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ARTICLE

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Invasive mammals disrupt sea–land nutrient inputs over 169 years on subtropical oceanic islands

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Abstract

Invasive mammals have severely impacted oceanic islands, reducing or extirpating seabird populations and driving the collapse of nutrient flows with lasting ecosystem effects. We investigated these dynamics on contrasting subtropical oceanic islands in the South Pacific: Rangitāhua, a large island where goats, cats, and rats caused the extinction of seabird populations, and the small mammal-free Meyer Islands, where seabird colonies remain dense. Using stable isotope analysis ($\delta^{13}C$ and $\delta^{15}N$) of 408 contemporary and historical specimens spanning 169 years, across plants to invertebrates and birds, we tested hypotheses about seabird-driven nutrient coupling across space and time. Spatially, we predicted stronger seabird-driven nutrient enrichment on the mammal-free Meyer Islands than on invaded Rangitāhua. Consistent with this, Meyer Islands' soils had higher phosphorus and lower pH, and terrestrial plants and herbivorous invertebrates were enriched in $\delta^{13}C$ and $\delta^{15}N$ relative to their Rangitāhua counterparts. In the nearshore marine system, $\delta^{15}N$ values—but not $\delta^{13}C$—were elevated in macroalgae and herbivorous and omnivorous invertebrates around the Meyer Islands compared with those around Rangitāhua, indicating stronger seabird-driven nutrient inputs to coastal food webs. By contrast, the lower values on Rangitāhua reflect slow seabird recovery more than 20 years after the eradication of invasive mammals. Temporally, we tested whether isotopic values in Rangitāhua plants and birds declined with seabird loss. Values for $\delta^{13}C$ declined steadily from the mid-19th century to the present, consistent with reduced seabird subsidies (and possibly volcanic activity), whereas $\delta^{15}N$ values showed no long-term

change. Together, these spatial and temporal perspectives show that while seabird nutrient pathways can recover within decades on small islands, recovery on large, degraded islands can take much longer. Adjacent islets can provide recolonists but may not serve as true analogues. Restoring sea–land nutrient connectivity on large islands may require not only invasive mammal eradication but also active facilitation of seabird return.

KEYWORDS
historical museum collections, island ecosystem restoration, long-term ecological change, seabird-driven nutrient cycling, soil nutrients, stable isotopes

INTRODUCTION

The cycling of organic matter and nutrients underpins ecosystem functions, supporting food webs across interconnected habitats. Despite physical boundaries, nutrient transfers occur between terrestrial and marine habitats through both abiotic processes, such as wave action and ocean currents, and biotic processes (Hilderbrand et al., 1999). Islands are useful systems for studying these interactions because they are geographically bounded and often support simpler food webs than continental systems (Warren et al., 2015). Oceanic islands, despite often having inherently low terrestrial productivity, can be substantially enriched by external subsidies from the marine environment (Anderson & Polis, 1998, 1999). Seabirds play critical roles as biological vectors for nutrient transfer from marine to terrestrial systems by feeding on marine prey and depositing nutrient-rich waste on island habitats where they breed and rest (Anderson & Polis, 1998; Bokhorst et al., 2019; Jones et al., 2025; Moss, 2017). Dense seabird colonies transfer large quantities of marine-derived nutrients—through guano, the remains of seabird adults, chicks, and eggs, and non-ingested or regurgitated prey remains—as well as physical disturbances from nesting and roosting (Kolb et al., 2011). These processes drive unique ecological relationships on seabird islands through bottom-up (enhancing primary production) and top-down effects (benefiting predators and scavengers) (Hentati-Sundberg et al., 2020; Jones et al., 2025; Kolb et al., 2011; Mulder, Jones, et al., 2011).

Invasive species have high impacts on oceanic island ecosystems. Notably, human introductions of non-native mammals to oceanic islands have severely reduced seabird populations, which predominantly evolved in the absence of mammals, especially predators (Croxall et al., 2012). Seabird loss disrupts marine-to-land nutrient transfer, altering soil and plant chemistry (Mulder, Anderson, et al., 2011; Wardle et al., 2012), invertebrate diversity and abundance (Fukami et al., 2006; Towns et al., 2009), and terrestrial vertebrate communities (Barrett et al., 2005; Bicknell et al., 2020; Markwell & Daugherty, 2002). Their loss also has impacts on adjacent marine ecosystems, affecting benthic nutrients (Hentati-Sundberg et al., 2020), phytoplankton growth and zooplankton biomass (McCauley et al., 2012), coral growth (Benkwitt et al., 2021), macroalgal diversity (Rankin & Jones, 2021), fish biomass and growth, and even fish behavior (Graham et al., 2018; McCauley et al., 2012). As seabirds are key vectors for marine-derived nutrients, their decline due to invasive species disrupts the nutrient balance of entire island systems. Detecting such change requires precise ecological tracers.

Introduced mammalian herbivores, absent from most oceanic islands, have markedly altered ecosystems (Courchamp et al., 2003; Vitousek, 1988). Goats, widely released as a food source, browse vegetation that typically lacks defenses against herbivory (Chynoweth et al., 2013; Coblentz, 1978), reducing or eliminating palatable plant species (Chynoweth et al., 2013; de la Luz et al., 2003) and driving vegetation state shifts—from woody cover to grasslands (Ohashi et al., 2024). These changes disrupt nutrient cycling and ecosystem functions (Bardgett & Wardle, 2003). Trampling and vegetation loss also increase erosion (Coblentz, 1978), with downstream impacts on nearshore marine environments (Chynoweth et al., 2013). On islands with seabirds, goats destabilize soils critical for burrow-nesting species and destroy nests through trampling (Hata et al., 2014; Hipfner et al., 2010).

Ecological studies over 10–60 years have provided valuable insights into the impacts of invasive mammals on oceanic islands and ecosystem recovery following eradication (Bellingham, Towns, et al., 2010; Hamann, 1993; Jones, 2010). However, because many mammal introductions occurred over a century ago (de Lima Martins et al., 2021), it is important to understand ecological change over longer timeframes. For example, palaeoecological techniques can detect historical shifts that are not apparent in contemporary systems

(Bellingham, Wiser, et al., 2010; Duda et al., 2020; Hawke, 2004; Swift et al., 2018).

