

RESEARCH ARTICLE

Island characteristics and sampling methodologies influence the use of stable isotopes as an ecosystem function assessment tool

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Funding information

National Geographic Society

Handling Editor: Michele Dechoum

Abstract

1. Monitoring seabird-derived nutrients on islands following invasive mammal eradications may provide a useful, cost- and time-efficient indication of the recovery of ecosystem function; however, the technique has only been investigated on environmentally similar islands. How seabird-derived nutrients recover on islands with different characteristics, and how differences in sampling regimes affect results is poorly understood.
2. To determine how different island characteristics (size, geographic location and invasion history) and aspects of the sampling regime (sample collection year, season and intra-island location) influence seabird-derived nutrients we collated nitrogen stable isotope ($\delta^{15}\text{N}$) data from three ecosystem components (soil, plants and spiders), collected on 28 islands around New Zealand. We investigated which variables best predict $\delta^{15}\text{N}$ using linear-mixed effects models. Accounting for these variables and using still-invaded and never-invaded islands as controls for recovery, we then investigated changes in $\delta^{15}\text{N}$ on islands at different stages following invasive mammal eradication.
3. Island size, invasion history and the presence of seabirds in the direct vicinity of a sampling location all influenced $\delta^{15}\text{N}$. After accounting for these variables, $\delta^{15}\text{N}$ increased with time since eradication in soils, plants and spiders, though there was still some variation that our chosen variables could not explain.
4. This study demonstrates the importance of considering island characteristics and sampling methods when assessing seabird-derived nutrient recovery and highlights the need for additional targeted sample collection on islands to help separate out the effects of time since eradication and other confounding variables affecting $\delta^{15}\text{N}$. Improved understanding of these factors will be prerequisite for furthering this technique as a useful addition to the post-eradication monitoring tool kit.

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KEYWORDS

ecosystem function, eradication, nutrients, recovery, seabird island, size, stable isotope

1 | INTRODUCTION

Invasive mammal eradication is a successful tool for conserving seabird populations and island ecosystems (Holmes et al., 2019; Jones et al., 2016; Kurle et al., 2021; Towns & Broome, 2003; Zavaleta et al., 2001). Removal of invasive species is just the first step in the ecosystem recovery process however, and recovery at a species or ecosystem level may not occur without assistance through active restoration (Jones & Schmitz, 2009; Kappes & Jones, 2014; Zavaleta et al., 2001). Ongoing monitoring may be required to ascertain if these broader recovery aims are being met, to provide eradication project stakeholders with feedback, inform decision making and allocation of funding around future eradication projects and to enable the detection of unexpected outcomes of an eradication (Bird et al., 2019). Eradications are expensive however, often leaving limited funding for post-eradication monitoring beyond verifying the successful removal of the target species. Monitoring is consequentially sporadic, either not occurring at all or limited to select native species (Jones et al., 2016). Species counts alone may not reflect whole ecosystem condition (Levin, 1998), and cryptic ecosystem components and community or ecosystem level recovery may be too challenging to monitor (Kurle et al., 2021). Even for more visible species, capturing population trends can require repeat visits over decades, which in addition to being resource expensive raises issues of increased disturbance, and risks further breaches of biosecurity. An alternative means for assessing ecosystem recovery to species level monitoring is to examine indicators of ecosystem functioning. Ecosystem functioning processes such as changing nutrient dynamics provide insight on a range of species and their interactions (Nigro et al., 2017).

Island ecosystems provide a system where assessing change in nutrient dynamics may prove a useful post-eradication assessment tool. Seabirds exert a major influence on many island ecosystems, such that those islands are often referred to as 'seabird islands' (Caut et al., 2012; Kolb et al., 2011; Mulder et al., 2011a). Foraging at sea, then returning to often dense breeding colonies, seabirds transport marine-derived nutrients to islands, primarily through guano deposition (Thoresen et al., 2017). This classic example of cross-ecosystem boundary nutrient subsidization provides the primary source of nutrients for many terrestrial island ecosystems (Fukami et al., 2006; Jones, 2010a; Mulder et al., 2009). Globally, seabirds are one of the most threatened animal groups, with invasive predators and habitat degradation at their breeding sites their greatest threats (Anderson & Mulder, 2011; Brooke et al., 2017). The integral role of seabirds in many island ecosystems means their loss likely has important implications for insular ecosystem functioning (Towns et al., 2006).

Several studies have compared seabird-derived nutrients in ecosystem components such as soil, plants and invertebrates on islands with and without invasive species, for example islands with and without

foxes in the Aleutian Archipelago (Croll et al., 2005) and islands with and without rats in New Zealand (Fukami et al., 2006; Jones, 2010a, 2010b), on islets around Palmyra Atoll in the Pacific (Nigro et al., 2017), islands off Mexico (Samaniego-Herrera et al., 2017) and in the Chagos Archipelago in the Indian Ocean (Graham et al., 2018). In all apart from the Mexican study system, seabird-derived nitrogen levels (as measured by enriched nitrogen isotope levels) in the assessed ecosystem components were higher on islands without invasive species than those with invasive species. Following introduced mammal eradication and the alleviation of disturbance and predation pressures on both seabirds and the rest of an island ecosystem, these seabird-derived nutrient levels should increase (Figure 1). If this increase can be attributed to the eradication, monitoring seabird-derived nutrient level changes may provide a good indication on whether whole-ecosystem recovery is occurring.

