mean NH_3 gas concentrations were 11.52 ± 2.68 μg NH_3-N m^{-3}. Island estimates ranged from 0.14 ± 0.048 μg NH_3-N m^{-3} on Motuhoropapa to 29.27 ± 7.49 μg NH_3-N m^{-3} on Motutapere (Table 5.2). Burrow-nesting seabirds are associated with less NH_3 volatilization than cliff- or ground-nesting birds (Blackall et al. 2008) making some of these estimates for small colonies and nearby off-colony sites slightly higher than expected, compared to compiled estimates from around the world (Table 5.1). Despite individual variability among islands, the average is comparable to other burrow nesters (Blackall et al. 2008; Blackall et al. 2007; Schmidt et al. 2010). Smith (1978) speculated that acidic soils may form effective “traps” for NH_3 volatilized from seabird colonies. Seabird nutrient additions are often acidic, and enhanced nitrification decreases soil pH even further (Chapter 4). In our study system, NH_3 gas is still produced with soil pH values of <3 to ~8, but islands with pH > 7 had the highest NH_3 concentrations (unpublished data). Soil pH may explain why some locations with few seabirds had higher NH_3 concentrations than the rat-free islands with the highest burrow densities (Table 5.2).

Contrary to our predictions, seabirds did not always increase NH_3 concentrations on these islands, either at the whole-island or within-island scale (Fig. 5.2). However, we collected NH_3 gas at each island on only 1-2 days (except for Motuhoropapa), and weather can be a strong source of variability. Seabirds often nest on exposed sites where wind could easily blow NH_3 away (Erskine et al. 1998; Lindeboom 1984; Schmidt et al. 2010), and on seabird cliffs in Scotland, Blackall et al. (2008) noted that moving a sampling location only 3 m away resulted in a 85% decrease in NH_3 gas measured. Seabird densities notably increase the spatial variability of NH_4^+, net mineralization, and pH (which controls volatilization) within islands (Chapter 3), so it is not surprising that NH_3 volatilization should also be highly variable within islands.

On Motuhoropapa, NH_3 gas concentrations increased seasonally, as more seabirds returned to the island to breed and feed their chicks (Fig. 5.5), although this island had the lowest NH_3 in the study (Table 5.2). Seasonal trends in nutrient cycles aligned with the nesting cycle are common (Lindeboom 1984), though the peak in NH_3 emissions may lag a month or so behind peak seabird occupancy (Blackall et al. 2008). Wet periods may also increase NH_3 concentrations (Staunton Smith and Johnson 1995), and the wet winter in this system coincides with chick rearing. Because NH_3 easily dissolves into rain, this may be a pathway for re-deposition of NH_4^+ onto the colony or sites nearby (Schmidt et al. 2010; Staunton Smith and Johnson 1995). We did not find consistent differences between our on- and off-colony sites on Motuhoropapa (ANOVA; p=0.536); thus we did not successfully apply a "treatment" of more concentrated NH_3 gas by placing plants at the seabird colony, as we had intended. For NH_3 gas concentrations, inter-island variability greatly exceeded intra-island variability (compare Figs. 5.2 and 5.5), demonstrating that the potential distance of NH_3 dispersal should be a key constraint on the design of future experiments. Gaseous NH_3 emissions from various industrial point sources, for example, take 0.6-4 km to fall by 50-95% (Krupa 2003), a distance which could not have been achieved on any one of our islands.

5.5.2 $\delta^{15}N$ values of NH_3 gas and lichens

Across all islands, the mean $\delta^{15}N$ value of NH_3 gas was -26.7 ± 2.9‰. On individual islands, this value ranged from -23.1 ± 1.9‰ on Ohinauiti to -32.3 ± 4.7‰ on Motutapere (Table 5.2). We expected NH_3 gas to be highly depleted in ^{15}N due to the large fractionation (-40 to -60‰) associated with ammonia volatilization (Högberg 1997; Robinson 2001). Compared with the $\delta^{15}N$ values of NH_3 reported from Macquarie Island penguin colonies, -10.0 ± 3.1‰ (Erskine et al. 1998), these $\delta^{15}N$ values are lower, but our soil $\delta^{15}N$ values were similar or even higher (Fig. 5.3, Table 5.3), indicating greater fractionation between bulk soil and NH_3 gas in our study system. On seabird colonies only (where burrows were dense and the soil had high $\delta^{15}N$ values) burrow density was correlated with lower $\delta^{15}N$ values of NH_3 gas. Yet the $\delta^{15}N$ of NH_3 gas was positively correlated with whole-island burrow density on off-colony sites (with few burrows and lower soil values). Together, this suggests that fractionation was highest at sites with the most seabirds and the highest nutrient input. This is consistent with strong isotopic enrichment of the soil NH_4^+ pool during volatilization, as well as the general understanding that isotopic fractionation is strongest when access to a source is unlimited, i.e., pools are large (Högberg 1997; Robinson 2001).

On Motuhoropapa, the $\delta^{15}N$ value of NH_3 gas varied by season, with highs in May (-15‰) and lows in December (-42‰; Fig. 5.5). This variability across seasons was greater than that of similar measurements across multiple islands within a month of each other, suggesting that strong seasonal controls on fractionation alter the $\delta^{15}N$ value of NH_3 gas present at a seabird colony. This pattern is inversely related to the seasonal increase in NH_3 concentrations (except for the $\delta^{15}N$ value increase from March to May) although further work is needed to distinguish between the effects of wetter weather and increasing bird occupancy.

Lichen $\delta^{15}N$ values can also reflect the $\delta^{15}N$ values of gaseous N sources including NH_3 gas (Tozer et al. 2005), and these were higher on rat-free islands, in agreement with the higher $\delta^{15}N$ values of NH_3 gas (Fig. 5.3). Some lichen $\delta^{15}N$ values (e.g., +5 to +9‰) are surprisingly high for epiphytes (Fogel et al. 2008; Stewart et al. 2002; Tozer et al. 2005), while others (e.g., -19 to -10‰) indicate that lichens are assimilating NH_3 gas. Lichens have been used as indicators of industrial NH_3 deposition because their physiology and community composition are particularly sensitive to high atmospheric N (Krupa 2003). Although *Usnea* lichens were widespread in the canopy on Motuhoropapa, we noticed that no *Ramalina* lichens grew near the seabird colonies. If related to NH_3 gas emissions as we suspect, this observation suggests that lichens may be useful indicators of the “ammonia shadow” surrounding a seabird colony.