Stable isotope analysis of carbon ($\delta^{13}C$, the ratio of ^{13}C to ^{12}C, expressed in ‰ units) and nitrogen ($\delta^{15}N$, the ratio of ^{15}N to ^{14}N expressed in ‰ units) provides powerful tools for tracing seabird nutrient inputs. Seabird guano has elevated $\delta^{15}N$ values due to their position as top predators in oceanic food webs, in which $\delta^{15}N$ values increase by 3–4 ‰ per trophic level (Minagawa & Wada, 1984; Post, 2002). Their guano also has elevated $\delta^{13}C$ values, as the carbon source of seabird prey comes from marine primary production dominated by phytoplankton and macroalgae. Within terrestrial systems, carbon and nitrogen isotopes reflect seabird influence through distinct mechanisms. Specifically, $\delta^{15}N$ provides a direct tracer of marine-derived nitrogen enrichment from guano, carrion, and detritus, whereas $\delta^{13}C$ values increase in response to improved nutrient status at the base of the food chain (Erskine et al., 1998; Szpak et al., 2012). Together, $\delta^{13}C$ and $\delta^{15}N$ track the extent of marine subsidies and connectivity between terrestrial and nearshore habitats (Estupiñán-Montaño et al., 2022). Contemporary stable isotope data provide insights into current ecosystem functioning, while data from historical specimens offer a window into past ecological conditions. Analyzing samples across invasion timelines enables reconstruction of long-term changes in nutrient flow. The combination of stable isotope techniques with archaeological, palaeofaunal, or museum collections is opening new avenues for understanding how human arrival and associated species have reshaped seabird-dominated island ecosystems (Swift et al., 2018).

Rangitāhua, the Kermadec Islands, is a remote subtropical archipelago in the south Pacific Ocean 1000 km northeast of Aotearoa New Zealand. The name Rangitāhua refers to both the largest island (also known as Raoul Island) and the wider group; hereafter, we use "Rangitāhua" for the main island and "Rangitāhua Islands" or "archipelago" for the group. Fourteen seabird species breed across the archipelago, totaling ~10–15 million birds (Gaskin, 2011; Taylor, 2000) and are a key component of the islands' ecosystems. Their populations benefit from one of the world's least modified marine ecosystems included within Aotearoa New Zealand's largest marine reserve (7480 km^2), resulting in exceptional protection for seabird and marine biodiversity (Duffy & Ahyong, 2015; Edgar et al., 2014; Trnski & de Lange, 2015).

Rangitāhua holds cultural, spiritual, and ecological significance for Ngāti Kuri, the legally recognized kaitiaki (guardians), who view the archipelago as a tupuna (ancestor). The largest island was where the Māori ancestors first settled in the 13th century, and it served as a critical stopover in voyages to and from Aotearoa New Zealand and tropical Pacific islands (Anderson, 1980; Furey et al., 2015; Matisoo-Smith et al., 1999).

The arrival of humans brought profound ecological changes to the Rangitāhua islands, particularly to Rangitāhua itself. Kiore (Pacific rat, *Rattus exulans*) were likely introduced by Polynesian voyagers in the 13th century (Anderson, 1980; Matisoo-Smith et al., 1999; Spriggs & Anderson, 1993). Major transformations followed European settlement in the 19th and early 20th centuries. Goats (*Capra hircus*) were introduced in 1836, followed by feral cats (*Felis catus*) (Gentry, 2013; Merton, 1970; Veitch, 2004), and Norway rats (*Rattus norvegicus*) invaded in 1921 after a shipwreck (Veitch et al., 2011).

These invasive mammals caused ecological degradation, reducing bird populations and damaging forests (Veitch, 2004). Seabird numbers likely reached many millions before the 1850s despite goat and cat introductions and in the early 20th century there were approximately 500,000 Kermadec petrel *Pterodroma neglecta*, "abundant" white-necked petrel *Pterodroma cervicalis*, and "immense numbers" of wedge-tailed shearwater *Ardenna pacifica* (Iredale, 1910). All these populations were exterminated soon after Norway rats invaded in 1921 (Gaskin, 2011; Merton, 1970). Some terrestrial birds also went extinct while others survived only on nearby predator-free islands such as the Meyer Islands (Gaskin, 2011; Veitch et al., 2011) (Figure 2). Goats were introduced to the Meyer Islands by whalers, and 12 goats were seen in July 1854 (MacGillivray, 1854), but no goats were present when a group went ashore in August 1887 (Cheeseman, 1887) and the islands have remained free of introduced mammals since.

Restoration on Rangitāhua began in 1936 with goat control, culminating in their eradication in 1984. Rat and cat eradication was conducted in 2002 and confirmed by 6 months of monitoring in 2004 (Bellingham, Wiser, et al., 2010). Since then, some extant seabird populations have grown, and other sea and terrestrial bird species have recolonized Rangitāhua from nearby mammal-free islands (Gaskin, 2011; Ortiz-Catedral et al., 2009). Yet, by 2011, Rangitāhua supported only around 50,000 seabirds, fewer than the approximately 70,000 breeding on the much smaller Meyer Islands (1.76% of Rangitāhua's area), where ecological processes remain intact (Gaskin, 2011). This contrast enables investigation into the long-term impacts of seabird loss, ecosystem degradation, and any post-removal recovery.

Since the mid-19th century, scientists have visited the Rangitāhua archipelago, particularly Rangitāhua itself, to collect plant and animal specimens, now lodged in

Aotearoa New Zealand and international museums and herbaria. We used a stable isotope approach to test two hypotheses:

1. From a contemporary perspective, the Meyer Islands, which have large, intact seabird populations providing significant marine-derived nutrient inputs, will have higher soil nutrient levels, $\delta^{13}C$ and $\delta^{15}N$ values across both terrestrial and marine ecosystem components than Rangitāhua, reflecting stronger ecological coupling between sea and land.
2. From a historical perspective, $\delta^{13}C$ and $\delta^{15}N$ values from terrestrial plants and birds of Rangitāhua, preserved in collections, would reflect the progressive loss of seabird-derived allochthonous inputs, decreasing across four invasive mammal regimes including Period 1: 1854–1920, when kiore, goats, and cats were present but seabirds remained abundant; Period 2: 1921–1983, when kiore, goats, cats, and Norway rats were present and seabirds were extirpated; Period 3: 1984–2001, when kiore, cats, and Norway rats were present and seabirds remained absent; and Period 4: 2002–2023, when invasive mammals were absent and seabirds exhibited a slow recovery (Figure 1). We hypothesized that $\delta^{15}N$ in at least primary producers would decline in the absence of allochthonous inputs, especially during Periods 2 and 3. Some studies have shown increases in $\delta^{13}C$ and $\delta^{15}N$ values after mammal eradication on islands, equivalent to Period 4 (e.g., Jones, 2010) but others have not (e.g., Pascoe et al., 2025).