Repeatedly sampling an island over decades following an eradication is logistically challenging and requires sustained funding. An alternative is to predict recovery trajectories by sampling multiple islands representing a range of times since eradication (i.e. a space for time substitution or chronosequence), enabling inferences about an individual island's recovery progression to be made. Across a selection of environmentally similar New Zealand islands, seabird-derived nutrient levels were found to increase with time since eradication (Jones, 2010b). However, many factors generate variation in nutrient dynamics (Boecklen et al., 2011), making attributing variation to a single cause, such as an eradication, challenging. To date, studies comparing seabird-derived nutrient levels have targeted islands with similar characteristics and geographic proximity (but see Caut et al. (2012) for a comparison of geographically distinct, rodent-invaded islands). How these trends may differ on islands ranging in size, latitude, biome, seabird assemblage, climate, and the timing and intra-island location of sample collection is largely unknown. These variables are critical to unpack if meaningful post-eradication island recovery trajectories are to be developed as ecosystem assessment and management tools.

From the eradication of Maria Island (0.01 km²) in the early 1960s (Moores, 1985), to the largest successful multi-species eradication programme completed to date on 128 km² Macquarie Island in 2011 (Springer, 2016) and the successful eradication of rats from South Georgia (3500 km²) (Martin & Richardson, 2019), eradications continue to grow in size and scope. Large islands represent the frontier of eradications, and as such even less is understood about their potential recovery trajectories. Large islands likely follow different recovery trajectories than smaller islands. For example, recovering small islands are likely to reach the high seabird densities required for local seabird dynamics to have a whole island effect more rapidly (Jones, 2010a), and overall the impact of seabirds as ecosystem engineers is likely to diminish with island size (Ellis et al., 2011). Large islands are also more likely

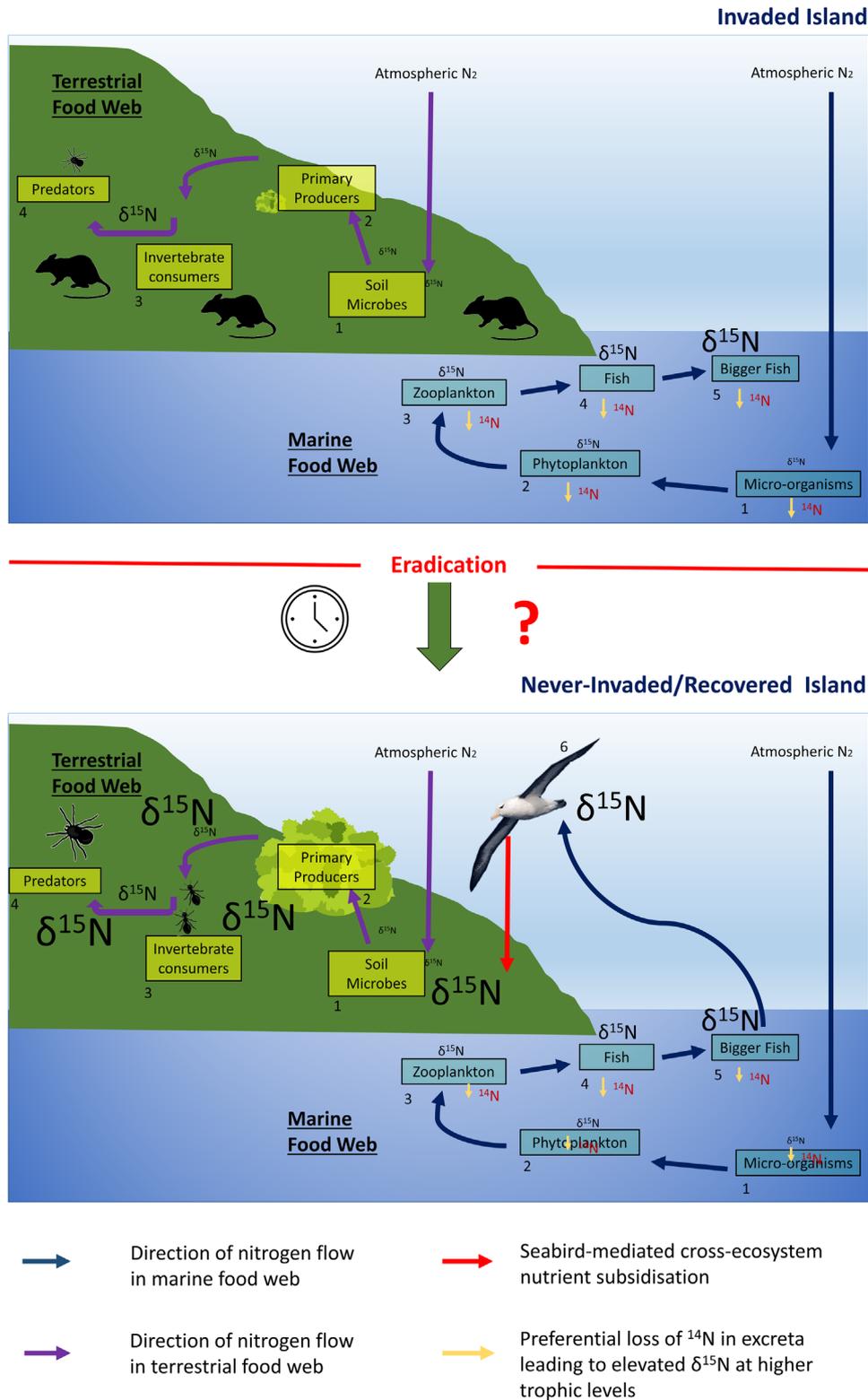


FIGURE 1 Conceptual diagram of the simplified marine-terrestrial food web linkages on an invaded and never-invaded or recovered island. The nitrogen isotopic signature ($\delta^{15}\text{N}$) is enriched as it passes through the food web (marine – blue and terrestrial – purple arrows), with ¹⁴N preferentially lost at each trophic level (yellow arrows). The marine food web is longer than the terrestrial food web (indicated by number of trophic transfer boxes). As top marine predators, seabirds transport enriched $\delta^{15}\text{N}$ to the terrestrial island food web (red arrow). Invasive mammals have deleterious effects on seabird populations, removing this marine-terrestrial linkage

to have heterogeneous seabird distributions with terrestrial nutrient sources more influential than seabird-derived sources in some regions.