5.5.3 Foliar uptake of NH_3 gas by island plants

Our mixing models confirmed that two plant species present on multiple islands assimilated NH_3 gas, which contributed up to 20% (*Melicytus*) and 30% (*Coprosma*) of their leaf N (Fig. 5.4). However, we expected plants on rat-free islands to assimilate proportionally more NH_3 gas where concentrations should have been substantially higher. None of our results (neither NH_3 gas concentrations, nor the mixing model) agreed with this prediction. *Coprosma* leaves were more variable in their NH_3 gas assimilation on rat-free islands, but group means were not significantly different, indicating that only some plants behaved as expected. The pattern was reversed for *Melicytus* leaves, which assimilated more NH_3 gas on rat-invaded islands (Fig. 5.4), where soil N is less available (Fukami et al. 2006). These species are both multi-stemmed early successional coastal trees, yet leaf N is much higher for *Melicytus* (Fukami et al. 2006), and this brief analysis suggests the two may differ by N preference, N uptake strategy, and/or N use efficiency. Plant $\delta^{15}N$ values in our study are comparable to those measured at other seabird colonies (e.g., Erskine et al. 1998; Mizota 2009b; Wainwright et al. 1998), and our estimates of foliar NH_3 uptake are comparable to those of northern coniferous forests on acid soils subjected to industrial NH_3 pollution (Gebauer 2000; Högberg 1997).

On Motuhoropapa, seedlings at the seabird colony received more of their N from NH_3 than those at the control site, though this trend was not significant for the experimental *Coprosma* cuttings. As predicted, nutrient demand caused greater NH_3 gas assimilation: plants in nutrient-limited control soil assimilated more NH_3 than those in nutrient-rich seabird colony soil (Fig. 5.7). Cuttings and seedlings from soil with added P used the most NH_3 (relative to leaf N), in accordance with our hypothesis that P addition would increase demand for N and thus stimulate NH_3 gas uptake. Over half the *Coprosma* cuttings with added P took up at least some NH_3, and NH_3 contributed up to 15% of leaf N for both cuttings and seedlings (Fig. 5.7).

No seedlings in soil with added N used any NH_3 gas, and no *Coprosma* cuttings survived under N addition (Fig. 5.7), suggesting N levels may have been toxic to this species; few *Coprosma* plants grow directly on seabird colonies (M. Durrett, pers. obs.). Together these results suggest that when N is in short supply compared to P, foliar uptake of NH_3 gas is a viable strategy for obtaining N, but leaf uptake is no longer beneficial when N is readily available at the roots. In contrast, mangroves in an oligotrophic ecosystem had the highest foliar NH_3

assimilation when extremely P-limited, as their root systems were inadequate for nutrient uptake, and N-fertilized plants had very low $\delta^{15}N$ values indicating strong fractionation (Fogel et al. 2008). Our study system is far from oligotrophic: some plants such as *Melicytus* have leaf N >3% on seabird colonies (Fukami et al. 2006). When internal leaf concentrations of NH_4^+ are high compared to the atmospheric NH_3 concentrations, NH_3 gas is emitted from the stomata (Farquhar et al. 1980; Sparks 2009; Stulen et al. 1998) and this may have been the case in our N-fertilized plants.

5.5.4 Implications for plant-soil relationships

The high *Coprosma* leaf $\delta^{15}N$ values throughout this study, which are similar to and sometimes exceed $\delta^{15}N$ values of the soil, may indicate a preference for soil NH_4^+ over NO_3^- as an inorganic N source. Though we did not measure the $\delta^{15}N$ values of NH_4^+, the process of ammonification involves little to no isotopic fractionation, while the $\delta^{15}N$ value of the soil NH_4^+ pool increases via strong fractionation during two processes: 1) volatilization of NH_3 gas up to 60‰ lower than NH_4^+, and 2) nitrification, which produces NO_3^- up to 20‰ lower than NH_4^+ (Högberg 1997; Robinson 2001). For example, on two temperate gull colonies in northern Japan, the $\delta^{15}N$ value of guano was estimated at 10.5‰; $\delta^{15}N$ values of NH_4^+ range from +10.1 to +29.6‰ and +33.3 to +43.3‰; and $\delta^{15}N$ values of NO_3^- ranged from -0.2 to +2.8‰ and +17.2 to +33.7‰ (Mizota 2009b; Mizota 2009a). Such high $\delta^{15}N$ values for NO_3^- were attributed to soil enrichment during denitrification, which is probably limited in our study system by well-aerated soils and steep slopes. Because we used bulk soil as the end-member in our mixing models, and the $\delta^{15}N$ value of NH_4^+ is likely even higher, our estimates of foliar NH_3 uptake may be conservative. However, NO_3^- concentrations on these islands are about twice those of NH_4^+ (Chapter 3, 4) and some NO_3^- assimilation cannot be discounted without measuring nitrate reductase activity, which has demonstrated plant use of seabird-deposited NO_3^- at Svalbard, Norway (Odasz 1994). Because the $\delta^{15}N$ values of NO_3^- in this system are likely to be in the range of -10 to 0‰, it would take far more NO_3^- than NH_3 uptake to account for the decrease in leaf $\delta^{15}N$ values that we found.

Isotopic fractionation during root uptake may further decrease the $\delta^{15}N$ value of any NO_3^- or NH_4^+ assimilated by the plant, especially when the N source is abundant (Högberg 1997), and yet the $\delta^{15}N$ values of some cuttings and seedlings exceeded those of the soil on Motuhoropapa. This cannot be explained by the lower $\delta^{15}N$ value of the shallow soil used in our experiment (from 0-15 cm deep), because cuttings were too small to access deeper soils with higher soil $\delta^{15}N$ values anyway. Instead, the increase was probably physiological: the cuttings were necessarily N-deprived until new roots were grown and thus forced to recycle N efficiently, increasing nitrogen use efficiency and leaf $\delta^{15}N$ values. Leaf uptake of NH_3 gas can also establish a positive feedback loop by stimulating stomatal conductance and decreasing water use efficiency (Krupa 2003), which partially explains very high leaf $\delta^{13}C$ values on these islands (Chapter 4).

In contrast to the experimental plants, we sampled leaves from a range of tree sizes for the across-island mixing models, and in most cases the soil end-member (from the top 30 cm) was probably shallower than the soil foraged by trees. Because soil $\delta^{15}N$ values increase with depth in this system (Fig. 5.3), trees were likely accessing N sources with higher $\delta^{15}N$ values. Within a mixing model, higher soil $\delta^{15}N$ values necessitate greater uptake of a low-$\delta^{15}N$ source to arrive at a similar leaf $\delta^{15}N$, again suggesting that our estimates of NH_3 contributions to plant N across islands may be conservative. Maximum estimates from cuttings and seedlings on Motuhoropapa are slightly lower, but comparable, to minimum estimates from the across-island analysis (compare Figs. 5.4 and 5.7).