METHODS

Study site

This study was conducted on Rangitāhua (Raoul Island; 29°16′ S, 177°52′ W; 2938 ha; maximum elevation 516 m) and the nearby Meyer Islands (combined 52 ha; maximum elevation 123 m), located 2 km northeast of Rangitāhua (Figure 2). All islands in the archipelago are volcanic in origin. Rangitāhua is an active volcanic island with a central caldera and three lakes, with recent eruptions in 1964 and 2006 (Brothers & Searle, 1970). The Meyer Islands are inactive and consist of basaltic tuff and breccia overlain by ash from Rangitāhua eruptions (Brook, 1998).

The region has a humid subtropical maritime climate with mild temperatures ranging from 16–17°C (minimum) to 21–24°C (maximum). Southeast trade winds are persistent, and tropical cyclones occur between November and April, about three to four times per decade.

The flora and fauna of Rangitāhua are species-poor relative to other southwest Pacific islands, reflecting the archipelago's young geological age and volcanism. Vegetation is subtropical evergreen forest with 127 native vascular plant species, 16% of them endemic (Sykes, 1977; Wardle, 1991). On Rangitāhua, *Metrosideros kermadecensis* dominates canopies, with *Rhopalostylis baueri* locally abundant; dry forest prevails below 250 m and wet forest above (Oliver, 1910). The Meyer Islands

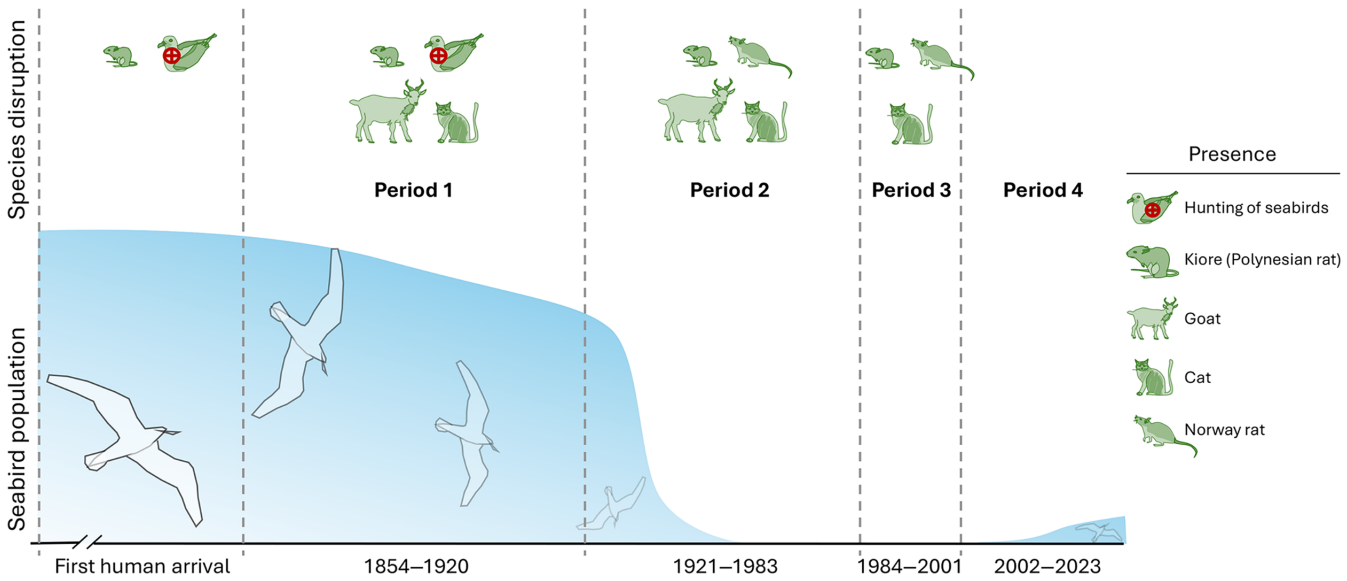

FIGURE 1 Contrasting periods on Rangitāhua that inform our data analyses showing predicted seabird decline (bottom section) in response to the human-induced disturbances (top section). Kiore/Polynesian rat (*Rattus exulans*) is hypothesized to have arrived between 1250 and 1700. Goats were introduced in 1836 and cats soon after (Veitch et al., 2011). Illustration credit: Marina Ferrari de Aquino Klemm.