An island's geographic location, climatic zone and seabird composition as well as sampling regimes can also influence nutrient dynamics. Guano toxicity to vegetation may be more prominent in arid regions (Ellis, 2005), while in wetter regions nutrient loss through leaching may be more significant (Kazama, 2019). Invasive species, such as rodents, are also likely to be at higher densities in tropical compared to temperate regions (Samaniego-Herrera et al., 2017), thus eradication, and the attendant alleviation of predation pressure, may also differ depending on initial invasive mammal densities. Moreover, the logistical challenges involved in accessing islands means post-eradication monitoring can rarely be perfectly timed or undertaken. Seabirds are highly seasonal, with different colony attendance levels throughout the breeding cycle leading to differing quantities of guano deposition throughout the year (e.g. Lindeboom, 1984). In addition to an island's characteristics and seabird composition, it is also important to ascertain how sometimes uncontrollable aspects of a sampling regime, such as where permits allow samples to be collected, season, or year of collection, and localized weather events (Anderson & Polis, 1999; Handley et al., 1999) influence results.

Here we used published and unpublished nitrogen stable isotope data to identify how island characteristics and different sampling regimes affect seabird-derived nutrient levels to expand the scope of stable isotope monitoring as a useful post-eradication ecosystem function assessment tool. Specifically, we aimed to explore:

1. What island characteristics (size, island location and invasion history) best predict seabird-derived nutrient levels at different trophic levels.
2. What aspects of the sampling regime (sample collected inside or outside a seabird colony, sample collection season, sample collection year) best predict seabird-derived nutrient levels at different trophic levels.
3. How seabird-derived nutrient levels vary with time since eradication for each trophic level, accounting for the important variables identified in aims 1 and 2.

2 | MATERIALS AND METHODS

Seabird-derived nutrients can be traced through terrestrial island food webs using stable isotopes. In nature, elements such as nitrogen (N) naturally occur in light (^{14}N) and heavy (^{15}N) stable isotopic forms (Fry, 2006). The isotopic ratio of a sample is generally expressed in terms of δ values, which is the isotopic ratio of the sample relative to an international standard for that element (atmospheric N_2 for nitrogen) in parts per thousand (‰) (Peterson & Fry, 1987) – termed isotopic enrichment. Each nitrogen isotope is incorporated into tissue and passed on between prey and consumers at a different rate, with ^{14}N disproportionately lost in waste products at each trophic level (Figure 1). This means that ^{15}N enrichment in plant and animal tissue generally increases with an organism's trophic position (McCormack et al.,

2019; Peterson & Fry, 1987). Marine food chains are typically longer than terrestrial ones, and seabirds are top order marine predators. The high trophic position of seabirds, in conjunction with the preferential volatilization of ^{14}N from waste means seabird guano, is enriched in ^{15}N (greater $\delta^{15}\text{N}$ value) compared to terrestrial N sources (Figure 1). Elevated $\delta^{15}\text{N}$ levels in island ecosystem components can therefore be used to infer the presence of seabird-derived nutrient input to an inland (Caut et al., 2012). Enriched ^{15}N reaching higher trophic levels indicates sufficient connectivity for these nutrients to be passed up the food web.

2.1 | Study islands

Nitrogen stable isotope data from soil, plant (*māpou* - *Myrzine australis*), and spider (Porrhothelidae family) samples from 28 islands around New Zealand were collated from published and unpublished datasets. Twenty-seven islands were less than 4 km² (mean \pm SD = 1.24 \pm 1.05 km²) and located in the Hauraki Gulf, northeast of Auckland (Jones, 2010b and unpublished data from Aorangi, Ohinaiti, Tawhiti Rahi and Otata islands), or Cook Strait (Jones, 2010a). These islands represented never-invaded ($n = 8$), eradicated ($n = 14$) and invaded ($n = 5$) invasion histories and were all sampled between 2006 and 2014 (Figure 2, Table 1). The dominant seabird species in these regions are summer breeding, burrowing procellariiforms (Borrelle et al., 2018; Jones, 2010a).

In 2015 and 2017 comparable soil, spider and plant samples were also collected from Te Hauturu-o-Toi/Little Barrier Island (hereafter referred to as Hauturu). Hauturu is an extinct volcanic island situated in the Hauraki Gulf approximately 80 km northeast of Auckland and in the vicinity of the other smaller Hauraki Gulf islands (Figure 2). It is much larger than the other islands in this study at ~ 30 km² and rises to 710 m above sea level (Rayner et al. 2007) and is invasive mammal free, with domestic cats (*Felis catus*) and kiore (Pacific rat, *Rattus exulans*) eradicated in 1981 and 2004, respectively (Griffiths et al., 2019; Veitch, 2001). While not as large as some islands undergoing eradications in recent years (e.g. Bester et al., 2002; Horn et al., 2019; McClelland, 2011; Springer, 2016), Hauturu represents the largest island in the Hauraki Gulf or Cook Strait regions to have been successfully eradicated to date (DIISE, 2018).

For each eradicated island ($n = 15$; 14 islands < 4 km² and Hauturu), a time since eradication value was calculated as the time between the removal of all invasive mammals and the year of sample collection and ranged from 6 to 21 years. For all eradicated islands, rodents were the final invasive mammal to be removed, excepting Korapuki where European rabbits (*Oryctolagus cuniculus*, eradicated: 1988) were eradicated one year after kiore/Pacific rat (eradicated 1987) (Table 1).