5.5.5 Conclusion

We have shown that even a rat-invaded island with only a few burrow-nesting seabirds can be a point source of NH_3 gas, and that multiple woody species depend on this N source for up to 30% of their leaf N. Concentrations of NH_3 gas are highly variable within and among islands, on- and off-colony, and seasonally according to the seabird breeding cycle. Conditions creating plant N demand encourage foliar NH_3 uptake, but seabird colony soils are both so acidic as to retard volatilization (or so windy that NH_3 gas blows away) and so N-rich that luxury consumption can occur for some plants. Therefore maximal NH_3 assimilation by plants is likely to occur at off-colony sites near seabird colonies, especially those downwind.

Most importantly, NH_3 gas uptake may be a small proportion of a plant's N budget, but it should not be ignored, especially in stable isotope mixing models attempting to distinguish the roles of marine and terrestrial N in plant nutrition (e.g., Helfield and Naiman 2001). Because ammonification and subsequent volatilization of a marine N source (with an already high $\delta^{15}N$ value) produces NH_4^+ with a very high $\delta^{15}N$ value and NH_3 gas with a very low $\delta^{15}N$ value, a plant assimilating a small amount of NH_3 gas may still have a relatively high $\delta^{15}N$ value. Crucially, though, the $\delta^{15}N$ value of a terrestrial N source will likely fall somewhere in between; thus a small uptake of NH_3 gas could be mistaken for more substantial uptake of a terrestrial N source. Leaving NH_3 gas out of such an ecosystem model underestimates the marine N contribution in two ways: first, it overestimates the terrestrial contribution, and second, it overlooks NH_3 gas which can be marine in origin. We suggest that NH_3 concentrations should always be evaluated, with a reminder of their inherent variability, wherever marine-derived N is deposited.

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5.8 Tables

Table 5.1 Measurements of NH_3 gas concentrations at seabird colonies

Seabird species	**Nesting habit**	**Location**	**NH_3 conc.[1] (μg NH_3-N m^{-3})**	**Reference**
Adelie penguins	ground	Isle de Petrels, Antarctica	5.39 ± 2.19	Legrande et al. (1998)
Adelie penguins	ground	Isle de Governeur, Antarctica	0.53	Legrande et al. (1998)
Atlantic puffins	burrow	Isle of May, Scotland	0.4 - 31.4	Blackall et al. (2007)
Common guillemots	cliff	Isle of May, Scotland	0.5 - 168.3	Blackall et al. (2007)
Common guillemots	cliff	Funk I, Newfoundland	710 - 1370	Blackall et al. (2007)
Cape gannets	cliff	Bird I, South Africa	54 - 560	Blackall et al. (2007)
Black-browed albatross	ground	Bird I, South Georgia	14	Blackall et al. (2007)
Macaroni penguin	ground	Bird I, South Georgia	55	Blackall et al. (2007)
Atlantic puffins	burrow	Isle of May, Scotland	16.1 ± 14.6 31 (max)	Blackall et al. (2008)
Common guillemots	cliff	Isle of May, Scotland	8.7 ± 9.1 83 (max)	Blackall et al. (2008)
White-capped Noddy terns, Wedge-tailed shearwaters	ground, burrow	Heron I, Great Barrier Reef (low density)	3.2 ± 4.5	Schmidt et al. (2010)
White-capped Noddy terns, Wedge-tailed shearwaters	ground, burrow	Heron I, Great Barrier Reef (medium density)	11 ± 7.3	Schmidt et al. (2010)
White-capped Noddy terns, Wedge-tailed shearwaters	ground, burrow	Heron I, Great Barrier Reef (high density)	17 ± 7.8	Schmidt et al. (2010)

[1] NH_3 gas concentrations are expressed as mean ± standard deviation, or as a range if means were not reported

Table 5.2 Mean NH_3 gas concentrations and $\delta^{15}N$ values for individual islands[1]

Island	**NH_3 (µg NH_3-N m^{-3})**	**$\delta^{15}N$ (‰)**
Mututapere	29.27 ± 7.49	-32.36 ± 4.66
Motuoruhi	19.14 ± 4.80	-25.58 ± 3.95
Motukaramarama	21.53 ± 5.38	-29.93 ± 2.07
Motuhoropapa	0.14 ± 0.05	-26.88 ± 3.80
Goat	2.90 ± 0.44	-26.69 ± 1.24
Motueke	7.25 ± 1.67	-24.76 ± 2.68
Ohinauiti	5.45 ± 1.08	-24.67 ± 2.78
Ruamahuaiti	8.99 ± 1.06	-23.05 ± 1.90
Ruamahuanui	18.20 ± 3.60	-28.03 ± 0.66
Middle Mercury	2.30 ± 1.19	-25.10 ± 5.55
Mean	**11.52 ± 2.68**	**-26.70 ± 2.93**

[1] Expressed as mean ± standard deviation

Table 5.3 Mean N content and $\delta^{15}N$ values of experimental soils used on Motuhoropapa[1]

			Soil $\delta^{15}N$ (‰)	
Soil type	**n**	**N (%)**	**Mean**	**Range**
Control	12	73.9 ± 0.18	10.08 ± 2.02	5.71 - 13.36
Control + N	2	75.7 ± 0.07	10.97 ± 0.54	10.58 - 11.35
Control + P	4	76.4 ± 0.05	9.86 ± 1.40	7.97 - 11.24
Seabird	11	79.0 ± 0.23	12.66 ± 1.56	9.76 - 14.01

[1] N and mean $\delta^{15}N$ expressed as mean ± standard deviation

5.9 Figures

Fig. 5.1 Baskets containing experimental cuttings of *Coprosma macrocarpa* hang above a seabird colony on Motuhoropapa. Cuttings were planted in one of four soil types: control, added N, added P, and seabird colony soil. Two rain catchment buckets irrigate four plant baskets each. This setup was duplicated at a control site nearby with no seabird burrows, as well as at one additional seabird colony and control site