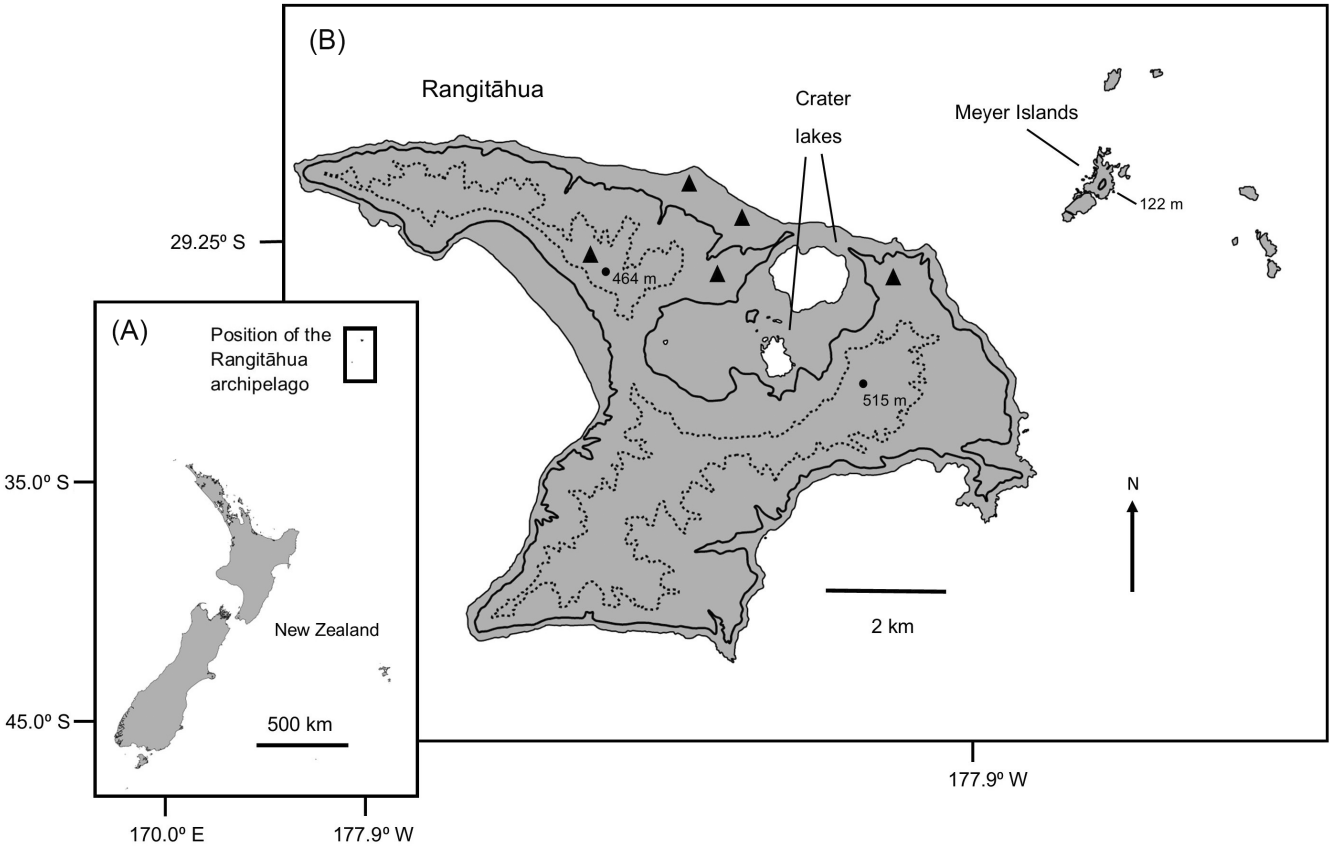

FIGURE 2 (A) The Rangitāhua archipelago in relation to mainland Aotearoa New Zealand and (B) Rangitāhua and the Meyer Islands. Topographic contours are represented as a solid line (100 m) and dashed line (300 m). Location of soil sampling sites on Rangitāhua are shown by solid black triangles. Soil samples were also collected on the Meyer Islands but are not shown.

support low-canopy vegetation dominated by *Myoporum rapense* (de Lange, 2011).

Terrestrial faunal diversity is also limited. About 500 invertebrate species are recorded, with very low endemism and many widespread, highly mobile or introduced taxa (e.g., *Geograpsus grayi*, *Aporrectodea caliginosa*) (Brown & Baker, 2009; Chinn, 2011). The terrestrial bird community comprises 10 resident species, most with ancestors dispersing from Aotearoa New Zealand (Veitch, 2004; Veitch et al., 2011).

Seabird populations on Rangitāhua are sparse but growing after mammalian predator eradication, with at least nine species currently breeding, of which the burrow-nesting *Pterodroma nigripennis* is the most widespread and common. In contrast, the Meyer Islands, which never had invasive predators, have dense populations of breeding burrowing, surface- and tree-nesting seabirds (13 species) (Gaskin, 2011).

The marine ecosystems of Rangitāhua are among the world's least modified. Most islands are steep-sided rocky outcrops exposed almost continuously to strong swells and wave action. Habitats in the shallow subtidal areas include low-relief sand, bedrock, and boulders, and rocky reefs with a diverse biota of macroalgae, invertebrates, and fishes. The coral fauna of Rangitāhua includes warm-water, reef-building corals that build reefs in the shallow depths but not at most sites since they are near their southern limit. Rangitāhua has the greatest number of fish species of anywhere within Aotearoa New Zealand across all examined depths, down to 1200 m.

Field and museum collections

Sampling spanned four periods (Periods 1–4) over 169 years (1854–2023; Appendix S1: Table S1). In total, 408 specimens from 58 terrestrial and marine taxa were analyzed, representing all trophic levels of interest. For Rangitāhua, 317 specimens were collected across Periods 1–4 (1854–2023); for the Meyer Islands, 91 contemporary specimens were collected in Period 4 (2003–2023). Sampling followed standard herbaria and museum collection protocols as directed by curators and collection managers. Tissues were selected based on preservation suitability for stable isotope analysis. Only frozen, ethanol-fixed, or dry-preserved specimens (herbarium

material and feathers) were included; formalin-preserved specimens were excluded owing to isotope alteration (Edwards et al., 2002).

Contemporary field sampling

Soil nutrients collection and analysis

Soils were collected in November 2023 from five sites on Rangitāhua under forest canopies at elevations ranging from 5 to 450 m. Additionally, samples were taken from five locations on North Meyer Island, which included sampling from coastal slopes to the summit 130 m above sea level. Each sample was collected using a 25-mm diameter auger to a depth of 10 cm.

Each soil sample was air dried at 35–40°C overnight. Soil total C and total N concentrations were determined using a Dumas dry combustion analyzer (Leco TruMac Analyzer, LECO, St. Joseph, MO, USA) as part of the stable isotope analysis. Total phosphorus (P) concentration was determined by heating soil at 550°C for 60 min, extracting with 0.5 M sulfuric acid for 16 h and analyzing with a flow injection analyzer (QuikChem 8500, Lachat Instruments, Milwaukee, WI, USA).

Biota

We analyzed 292 contemporary specimens from Period 4 (2003–2023): 91 from the Meyer Islands and 201 from Rangitāhua (Appendix S1: Table S1).