2.2 | Sample collection

The methods used for sample collection and processing across the small islands are outlined in Jones (2010a, 2010b). In brief, samples

TABLE 1 Summary of the study islands

Island	Group	Collection year(s)	Size (km ²)	Treatment	Invasive species (year of eradication)	Data source
Aorangaia	Poor Knights	2008	0.06	NI		Jones (2010b)
Aorangi	Poor Knights	2008	1.10	ER	pig (1936), house mouse (2002)	This study
Archway	Poor Knights	2008	0.06	NI		Jones (2010b)
Atihau	Mokohinaus	2008	0.16	ER	goat (1940), Pacific rat (1990),	Jones (2010b)
Coppermine	Hen and Chickens	2009	0.76	ER	Pacific rat (1997)	Jones (2010b)
Moturehu/Double	Mercury Islands	2009	0.27	ER	Pacific rat (1989)	Jones (2010b)
Motukino/Fanal	Mokohinaus	2009	0.77	ER	Pacific rat (1997)	Jones (2010b)
Green	Mercury Islands	2007	0.03	NI		Jones (2010b)
Korapuki	Mercury Islands	2009	0.18	ER	European rabbit (1988), Pacific rat (1987)	Jones (2010b)
Mauimua/Lady Alice	Hen and Chickens	2009	1.42	ER	Pacific rat (1994), black rat (2009)	Jones (2010b)
Hauturu/Little Barrier	Hauraki Gulf	2015, 2017	31.69	ER	domestic cow (unk), domestic sheep, (unk), pig (unk), domestic cat (1980), Pacific rat (2004),	This study
Mana	Cook Strait	2006, 2007	2.22	ER	domestic sheep (1978), domestic cow (1986), house mouse (1990),	Jones (2010a)
Maud	Marlborough Sound	2006, 2006	3.14	IN	House mouse (2014, samples collected prior to eradication), stoat (1993), domestic sheep (unk)	Jones (2010a)
Atiu/Middle	Mercury Islands	2008	0.14	NI		Jones (2010b)
Middle Trio	Cook Strait	2006, 2007	0.13	NI		Jones(2010a)
Nukuwaiata	Chetwodes Islands	2006, 2007	1.82	ER	Pacific rat (1994), pig (1963), goat (1993)	Jones (2010a)
Ohinauiti	Coromandel	2008	0.06	NI		This study
Otata	Noises	2014	0.23	ER	stoat (1955), European rabbit (1945), Norway rat (2002)	This study
Pauanui/Penguin	Slipper Islands	2009	0.10	IN	Pacific rat (current)	Jones (2010b)
Rabbit	Slipper Islands	2009	0.11	IN	Pacific rat (current)	Jones (2010b)
Whakau/Red Mercury	Mercury Islands	2010	2.25	ER	Pacific rat (1993)	Jones (2010b)
Stanley/Kawhitihu	Mercury Islands	2009	2.40	ER	European rabbit (1992), Pacific rat (1992)	Jones (2010b)
Takapourewa/Stephens	Marlborough Sound	2006, 2007	1.05	NI		Jones (2010a)
Tawhiti Rahi	Poor Knights	2007	1.46	NI		This study
Tawhitinui	Marlborough Sound	2006, 2007	0.22	IN	Pacific rat (current), black rat (1983), pig (unk)	Jones (2010a)
Victory	Marlborough Sound	2007	0.16	IN	Pacific rat (current)	Jones (2010a)
Wakaterepapanui	Cook Strait	2006, 2007	0.74	ER	Pacific rat (1999), Norway rat (1999)	Jones (2010a)
Whatapuke	Hen and Chickens	2009	0.90	ER	Pacific rat (1993), black rat (2009)	Jones (2010b)

'Treatment' indicates an islands invasion status at the time of sample collection: ER, eradicated of all invasive mammals; NI, never-invaded by invasive mammals; and IN, currently invaded by invasive mammals. 'Invasive species' indicates the species eradicated or still present on an island with eradication year listed in parenthesis, if applicable (DIISE, 2018): house mouse (*Mus musculus*), Pacific rat (*Rattus exulans*), Norway rat (*Rattus norvegicus*), black rat (*Rattus rattus*), European rabbit (*Oryctolagus cuniculus*), domestic cow (*Bos taurus*), domestic sheep (*Ovis aries*), domestic cat (*Felis catus*), goat (*Capra hircus*), pig (*Sus scrofa*) and stoat (*Mustela erminea*).

from islands in the Hauraki Gulf consisted of one soil sample and triplicates of new-growth leaf and spider samples per island. All samples were collected from a single location outside seabird colonies to obtain a measure of island-wide dynamics, rather than a localized seabird

effect (Jones, 2010b). For islands in Cooks Strait, multiple soil, new-growth leaf and spider samples were collected along transects with samples collected both inside and outside seabird colonies. Sampling locations were defined as being inside a seabird colony if burrows were