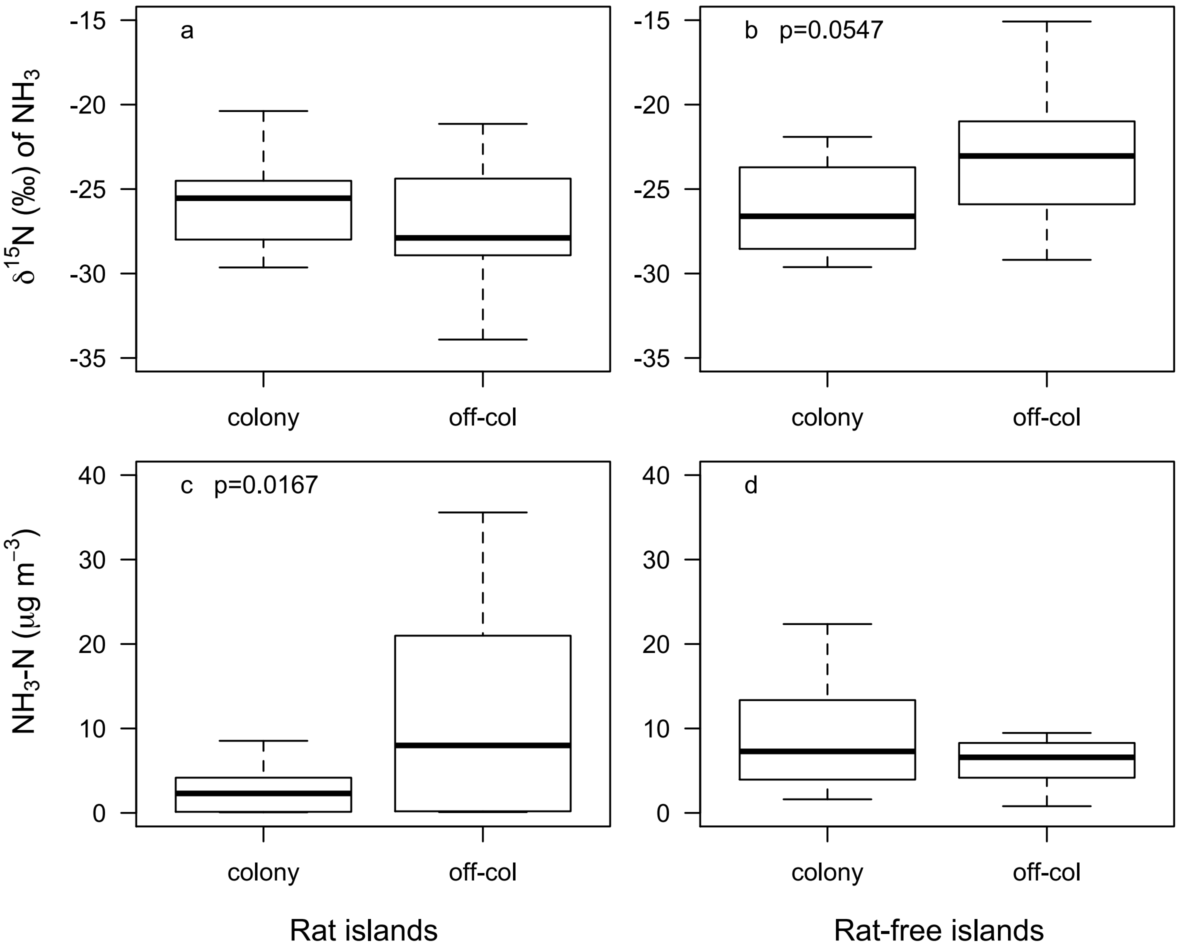

Fig. 5.2 Ammonia gas $\delta^{15}N$ and concentrations, on rat-invaded and rat-free islands (low and high seabird density, respectively), measured on seabird colonies and on nearby control sites with few burrows. P-values indicate significant differences between means

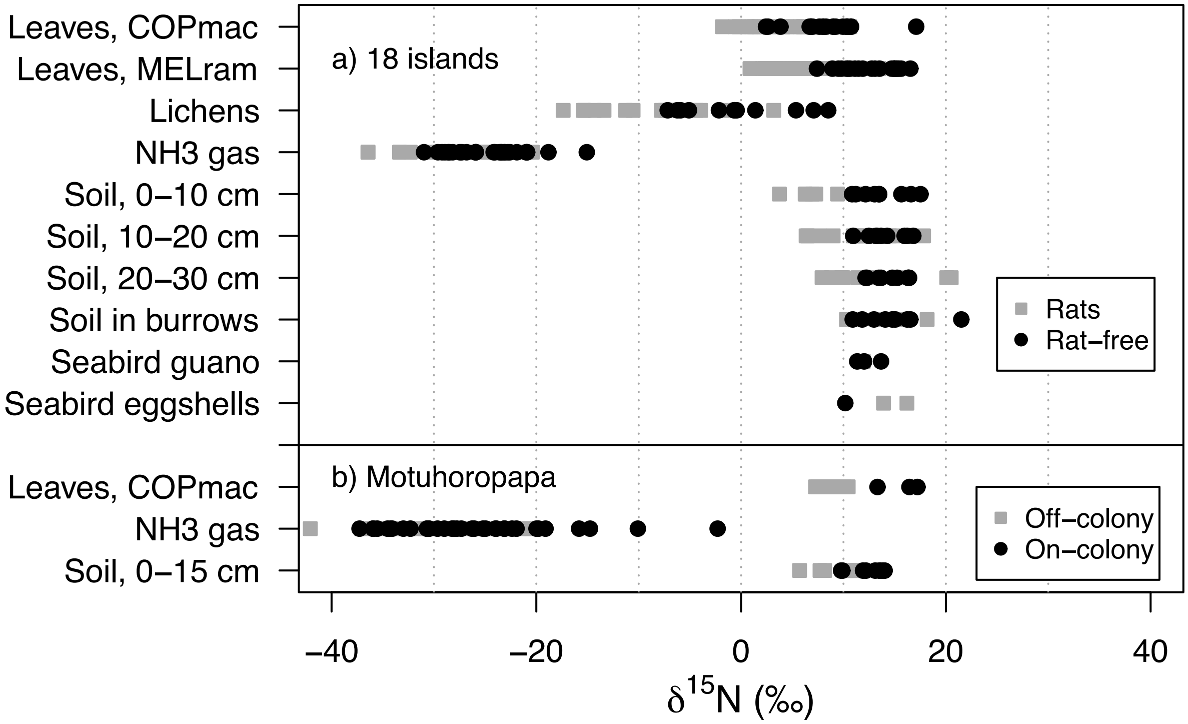

Fig. 5.3 Seabird N sources, soil, NH_3 gas, lichens, and plant leaf $\delta^{15}N$ values from a) across our study system and b) our field experiment on Motuhoropapa. COPmac, *Coprosma macrocarpa*; MELram, *Melicytus ramiflorus*