Contemporary marine specimens

Sampling targeted nearshore reef habitats (<30 m depth) to examine terrestrial–marine ecosystem boundary interactions. Primary producers included red, green, and brown macroalgae (e.g., *Asparagopsis taxiformis*, *Caulerpa* spp., *Sargassum* spp.) and were hand-collected on SCUBA. Consumers were sampled across feeding guilds and mobility spectra. Benthic invertebrates were collected on SCUBA by hand, and in baited traps ranging from small to large; they comprised gastropods, bivalves, echinoderms, and crustaceans from intertidal and shallow subtidal habitats (e.g., limpets, oysters, sea urchins, starfishes, barnacles, crabs). Sessile taxa (barnacles, mussels) were taken from rocky substrates. Reef fishes were collected on SCUBA using rotenone and hand nets, spear, night lighting from the research vessel, and on hook and line; they spanned 10 species representing three mobility classes: pelagic species ranging widely across the archipelago (e.g., *Seriola lalandi*), site-attached territorial species (e.g., *Pseudolabrus luculentus*, *Chrysiptera rapanui*), and benthic species of intermediate mobility (e.g., *Engyprosopon raoulense*, *Gymnothorax nubilus*).

Species identities and sample sizes for all taxa are detailed in Appendix S1: Table S1.

Contemporary terrestrial specimens

Plant material was collected from seven woody species and one fern species across both islands (Appendix S1: Table S1). For each species, sunlit canopy leaves were sampled from mature plants, pressed, and dried before analysis.

Terrestrial invertebrates were obtained by pitfall traps and hand collection, targeting comparable feeding groups across islands. Herbivores included bees and planthoppers, while omnivores/detritivores included invasive ants and beetles (see Appendix S1: Table S1).

Birds were sampled on Rangitāhua by mist-net capture, focusing on six resident species spanning trophic guilds: herbivorous parakeets (*Cyanoramphus novaezelandiae*), omnivorous tūī (*Prosthemadera novaeseelandiae*), and two thrushes (*Turdus* spp.), carnivorous kingfisher (*Todiramphus sanctus*), and the rail pūweto (*Zapornia tabuensis*). Sample sizes are provided in Appendix S1: Table S1.

Historical terrestrial specimens

In total, 116 historical specimens of terrestrial plants and birds from Rangitāhua were obtained from museums and herbaria focusing on the same species/genera collected in the contemporary sampling (Appendix S1: Table S1). All museum samples were stored in paper envelopes or sterile cryotubes until further processing.

For plant specimens, entire leaves or small sections of large leaves were removed from adult plants. Samples were taken from specimens collected on both Rangitāhua and the Meyer Islands, with collection dates spanning all historical Periods 1–4 (Appendix S1: Table S1).

For bird specimens, three to five body feathers were removed from the breast of study skins of adult birds. Samples were collected from historical specimens across Periods 1–4, representing five of the six species sampled in 2023 from Rangitāhua (excluding pūweto) (Appendix S1: Table S1). Feathers were triple-rinsed in ethanol followed by distilled water, then oven-dried prior to stable isotope analysis.

Processing of contemporary and historical specimens

Terrestrial plant samples were rinsed with distilled water to remove surface contaminants. For terrestrial invertebrates, one to three legs (larger specimens such as bees) and whole bodies (smaller specimens such as ants) were sampled and rinsed in distilled water. Terrestrial bird feathers were triple-rinsed in ethanol and double-rinsed in distilled water before being sent for further analysis.

For macroalgae samples, sections were cut from the mid-portion of the thalli, avoiding reproductive structures, epiphytes, and damaged areas. Marine invertebrates were processed as follows: for mollusks (gastropods and bivalves), foot muscle tissue was extracted; for echinoderms (sea urchins, starfish), tube feet (three to five) were collected. For most crustaceans, muscle tissue from the appendages was sampled, except for some smaller specimens for which the whole organisms were processed.

For fishes, approximately 1 cm^3 of white dorsal muscle tissue was excised from each specimen. For the smallest species, whole muscle tissue was collected from the lateral body wall. In some specimens, fin clips were used instead, which previous studies have shown to be comparable for stable isotope analysis (Willis et al., 2013). Fish muscle tissue was rinsed with distilled water to remove potential contaminants.

Stable isotopes sample preparation and analysis

All tissue samples were freeze-dried for 48 h, homogenized, and ~0.5–1.0 mg weighed for $\delta^{13}C$ and $\delta^{15}N$ analyses. Carbonate-bearing tissues (e.g., echinoderms) were acidified. Stable isotope analyses were carried out on a DELTA V Plus continuous flow stable isotope ratio mass spectrometer linked to a Flash 2000 elemental analyzer using a MAS 200 R autosampler (Thermo-Fisher Scientific, Bremen, Germany) at Earth Sciences New Zealand's Stable Isotope Facility in Wellington, New Zealand. For more details of the analysis, refer to supplementary materials in Bury et al. (2024). For details of the standards and normalization process used, refer to Appendix S1. Where relevant, carbon stable isotope data were corrected for lipid content following equations in Fry et al. (2003). Repeat analysis of a suite of international standards produced data accurate to within 0.4% and a precision of better than 0.25% for total N% and total C% content, and data accurate to within 0.15 ‰ and a precision of better than 0.25 ‰ for both δ15N and δ13C values.

Statistical analysis

All analyses were performed in R (v4.1.2; scripts available at https://doi.org/10.5281/zenodo.20788131). Significance was assessed at $\alpha = 0.05$. Since the onset of the industrial era, the combustion of fossil fuels—characterized by low $\delta^{13}C$ values—has led to a decline in the $\delta^{13}C$ values composition of atmospheric CO_2, known as the Suess effect (Keeling, 1979). As this isotopically lighter CO_2 is absorbed by the oceans, the $\delta^{13}C$ values of dissolved inorganic C has decreased over time, producing lower $\delta^{13}C$ values from primary producers such as phytoplankton to apex predators (Lorrain et al., 2020). Accounting for this $\delta^{13}C$ baseline shift is crucial to distinguish genuine ecological or behavioral shifts in focal species—such as changes in diet or foraging zones—from fossil fuel-biased atmospheric trends (Quillfeldt et al., 2008). To address this, $\delta^{13}C$ values from historical specimens were adjusted to a common reference year (i.e., the year of analysis) using a temporal correction factor: $\delta^{13}C\ \text{adjusted} = \delta^{13}C\ \text{raw} - 1 + 1.1 \times (\text{analysis year} - \text{sample year}) \times 0.027$, as described by Hilton et al. (2006) and Quillfeldt et al. (2008).