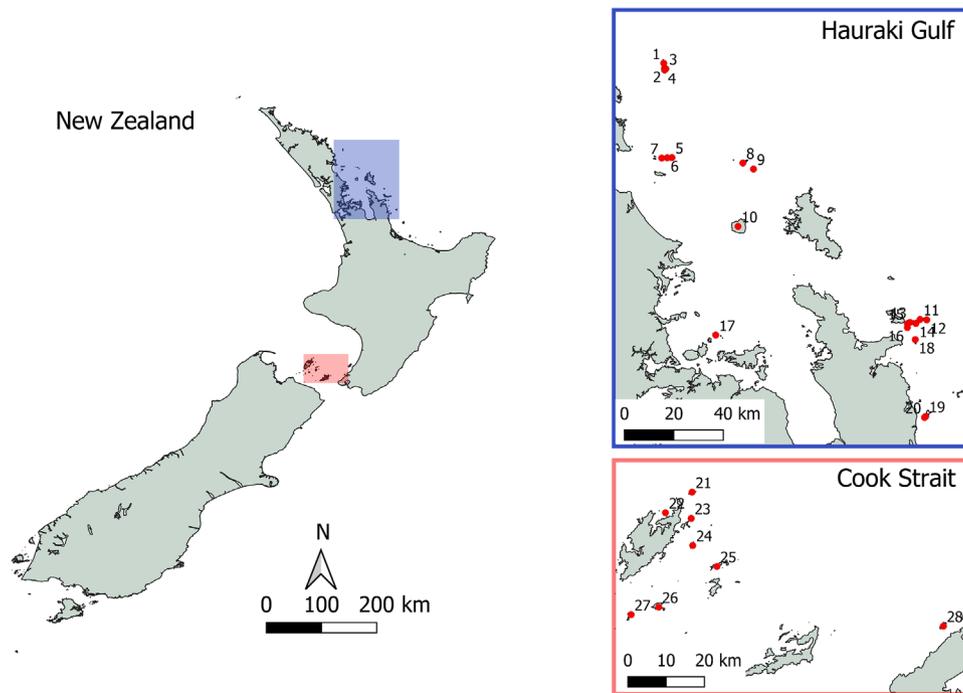


FIGURE 2 Locations of the study regions and islands. Insert panels show island locations (red points) within the Hauraki Gulf (blue-shaded area and panel) and Cook Strait (red shaded area and panel). Island names north to south are: 1, Tawhiti Rahi; 2, Aorangī; 3, Aorangāia; 4, Archway; 5, Coppermine; 6, Whatapuke; 7, Mauimua/Lady Alice; 8, Atihau; 9, Motukino/Fanal; 10, Hauturu/ Little Barrier; 11, Moturehu/Double; 12, Whakau/Red Mercury; 13, Atiu/Middle; 14, Stanley/Kawhitihu; 15, Green; 16, Korapuki; 17, Otata; 18, Ohinaiti; 19, Pauanui/Penguin; 20, Rabbit; 21, Takapourewa/Stephens; 22, Victory; 23, Wakaterepapanui; 24, Middle Trio; 25, Nukuwaia; 26, Maud; 27, Tawhitinui; and 28, Mana

present within a 3-m² radius, and outside a colony when the nearest known burrow location was >50 m from the sampling location. Samples were collected from areas with no known history of human disturbance. Additional samples collected from islands not included in these studies followed the same methods (Table 1). Soil samples were collected from all islands; however, spider and plant samples were not. Samples were collected throughout the year; however, the majority (90.56%) were collected during 'dry' season months (October–March). All samples were processed according to Jones (2010a) with samples washed with distilled water, dried at 60°C for 48 h, ground to a fine powder and analysed using a mass spectrometer for $\delta^{15}\text{N}$.

2.3 | Statistical analysis

All analyses were conducted using R version 4.0.2 (R Core Team, 2020). Code and raw data used are available at <https://doi.org/10.25959/zdc1-6z61> (Pascoe & Jones, 2021).

2.3.1 | Effects of island characteristics and sampling regime on $\delta^{15}\text{N}$

To test whether select island characteristics and aspects of the sampling regime (aims 1 and 2, respectively) influenced $\delta^{15}\text{N}$ in each sample type we fit two linear mixed effect models. Model 1 predicted $\delta^{15}\text{N}$

based on the island characteristics of island size (very small; < 1 km², small; 1–4 km² and large; Hauturu Island at ~ 30 km²), geographical area (Hauraki Gulf or Cook Strait) and invasion history (invaded, eradicated, never-invaded). Model 2 predicted $\delta^{15}\text{N}$ based on variable aspects of the sampling regimes: sampling season (wet or dry), collection year (2006–2017) and intra-island sampling location (inside or outside a seabird colony). Both models included the random effects of sample type (soil, plant or spider) and island to account for non-independence of multiple samples collected from the same island (the inclusion of each random effect improved model fit based on difference in the Akaike's information criterion (dAIC) value – Supplementary Table S1). The effect size of each categorical parameter estimate was visualized using R package sjPlot (Lüdtke, 2020). For ease of interpretation of the relative effect sizes, each input variable was centred and standardized for plotting by subtracting the mean and dividing by two standard deviations (Schielzeth, 2010).

2.3.2 | Change in $\delta^{15}\text{N}$ with time since eradication

We examined change in $\delta^{15}\text{N}$ with time since eradication by expanding on the initial work by Jones (2010b). By incorporating an additional 13 islands to the 15 environmentally similar islands used in this original study and assessing isotope levels separately both between islands (the original study pooled islands with the same times since eradication) and within an island to account for other potential sources of isotope

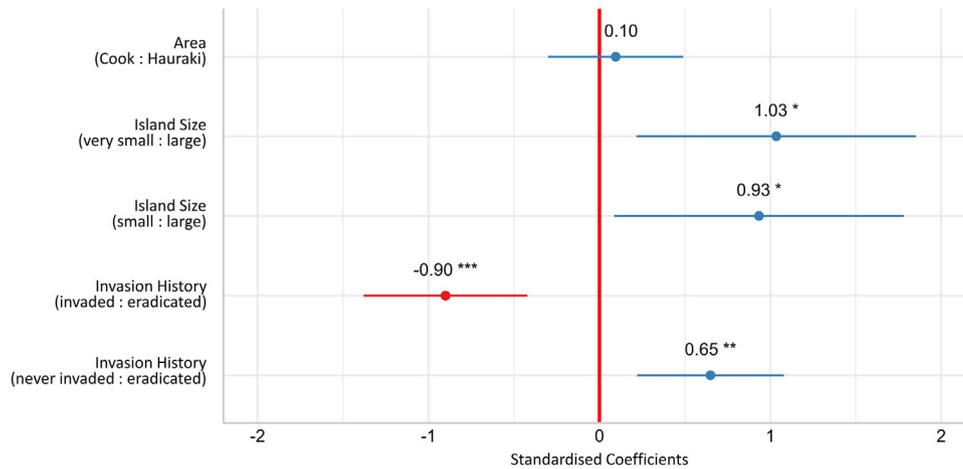


FIGURE 3 Standardized predictor coefficients (mean = 0, SD = 2) and 95% confidence intervals for the relationships between island location, size and invasion history with $\delta^{15}\text{N}$. For each parameter, the reference level is indicated by the latter part of the ratio in parenthesis. Based on when the 95% confidence interval does not intercept 0 (highlighted by the red vertical line), there is strong evidence for a positive effect of sampling on both small and very small islands compared to the larger Hauturu island, invaded islands compared to eradicated islands and eradicated islands compared to never-invaded islands on $\delta^{15}\text{N}$. There was no evidence for an effect of collection area (Cooks Strait vs Hauraki Gulf) on $\delta^{15}\text{N}$