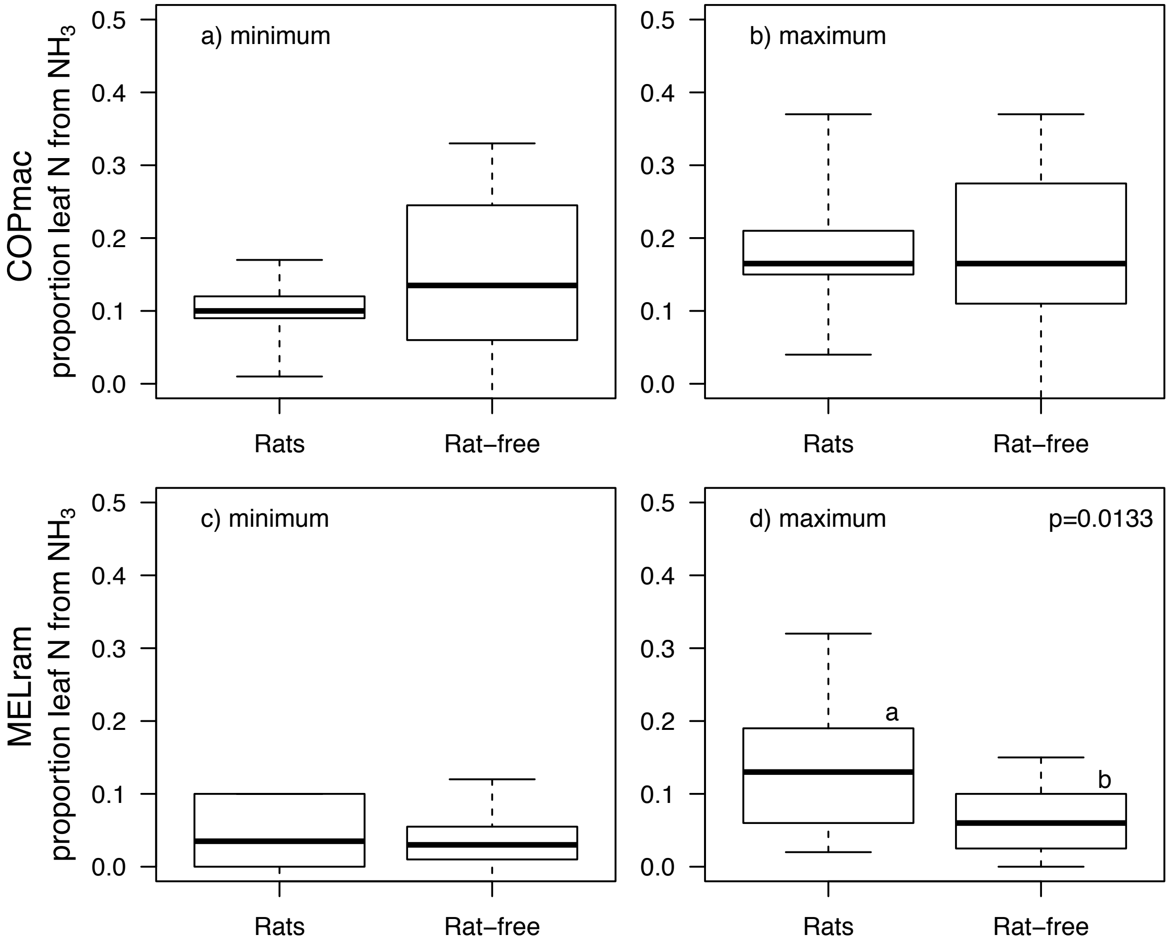

Fig. 5.4 Results of a one-isotope mixing model for two species on rat-invaded islands with few seabirds and rat-free islands with many seabirds, considering NH_3 gas and bulk soil N as potential plant N sources. P-values indicate significant differences between means. COPmac, *Coprosma macrocarpa*; MELram, *Melicytus ramiflorus*