To compare $\delta^{13}C$ and $\delta^{15}N$ values between Rangitāhua and the Meyer Islands (Hypothesis 1), data were grouped into four terrestrial and five marine trophic guilds. Normality was assessed with Shapiro–Wilk tests and Q–Q plots; non-normal data were analyzed with two-way ANOVA (island × guild) followed by Wilcoxon rank sum tests for pairwise contrasts (Shapiro & Wilk, 1968).

To assess changes over time (Hypothesis 2), $\delta^{13}C$ and $\delta^{15}N$ values in plants and birds sampled during Periods 1–4 from Rangitāhua were compared using one-way ANOVA, with Wilcoxon rank sum tests (with multiple comparison corrections) for post hoc contrasts.

Older herbarium specimens may have been treated with mercuric chloride or dichlorodiphenyltrichloroethane (DDT), commonly used before the 1950s. Although specific treatment records were unavailable, this raised concerns about contamination in our older specimens. To help determine whether low $\delta^{15}N$ values in plant tissues reflected ecological signals or preservation effects, $\delta^{13}C$ and $\delta^{15}N$ values from land plants in Period 1 were compared with untreated contemporary samples from the Meyer Islands' seabird-dominated ecosystem (Period 4), using Wilcoxon rank sum tests.

RESULTS

Comparisons of soil nutrients and stable isotopes of contemporary food webs between Rangitāhua and the Meyer Islands

Soil on the Meyer Islands had significantly lower pH (4.09 ± 0.21 [mean ± SE]) than that on Rangitāhua (6.16 ± 0.224, $p < 0.0001$) and higher total P concentrations than soil on Rangitāhua (3479.03 ± 742 mg kg^{-1} vs. 857.06 ± 81 mg kg^{-1}, $p = 0.01$; Figure 3). There was no significant difference in soil N concentrations between the Meyer Islands and Rangitāhua, and concentrations were more variable on the Meyer Islands (Meyer Islands: 0.79% ± 0.18%; Rangitāhua: 0.59% ± 0.04%, $p > 0.05$).

The $\delta^{13}C$ values of the Meyer Islands' terrestrial ecosystem were higher than those of Rangitāhua for plants ($W = 107$, $p < 0.05$) and herbivorous invertebrates ($W = 29$, $p < 0.01$), but not for omnivorous/detritivorous invertebrates ($W = 16$, $p > 0.05$; Figure 4). There were no significant differences in $\delta^{13}C$ values between Rangitāhua and the Meyer Islands for any marine ecosystem component, including herbivorous invertebrates, omnivorous/detritivorous invertebrates, carnivorous invertebrates, omnivorous/planktivorous fish, and carnivorous fish ($W \geq 10$, $p \geq 0.19$).

The Meyer Islands' terrestrial ecosystem had higher $\delta^{15}N$ values than Rangitāhua for plants ($W = 122$, $p < 0.05$) and herbivorous invertebrates ($W = 28$, $p < 0.05$), but not for omnivorous/detritivorous invertebrates ($W = 17$, $p > 0.05$; Figure 5). The Meyer Islands' marine ecosystem had higher $\delta^{15}N$ values for algae ($W = 274$, $p < 0.01$), herbivorous invertebrates ($W = 119$, $p < 0.05$), and omnivorous/detritivorous invertebrates ($W = 451$, $p < 0.01$) than that of Rangitāhua; but there were no significant differences for carnivorous invertebrates, omnivorous/planktivorous fishes, or carnivorous fishes ($W \geq 12$, $p \geq 0.44$).

Temporal variations of stable isotope values in the terrestrial Rangitāhua ecosystem

Terrestrial plant leaf $\delta^{13}C$ values from Rangitāhua declined from 1854 to 2023 (Figure 6A), with $\delta^{13}C$ in Period 1 higher than Period 2 ($W = 392$, $p < 0.001$), Period 3 ($W = 190$, $p < 0.0001$), and Period 4 ($W = 266$, $p < 0.0001$), and Period 2 higher than Period 3 ($W = 188$, $p < 0.05$). Terrestrial plant leaf $\delta^{13}C$ values on the Meyer Islands from Period 4 were not significantly different from those of the same species from Period 1 on Rangitāhua ($W = 58$, $p = 0.14$; median: Meyer Islands = −27.10, Rangitāhua = −25.20). Terrestrial bird feather