variability, we hoped to further investigate the influence of confounding variables on $\delta^{15}\text{N}$ trajectories. For each sample type on each island, sample $\delta^{15}\text{N}$ values were averaged across the variables identified as influencing $\delta^{15}\text{N}$ levels in the previous models (e.g. if seabird presence was found to influence $\delta^{15}\text{N}$ an averaged inside and an outside seabird colony $\delta^{15}\text{N}$ value was calculated for each sample type on each island). A linear model was fitted to the averaged results to assess the relationship between time since eradication and $\delta^{15}\text{N}$ for each sample type (aim 3) using R package lm (R Core Team, 2020). The effect size of time since eradication on $\delta^{15}\text{N}$ for each sample type was centred and standardized by subtracting the mean and dividing by two standard deviations (SD) then plotted using sjPlot (Gelman, 2008; Lüdtke, 2020). Mean $\delta^{15}\text{N} \pm \text{SD}$ for never-invaded and invaded islands was used as positive and negative controls for ecosystem recovery (Jones, 2010a).

3 | RESULTS

3.1 | Influence of island characteristics on $\delta^{15}\text{N}$

Island size and invasion history were the most influential island characteristics to impact $\delta^{15}\text{N}$ levels (Figure 3). $\delta^{15}\text{N}$ levels on the larger Hauturu island were lower than those found on the small or very small islands. Samples collected from islands with invasive mammals had lower $\delta^{15}\text{N}$ than those from eradicated islands, and islands that were never-invaded by invasive mammals had higher $\delta^{15}\text{N}$ than both invaded and eradicated islands. The location of islands in the Hauraki Gulf or Cook Strait did not affect $\delta^{15}\text{N}$ levels (Figure 3).

3.2 | Influence of sampling regime on $\delta^{15}\text{N}$

The most influential aspect of the sampling regime on $\delta^{15}\text{N}$ was whether samples were collected inside or outside seabird colonies,

with colony presence leading to elevated $\delta^{15}\text{N}$ (Figure 4). The year samples were collected, and the sampling season did not have a notable effect on $\delta^{15}\text{N}$ (Figure 4).

3.3 | Change in $\delta^{15}\text{N}$ with time since eradication

Sample collection year, season and island location were not found to affect $\delta^{15}\text{N}$ so samples were pooled to examine change in $\delta^{15}\text{N}$ with time since eradication. Collecting samples inside or outside a seabird colony did affect $\delta^{15}\text{N}$, however. Each sample type was collected within seabird colonies on fewer than seven eradicated islands (soil = seven islands, spider = five islands, plant = four islands) so it was not possible to examine within colony trends in $\delta^{15}\text{N}$. These samples were therefore omitted, and only samples collected outside colonies were used to investigate trends in $\delta^{15}\text{N}$ with time since eradication. $\delta^{15}\text{N}$ increased with time since eradication for each sample type, with the trend strongest in spider samples (standardized effect sizes: soil = 0.24, plant = 0.29 and spider = 0.57) (Figure 5, Supplementary Figure S1 and Supplementary Table S2). The larger Hauturu Island had $\delta^{15}\text{N}$ levels within the range of invaded islands for all three sample types. While the difference in size between the very small and small islands did not affect $\delta^{15}\text{N}$ (Figure 3), there was still variation in $\delta^{15}\text{N}$ on these islands sampled at similar times since eradication, suggesting that additional variables not examined here still need to be accounted for.

4 | DISCUSSION

Our results highlight that, if stable isotope analysis is to be developed into a useful post-eradication island-ecosystem function assessment tool, island characteristics and sampling regimes must be accounted for. Of the variables investigated in this study, island size and the

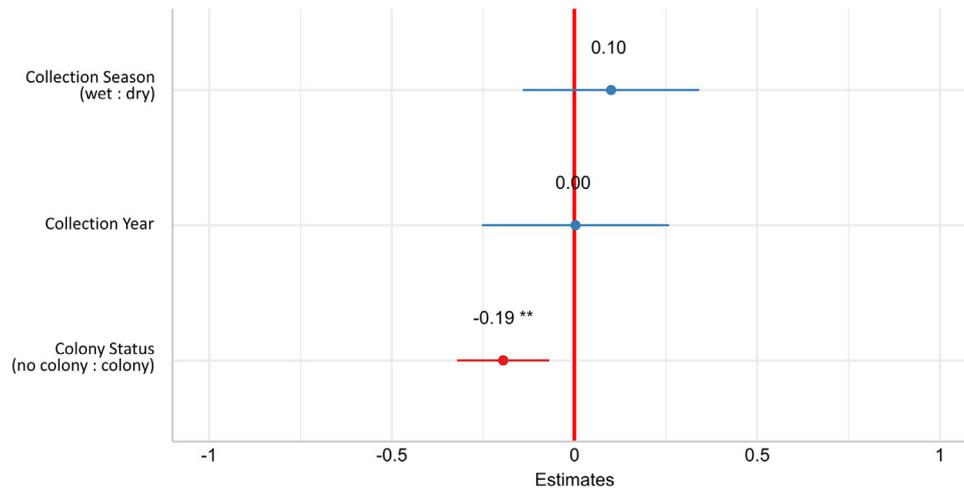


FIGURE 4 Standardized predictor coefficients (mean = 0, SD = 2) and 95% confidence intervals for the relationships between sample collection season, collection year and intra-island sampling location (inside or outside a seabird colony) with $\delta^{15}\text{N}$. For each parameter, the reference level is indicated by the latter part of the ratio in parenthesis. Based on when the 95% confidence interval does not intercept 0 (highlighted by the red vertical line), there is strong evidence for a negative effect of sampling outside seabird colonies on $\delta^{15}\text{N}$ levels but no evidence for an effect of collection year or season on $\delta^{15}\text{N}$