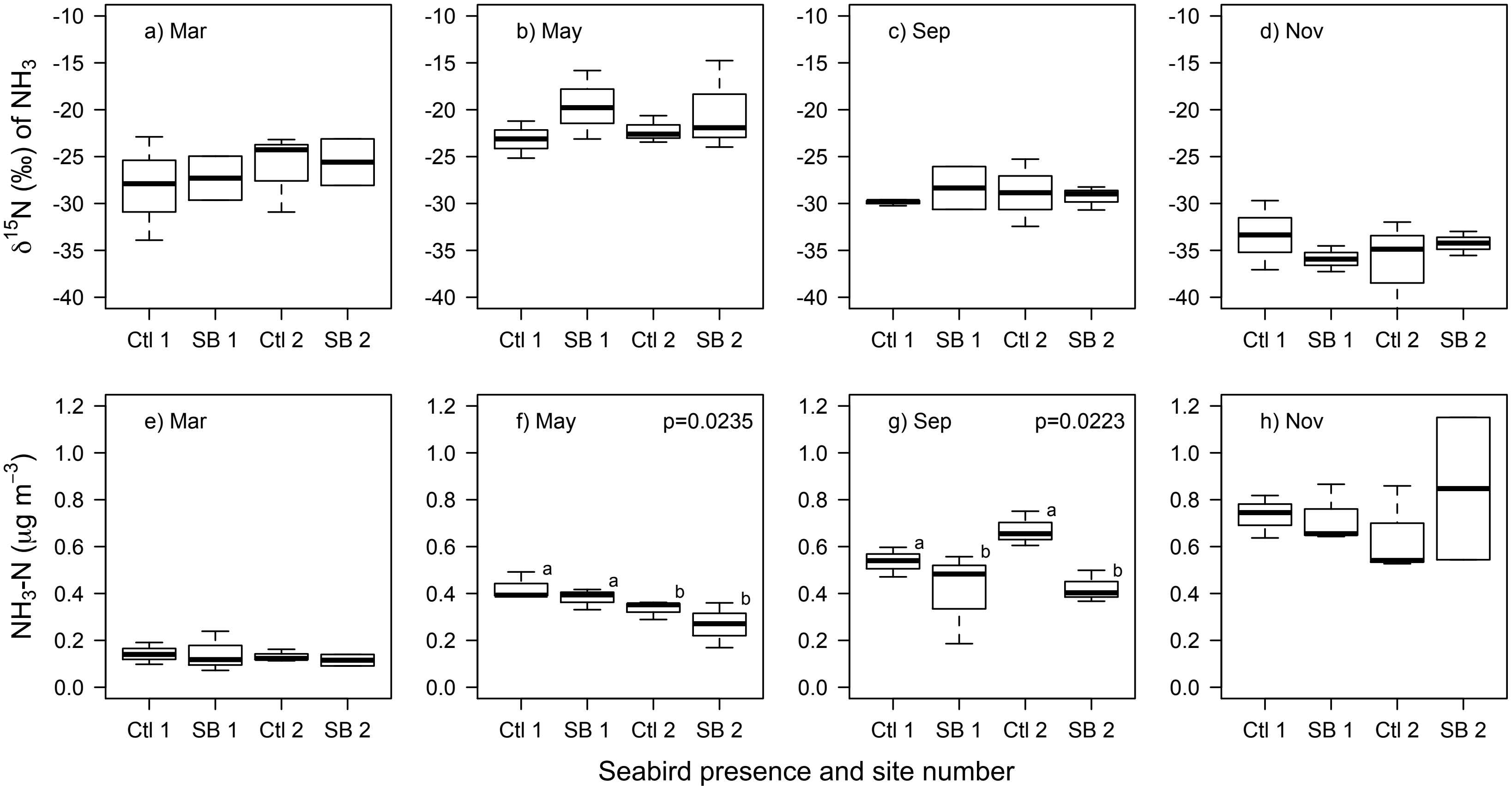

Fig. 5.5 Ammonia gas δ^{15}N values and concentrations on four visits to Motuhoropapa, at two seabird colonies and two control sites. Site 1 was located at the southernmost tip of the island, and site 2 on the southeastern peninsula known as Petrel Point. Ctl, control; SB, seabird colony

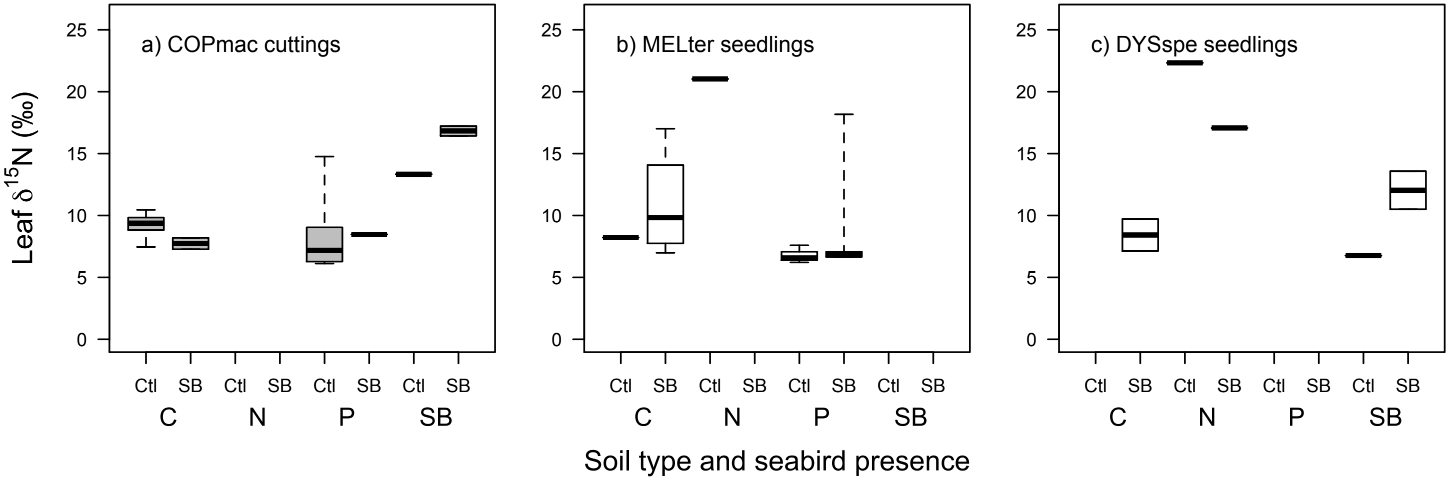

Fig. 5.6 Plant leaf δ^{15}N values from experimental cuttings and volunteer seedlings growing in one of four soil types (C-control, N-control with added N, P-control with added P, and SB-seabird colony soil) at the Petrel Point seabird colony on Motuhoropapa (SB) or a matching control site with no seabirds (Ctl). COPmac, *Coprosma macrocarpa*; DYSspe, *Dysoxylum spectabile*; MELter, *Melicope ternata*