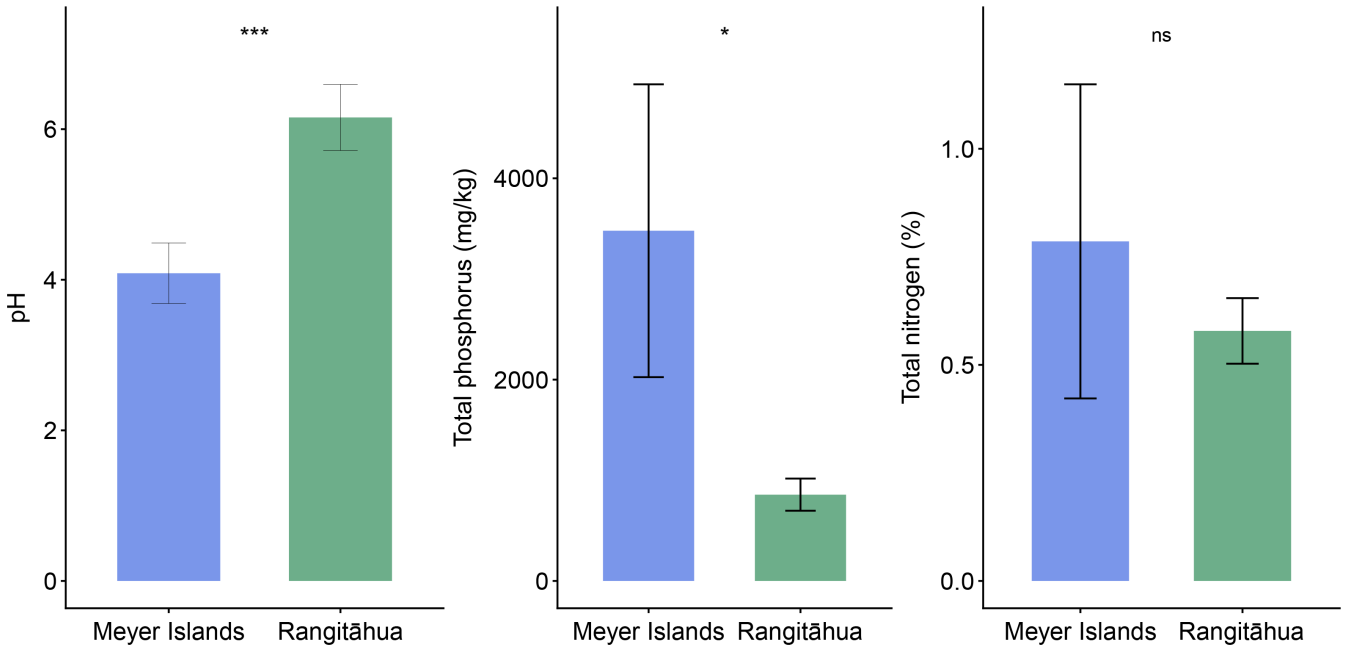

FIGURE 3 Key soil properties (mean ± 95% CI) across the Meyer Islands and Rangitāhua. Bar plots show soil pH, total phosphorus concentration, and total nitrogen concentration for each island. Statistically significant differences between islands were assessed using Welch's *t* tests. Rangitāhua soils were significantly more alkaline (***$p < 0.001$) and had lower phosphorus concentrations (*$p < 0.05$) than those on the Meyer Islands. Total nitrogen content did not differ significantly between the islands ($p > 0.05$). ns, non significant.

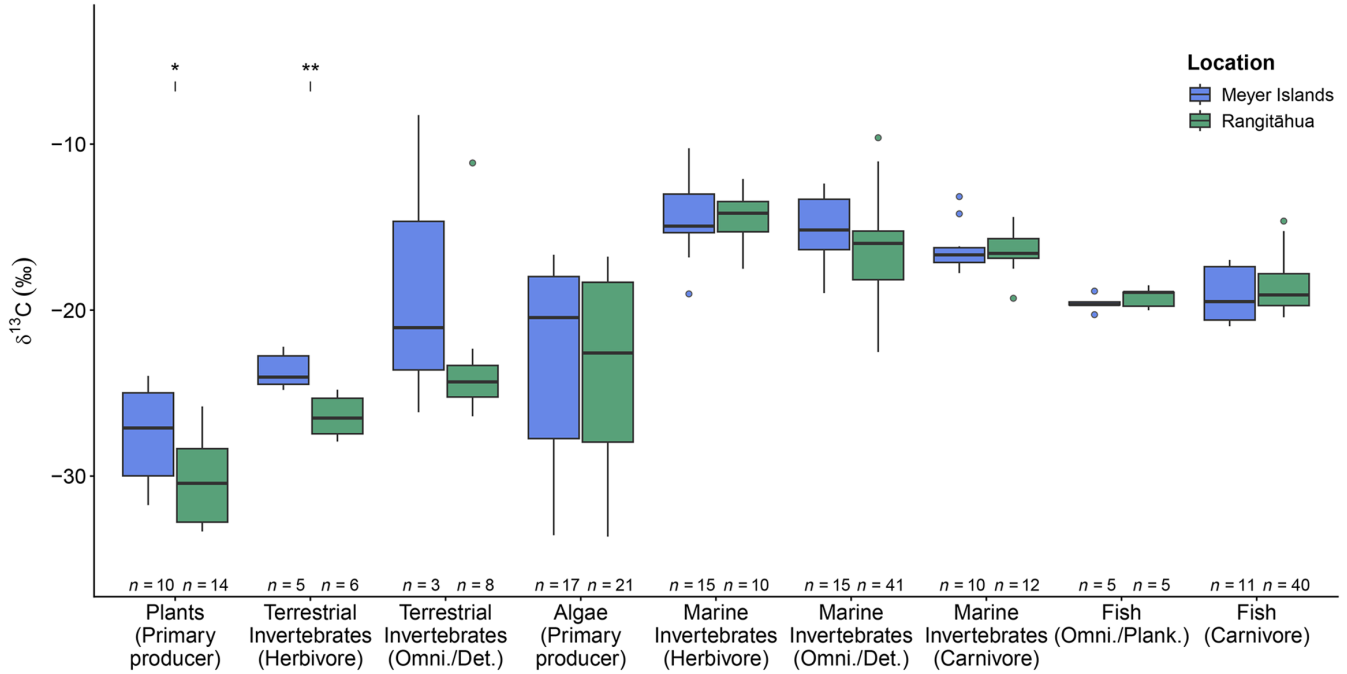

FIGURE 4 Comparison of $\delta^{13}C$ values (‰) across trophic guilds within terrestrial and marine environments for specimens from Rangitāhua and the Meyer Islands. Boxplots show the distribution of $\delta^{13}C$ for each guild, grouped by terrestrial or marine environment; the midline indicates the median, box limits represent the first and third quartiles (interquartile range), and whiskers extend to the smallest/largest values up to 1.5 times the interquartile range; outliers beyond the 1.5 interquartile range are shown as solid circles. Trophic guilds are ordered from lower to higher trophic levels. Sample sizes are indicated below each group. Paired Wilcoxon signed-rank tests were used to assess differences between islands within each guild; only statistically valid comparisons are shown. *$p < 0.05$; **$p < 0.01$. Det., detritivores; Omni., omnivores; Plank., planktivores.

$\delta^{13}C$ values also declined from 1887 to 2023, with values of Periods 1 ($W = 471$, $p < 0.0001$) and 2 ($W = 1943$, $p < 0.0001$) greater than Period 4 (Figure 6B).

There were no significant changes in $\delta^{15}N$ values of terrestrial plant leaves from Rangitāhua from 1854 to 2023 ($W \geq 15$, $p \geq 0.06$; Figure 6C) or terrestrial bird feathers from 1887 to 2023 ($W \geq 5$, $p \geq 0.056$; Figure 6D). However, $\delta^{15}N$ values of terrestrial plant leaves on the Meyer Islands in Period 4 were greater than those of the same species on Rangitāhua in Period 1 ($W = 181$, $p < 0.01$; median: Meyer Islands = 11.85, Rangitāhua = −0.73; Figure 6).