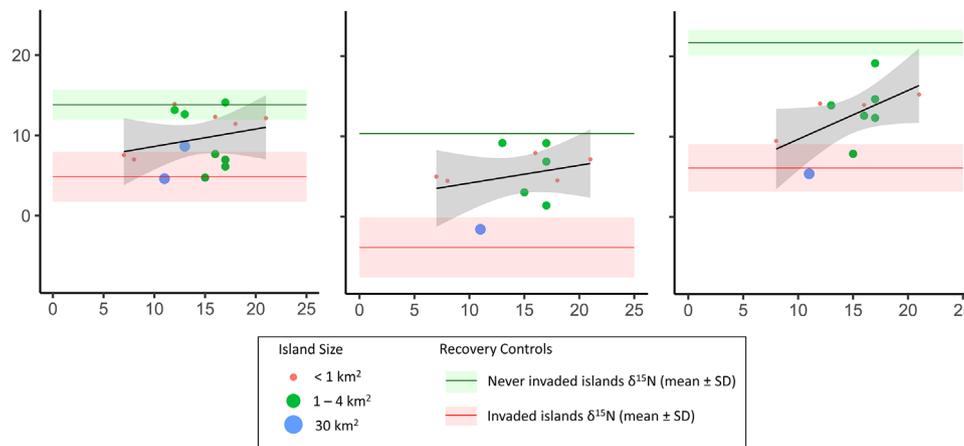


FIGURE 5 Trends in $\delta^{15}\text{N}$ with time since invasive mammal eradication for soil, plant (*Myrsine australis*) and spider samples collected from outside seabird colonies. A linear model is fitted across all islands and displayed with \pm SD

presence of seabird colonies around a sampling location both significantly affected sample $\delta^{15}\text{N}$.

4.1 | Island size

Samples collected from the largest island in this study, Hauturu, still had $\delta^{15}\text{N}$ values similar to those found on invaded islands. With only a single large island, we cannot conclusively attribute the low $\delta^{15}\text{N}$ levels on Hauturu to island size. However, with large islands at the forefront of eradication this finding highlights the importance for more research to understand the effects of island size on post-eradication recovery. Due to its size, Hauturu may not be comparable to the other islands in this study, with recovery following a different or lengthened trajectory. We were only able to examine small never-invaded islands as controls for a recovered ecosystem state. These may not be representative of

larger islands. With size comes increased heterogeneity in island geology, soil types, dominant plant communities, climates and distribution of seabird species – all factors likely to contribute to variation in $\delta^{15}\text{N}$ (Ellis et al., 2011). Hauturu has a range of habitat types absent on the other islands such as higher altitudes and wet cloud forests (Rayner et al. 2007). Larger islands may need to be considered as a matrix of seabird and non-seabird influenced zones with different recovery trajectories for each.

An island size threshold is likely to exist where islands stop being true ‘seabird islands’ with seabirds able to reach densities to act as island-wide ecosystem engineers and drive whole-island nutrient dynamics (Anderson & Mulder, 2011; Ellis et al., 2011). What this threshold is, and whether Hauturu is above it, is unknown. Determining this threshold will be informative for planning both monitoring and restoration strategies. Where seabirds are no longer the key ecosystem drivers, management focused on seabird conservation alone may not

bring about the wider ecosystem benefits expected on smaller seabird islands. In such instances, targeted conservation of multiple individual ecosystem components may be required. Such knowledge prior to the commencement of an eradication project would allow sufficient post-eradication restoration funding to be budgeted for.

4.2 | Presence of seabirds

The elevated $\delta^{15}\text{N}$ levels in samples collected in the vicinity of seabird burrows supports findings from previous studies (Bokhorst & Convey, 2016; Bokhorst et al., 2019; Caut et al., 2012; Crittenden et al., 2015; Jones, 2010b). Within colonies, higher seabird burrow densities have also been correlated with enriched isotopic signatures in several island systems globally (Mulder et al., 2011b). Interestingly, field observations from islands in this study indicated that seabird burrow densities around the depleted $\delta^{15}\text{N}$ samples collected on Hauturu island were higher than those on many of the smaller islands (Jones (2007) and Kong (2017) personnel communication). Invasive mammals affect numerous ecosystem components and the interactions between them (Drake et al., 2011; Harper & Bunbury, 2015) (Figure 1). The absence of enriched $\delta^{15}\text{N}$ at each trophic level on Hauturu may indicate that food web components, their interactions or functional roles had not yet recovered at the time of sample collection to enable the incorporation and transmission of the seabird-derived nutrients through the terrestrial food web.

4.3 | Recovery trajectories

For each sample type, $\delta^{15}\text{N}$ increased with time since eradication, with the most positive trend evident in spider samples. However, substantial variability still existed between islands at similar times since eradication. With additional research and a larger sample size of islands, more variables influencing $\delta^{15}\text{N}$ levels could be accounted for and we will be able to determine more clearly if an island with lower $\delta^{15}\text{N}$ levels than other islands at a similar time since eradication is in fact displaying a delay in its recovery and requires additional assistance.