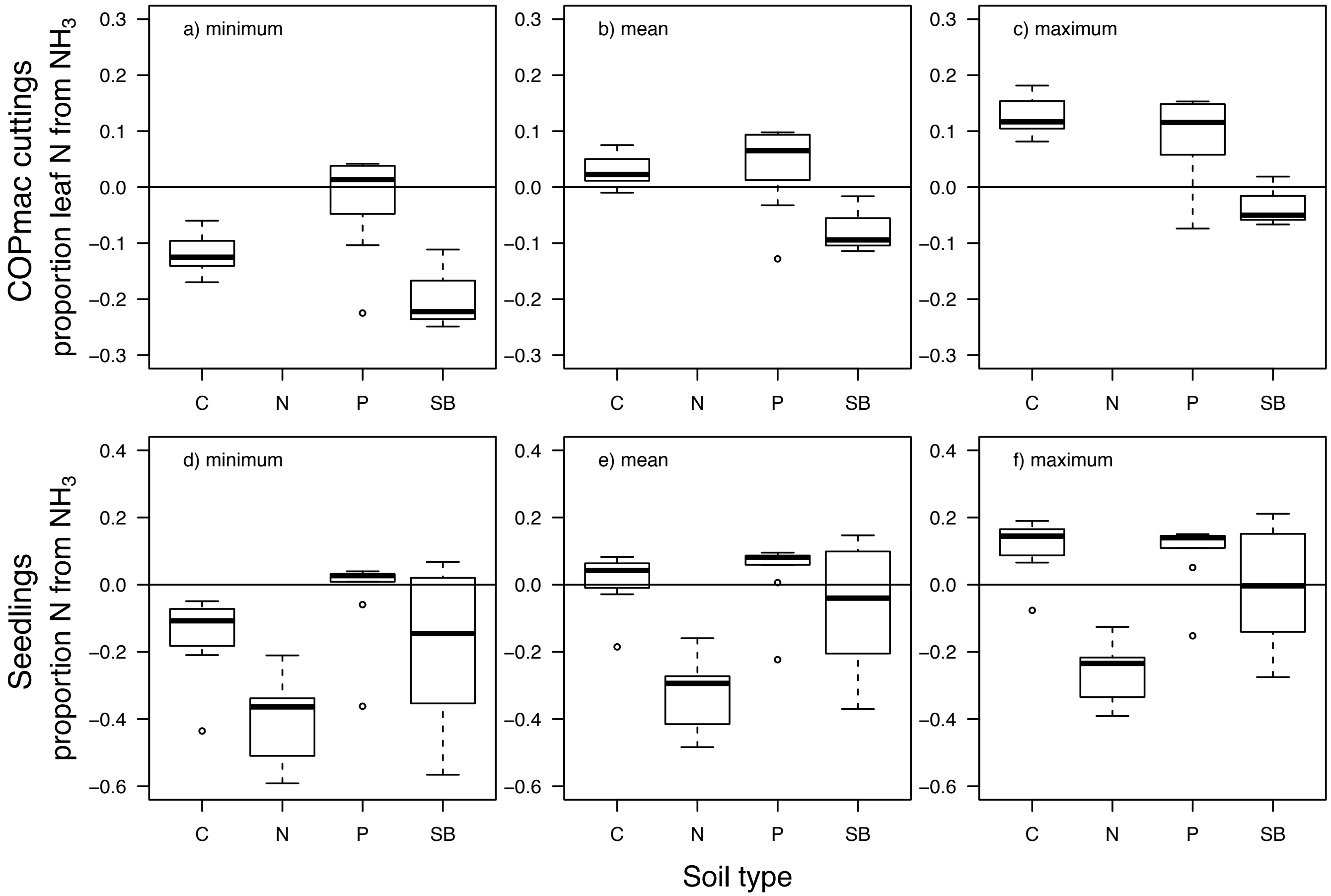

Fig. 5.7 Results of a one isotope, two end-member mixing model for experimental cuttings and volunteer seedlings (pooled; for species, see Methods) growing at the Motuhoropapa Petrel Point seabird colony (SB) and a nearby control site (Ctl), considering NH_3 gas and bulk soil N as potential plant N sources. Negative contributions are the result of plant leaves with higher $\delta^{15}N$ values than the soil, implying no contribution of NH_3 gas (see Eq. 5.1). COPmac, *Coprosma macrocarpa*

Chapter 6.

General conclusion

Burrowing seabirds add a great deal of spatial variability to island systems. In Chapter 3, I found that spatial variability within islands increases, rather than decreasing, at high seabird densities, though some variables become homogenous past a burrow density threshold. In Chapter 4, I showed that rat invasion alters the mechanisms by which seabirds control island N cycles, changing within-island patterns in ecosystem function. In Chapter 5, I demonstrated that volatilization of ammonia (NH_3 gas) is another source of spatial and temporal variability in island systems, and that plants can assimilate this underappreciated source of available N. These conclusions add to our overall understanding of seabird island ecology and the effects of rat invasion, with implications for how we study and restore islands, including avenues for future research.

Burrows themselves were more spatially dependent or "patchier" on low- and high-density islands, but not on intermediate-density islands (Chapter 3). This is probably a reflection of the colonial lifestyle; on low-density islands, it will be easier to dig near another burrow, either because the first bird has found the softest soil or because she has actively loosened it (Warham 1990). On high-density islands, "prime" habitat, perhaps that with an easy takeoff point or thin canopy (Chapter 1), may attract more birds than other sites, even in very good habitat; or there may be a few sites that are unsuitable, causing patchiness at the island scale. Why did this pattern not hold true for intermediate-density islands? One possibility is that habitat was inherently structured on these islands at small scales, spreading burrows out by necessity. For instance, parts of Ohinauiti were quite rocky and the soil is comparatively shallow, allowing only a few burrows in a cluster with a great deal of space in between (M. Durrett, pers. obs.). Because of the 10-m spacing of my sampling points, I may not have been able to detect such fine-scale patterns (Chapter 3). Future studies quantifying ecosystem responses to seabirds at the within-island scale may wish to employ a nested design including even smaller, plot-scale measurements, especially if smaller organisms like individual plants are of interest.

Some properties were most spatially variable on these intermediate-density islands (Chapter 3). These included soil pH, compaction, and δ^{15}N, three of the variables that respond most consistently to burrow density (Chapter 2, 4). Reduced soil pH and increased δ^{15}N are a direct result of marine nutrient input, while reduced soil compaction is a result of digging. At higher seabird densities, where it is difficult to find un-burrowed terrain, these variables became more spatially homogenous (Chapter 3). According to my spatial models from six islands of varying densities, this shift in variability happens at a threshold of ~0.15-0.50 burrows m^{-2}. The sampling implications are obvious: more samples will be needed to capture variability in these properties where burrows are spread widely across the island. On islands where burrows are ubiquitous, fewer samples are needed.

The spatial patterns in burrow density did not predict spatial patterns in other variables very well at the within-island scale, nor did nest site topography (Chapter 3). This is an advantage in that many statistics rely on the assumption of spatial independence, which enabled me to use structural equation models in Chapter 4. The lack of spatial correlation does not mean that burrow density did not correlate well with soil and plant properties. Rather, it implies that a burrowing seabird “colony” in this system does not have distinct boundaries, nor do many of the ecosystem properties that respond to seabirds. Unlike cliff-nesters, whose impacts are concentrated at the cliff, or ground nesters that may cover all available horizontal space in regularly spaced, guano-cemented mounds (Chapter 2), burrow-nesters affect their islands in ways that are not determined by the spatial arrangement of their burrows.

Surprisingly, seabirds did not completely homogenize the soil at very high burrow densities (Chapter 3). Net ammonification, net nitrification, soil NH_4^+ and NO_3^- all grew more spatially variable on densely colonized islands (Chapter 3), warranting further research into the mechanisms that control N cycling at the within-island scale. Within three rat-invaded and three rat-free seabird islands, soil C (which was strongly correlated with total soil N, less strongly with organic N) increased soil NH_4^+-N and NO_3^--N (Chapter 4). Microbes in my laboratory incubations quickly immobilized or nitrified NH_4^+-N pools from rat-invaded and rat-free islands alike (Chapter 4). I did not measure gross ammonification or nitrification rates, but this pattern of large, correlated pools of soil C and inorganic N probably indicates that these processes are stimulated by seabird-mediated organic substrates. Substrate quality, measured both as C:N ratio and as soil respiration per unit C, failed to correlate with net ammonification, net nitrification, NH_4^+-N or NO_3^--N (Chapter 4), despite the higher leaf and litter N content on uninvaded islands (Wardle et al. 2009). This may indicate that substrate quantity trumps quality for microbial communities on these islands, or at least that quality is not highly variable. After all, guano is quickly and easily decomposed and has been shown to stimulate microbial activity and biomass elsewhere (Cocks et al. 1999; Lindeboom 1984; Orchard and Corderoy 1983; Wright et al. 2010). On rat-invaded islands, however, reduced soil pH at seabird burrows locally inhibited NO_3^- production (Chapter 4), implying a negative feedback to microbial activity that is clearly lost at high seabird densities (pH and NO_3^- were not correlated on uninvaded islands).

If marine inputs or dead plant materials are tilled into the soil at small spatial scales, this could account for the increasing heterogeneity in inorganic N pools at high seabird densities observed in Chapter 3. Within rat-invaded islands, the few seabird burrows were hotspots of increased soil C and organic N, but on uninvaded islands, $\delta^{15}N$ was linked to local decreases in these substrate pools (Chapter 4)—a pattern which could indicate increased N cycling rates, or potentially C loss during increased soil respiration. This decreased C at very high seabird densities on uninvaded islands resulted in decreased soil moisture, presumably due to decreased water holding capacity. Seabirds locally reduced soil moisture within rat-invaded islands as well through reduced soil compaction, demonstrating that seabirds can have similar effects on the same soil property via two different mechanisms, and that rat invasion can alter that mechanism.

Larger trees were more vulnerable to water stress: seabirds burrow under them more often, increasing their leaf $\delta^{13}C$, indicative of plant water stress (Chapter 4). The large pools of seabird-mediated NH_4^+ and NO_3^-, however, contributed directly to plant N nutrition. Though seabird burrows increased leaf N on intermediate-density islands, tree size was the best predictor of this variable, with large trees achieving the highest leaf N concentrations (within the same species). Researchers collecting leaves on seabird islands for chemical analysis should therefore explicitly account for tree size, either by measuring it or by controlling for it during collection. Soil $\delta^{15}N$ directly correlated with leaf $\delta^{15}N$, demonstrating plant use of marine N deposited by seabirds (Chapter 4).

Volatilization of NH_3 gas can add further variability to island N cycles. This process is pH and temperature dependent which makes it both spatially and temporally variable (Chapter 5). Measurements of NH_3 concentrations were comparable to those near other burrow-nesting seabird colonies at 11.52 ± 2.68 μg NH_3-N m^{-3}. Seasonal variability in both NH_3 gas and its $\delta^{15}N$ value tracked well with the seabird breeding cycle (Chapter 5). Burrow densities did not, however, predict NH_3 concentrations across or within islands. Two species of broadleaf evergreen coastal tree, *Melicytus ramiflorus* and *Coprosma macrocarpa*, both exhibited foliar uptake of NH_3 gas, using it for up to 20% and 30% of their leaf N, respectively. Plant N demand stimulates NH_3 gas assimilation, but seabird colony soils are very N-rich. It follows that nearby plants without access to seabird-derived soil N are more likely to use NH_3 gas when it is available—when the wind blows it toward them (e.g., Erskine et al. 1998) or in winter when it is dissolved in raindrops (Schmidt et al. 2010; Staunton Smith and Johnson 1995).

The mean $\delta^{15}N$ of NH_3 was -26.70 ± 2.93‰, almost 40‰ lower than that of the soil, and plants that use even a little of this isotopically depleted source in addition to soil N sources can lower their $\delta^{15}N$ values dramatically (Chapter 5). If NH_3 gas is ignored as a potential plant source, and especially if a plant made use of more isotopically depleted soil N sources, like NO_3^-, a leaf's $\delta^{15}N$ value might be low enough to mislead a researcher into the conclusion that a plant did not assimilate any seabird-derived N at all. Thus seabird nutrient inputs would be underestimated twice: first by masking the contribution of marine-derived soil N, and second by failing to acknowledge NH_3 gas volatilized from marine sources. This possibility for misinterpretation of leaf $\delta^{15}N$ carries implications not just for seabird islands, but also for any system where marine-derived N deposition allows for NH_3 gas volatilization.

I have shown that ecosystem properties respond to seabirds at different spatial scales. Burrow density, as an indicator of current seabird occupancy, and soil $\delta^{15}N$, as an indicator of seabird legacy or cumulative seabird impacts, gave complementary rather than identical insights into the mechanisms controlling N cycles in Chapter 4. This raises the question of how to measure seabird "impact" or "use" of an island or small plot, especially where seabird populations are unknown. I demonstrated in Appendix 3.A a way to model burrow densities from easy-to-measure distances to the nearest burrow, rather than burrow counts per unit area (which can be very time consuming). However, this distance-to-burrow measure may be a more useful indicator of seabird impact on its own in some cases, e.g., seed germination or seedling nutrition. Soil pH has large impacts on soil microbial activity and consistently responds to burrow density; in investigations where it is not a response variable of interest, it may be a useful proxy of seabird visitation (especially since hand-held pH meters are far easier and cheaper to use than, say, isotope analysis).

6.1 Directions for future research

The controls on plant production on seabird islands are still poorly understood. For more insight into island N cycles and the availability of soil N, I recommend measuring gross rates of N cycling and examining their seasonal variability. Though seabirds increase N availability and uptake for island plants, whether plants can use this to boost production is unknown—especially when seabirds simultaneously decrease water availability and soil pH. Seed germination depends upon these soil chemical properties, which are likely to respond to seabird burrowing at small spatial scales. Effects on seed germination or individual plant production could scale up to influence island-wide plant productivity. Additionally, plants may change their patterns of C allocation in response to belowground damage from burrowing, but root damage has yet to be quantified.

My work also raises questions about N loss from seabird islands. Seabird-related NH_3 gas emissions should be estimated for New Zealand islands, as done for seabird colonies in the UK (e.g., Blackall et al. 2007), considering its potential to contribute to plant N at off-colony sites. At high concentrations, NH_3 gas can be toxic to plants, and this should be evaluated in our system given that at least one species, *Coprosma macrocarpa*, is already suspected to be N-sensitive (Chapter 5). Finally, the large NO_3^- pools on these islands combined with steep, loose slopes suggest that leaching of NO_3^- may return some of this seabird-derived N to the marine system, probably influencing nearshore productivity and community dynamics (Chapter 2).

Between gaseous and dissolved N transfers and the marine subsidies from seabirds and coastal wrack, the “boundary” surrounding a seabird island is more diffuse than our maps describe: a continuum, as the Māori explained it to me, between land and sea. Global change threatens this boundary directly through sea level rise and a host of other island-based and ocean-based threats to seabird populations (Chapter 2). One of the most pressing questions to address, therefore, is what makes islands resilient to invasion and how predator-invaded islands can be actively restored. My work has explained how even a few seabird burrows on a rat-invaded island can turn it into a seabird-controlled hotspot, a sort of island-within-an island where some of the mechanisms that work at large scales on uninvaded islands can still function. I suggest that future work at this within-island scale should focus on predicting a threshold of burrow density at which “restoration” of a given property or process is achieved; ammonification, nitrification, pH, soil C and N, and $\delta^{15}N$ would all be good starting points. This work could easily be done on currently invaded islands, or even inland, if omnivores could be kept out of the study site; guano inputs and tunneling are easy to mimic, and experimental “colonies” without birds may be useful. Results are likely to be system-specific, like many aspects of seabird island ecology, but outcomes would contribute greatly to island restoration and monitoring.

6.2 References

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