Several smaller islands also had $\delta^{15}\text{N}$ values within one standard deviation of the mean of invaded islands. Jones (2010b) found recovery of nutrient dynamics did not commence for at least 15 years post-eradication. The 13 islands included in this study in addition to those examined by Jones et al. (2010b) support a delay in the commencement of the recovery of seabird-derived nutrients. In all instances, islands still within the range of an invaded island were sampled within 17 years of eradication. Re-sampling islands would increase the temporal spread of the data and the proportion of samples from islands beyond this 15 to 17-year mark and would help to further our understanding of the trajectories of the recovery of seabird-derived nutrients.

4.4 | Future research directions

The variability in $\delta^{15}\text{N}$, even for islands at similar times since eradication highlights the need for additional research. Here we outline some key continuing knowledge gaps which would benefit from additional research through targeted island sample collection.

4.4.1 | Identification of a 'seabird island' size threshold

Additional investigation into a range of larger islands with varying invasion histories is required to ascertain at what size threshold an island can no longer be considered a true 'seabird island' with seabirds driving nutrient dynamics. Sub-Antarctic islands present some of the world's largest eradication projects undertaken to date (e.g. Bester et al., 2002; Horn et al., 2019; Martin & Richardson, 2019; McClelland, 2011; Springer, 2016), potentially providing a study system to better explore the effect of island size. The added logistical challenges of accessing many sub-Antarctic islands means that the development of a cost- and time-efficient post-eradication monitoring technique could be particularly beneficial for this region.

4.4.2 | Influence of seabird species assemblages

Seabirds are taxonomically diverse and the assemblage of species present, or re-colonizing an island is likely to influence seabird-derived nutrient recovery. Seabirds of differing body sizes contribute different quantities of nutrients (Smith et al., 2011). Nesting type (surface, tree or burrow) also influences the input of nutrients, with surface nesting species able to attain higher colony densities and deposit concentrated quantities of guano around their nests. In contrast, burrowing seabirds defecate less around their nest sites, and through burrow space requirements, nest at lower densities (Smith et al., 2011). Different species also have different re-colonization rates following eradications, with burrowing species often slow to re-colonies due to natal philopatry (Buxton et al., 2014). Islands that support a greater proportion of surface nesters may therefore be expected to reach higher seabird densities more quickly than burrowing seabird-dominated islands, such as those in this study. Similarly, islands with seabirds present all year round will have year-round nutrient input. Seabirds also forage in different oceanic regions, and on different prey types, both of which can affect the isotopic signature of nutrients they transport to an island. With different seabird community compositions present on each island (Borrelle et al., 2018), it may be expected that the baseline isotope values entering each island also differs. Direct analysis of seabird guano and an assessment of the likely seabird assemblage on each island would provide additional insight.

4.4.3 | Intra-island sampling location

Intra-island sampling location features may influence $\delta^{15}\text{N}$ levels. The reported reach of seabird influence ranges from 50 m to tens of kilometres (Bokhorst & Convey, 2016; Bokhorst et al., 2019; Caut et al., 2012; Crittenden et al., 2015; Jones, 2010b). Additional investigation into what factors influence this range on different islands such as terrain, rainfall and vegetation type would assist in ensuring that samples collected within and between islands are comparable.

4.4.4 | Seasonality of sample collection

The collection of samples in the wet and dry season did not affect $\delta^{15}\text{N}$ levels in this study. However, with over 90% of samples collected in the dry season, additional investigation would be beneficial. Studies on Heron Island, Australia, found seabird guano input varied from 16 to 738 kg per day due to seasonal changes in wedgetailed shearwater (*Puffinus pacificus*) and black noddy (*Anous minutus*) population sizes (Staunton Smith & Johnson, 1995). Such variation in seabird-derived nutrient availability may be expected to have some reflection in isotopic enrichment levels over a season. Repeat sampling locations on islands over the course of a seabird breeding cycle would help confirm if seabird colony attendance and seasonality in weather needed to be accounted for to make samples comparable between islands and individual islands sampled at different times of year.

5 | CONCLUSIONS

Strengthening our understanding of the dynamics of stable isotopes following invasive mammal eradications, and the factors that influence this will require targeted sample collection. Selecting easily accessible islands or those with permanent personnel, where repeat visits will not cause great disturbance or biosecurity risks, could further our understanding of how timing and location of sampling, as well as the sample type, influence isotope levels. Accounting for these variables, sampling across islands with differing characteristics, such as size and biome could then inform us how comparable islands are. Stable isotope data are inherently noisy (Boecklen et al., 2011), improving our understanding of the island characteristic and sampling regime can reduce some of this noise. Addressing these questions would help realize the potential for stable isotope analysis as a cost- and time-efficient indicator of the recovery of an islands' ecosystem function in response to eradication, something currently not widely available in the post-eradication monitoring tool kit.

ACKNOWLEDGEMENTS

We would like to acknowledge the Traditional Owners and ongoing custodians of the land on which this research took place: Ngātiwai, Ngāti Hei, Ngāti Whanaunga, Ngāti Koata, Ngāti Kuia, Ngāti Toa and Ngāi Tahu. We would like to thank the National Geographic Society for funding this work, and all field assistants, island rangers and

Department of Conservation personnel for logistical support. We would like to thank Ana Miller-ter Kuile and Thomas Bodey for their helpful and constructive feedback on the manuscript.

CONFLICTS OF INTEREST

The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS

PP, JS, RT, SK and HJ conceived the ideas and designed methodology. HJ and SK undertook data collection. PP led the analysis and writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data and R code has been lodged with the University of Tasmania data portal: <https://doi.org/10.25959/zdc1-6z61> (Pascoe & Jones, 2021).

PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1002/2688-8319.12082>

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How to cite this article: Pascoe, P., Shaw, J., Trebilco, R., Kong, S., & Jones, H. (2021). Island characteristics and sampling methodologies influence the use of stable isotopes as an ecosystem function assessment tool. *Ecol Solut Evidence*, 2, e12082. <https://doi.org/10.1002/2688-8319.12082>