DISCUSSION

Our comparison of ecosystem components between two islands with contrasting histories of human-mediated changes underscores the role that seabirds perform in nutrient enrichment of island and nearshore food webs (Benkwitt et al., 2025; Mulder, Anderson, et al., 2011; Rankin & Jones, 2021). By comparing Rangitāhua, with depleted seabird populations, and the Meyer Islands, with dense seabird populations (Hypothesis 1), we aimed to document the differing footprint of seabird nutrient subsidies on soil chemistry, food web function, and connectivity between terrestrial and marine habitats. By tracking changes in stable isotope values of historical specimens from Rangitāhua (Hypothesis 2), we explored the temporal legacy of seabird population decline following invasive mammal introductions. By combining ecological, isotopic, and chemical lines of evidence, our study offers new insights into major agents of global change on island ecosystems, especially the ecological legacies of loss of seabird-derived nutrients.

Stable isotope and soil nutrient differences between an invaded and an uninvaded island: Spatial evidence for seabird-driven nutrient enrichment

Soils from the Meyer Islands had high concentrations of total N and P, as well as a highly acidic pH, typical of islands with dense seabird colonies worldwide (Benkwitt et al., 2021; Erskine et al., 1998; Wilder et al., 2022). Soil total P concentrations were much higher on the Meyer Islands than on Rangitāhua. The Meyer

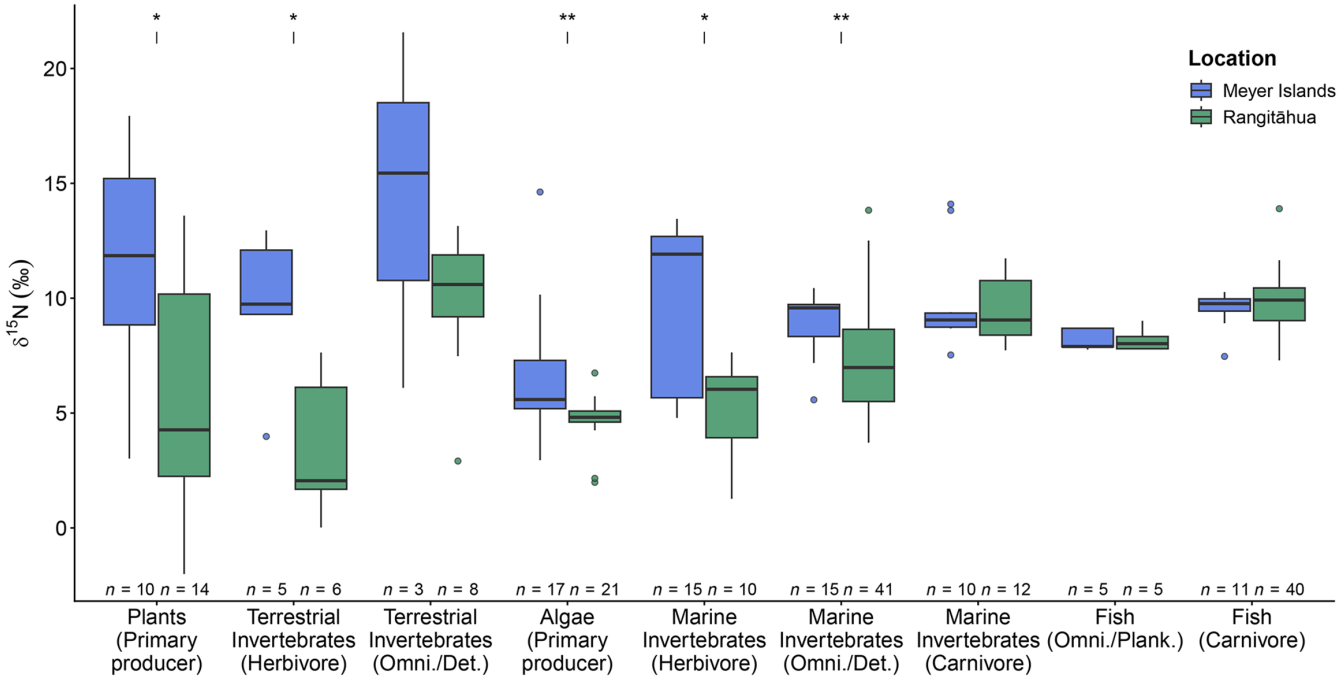

FIGURE 5 Comparison of $\delta^{15}N$ values across trophic guilds within terrestrial and marine environments for specimens from Rangitāhua and the Meyer Islands. Boxplots show the distribution of $\delta^{15}N$ for each guild, grouped by terrestrial or marine environment; the midline indicates the median, box limits represent the first and third quartiles (interquartile range), and whiskers extend to the smallest/largest values up to 1.5 times the interquartile range; outliers beyond the 1.5 interquartile range are shown as solid circles. Trophic guilds are ordered from lowest to highest trophic levels. Sample sizes are indicated below each group. Paired Wilcoxon signed-rank tests were used to assess differences between islands within each guild; only statistically valid comparisons are shown. $^{*}p < 0.05$; $^{**}p < 0.01$.

Islands, influenced by dense seabird colonies and never supporting established invasive mammals, had higher soil P concentrations and consistent $\delta^{15}N$ and $\delta^{13}C$ enrichment across marine and terrestrial trophic levels compared with Rangitāhua, where seabird colonies were exterminated. Although these islands differ in size, geology, and vegetation (de Lange, 2011), they lie <2 km apart and share near-identical marine environments. Given this similarity offshore, the elevated $\delta^{13}C$ and $\delta^{15}N$ values across multiple taxa on the Meyer Islands are best explained by seabird abundance rather than habitat differences. These inter-island contrasts mirror findings from other archipelagos where invasive mammals have suppressed seabirds, leading to nutrient depletion, isotopic declines, and simplified food webs (Benkwitt et al., 2021; Graham et al., 2018; Mulder, Anderson, et al., 2011).

Higher $\delta^{13}C$ values on the Meyer Islands likely reflect seabird-driven soil nutrient enrichment from guano. Elevated soil N and P can reduce stomatal conductance and discrimination against ^{13}C, leading to higher plant $\delta^{13}C$ (Dercon et al., 2006). The consistent differences in $\delta^{13}C$ values in the same plant species between the Meyer Islands and Rangitāhua support the use of $\delta^{13}C$ as an indicator of seabird-derived nutrients. Isotopic values are also shaped by local factors such as light (canopy plants showing less negative $\delta^{13}C$ than forest-floor plants; Berry et al., 1997) and moisture stress with drier sites having higher $\delta^{13}C$ in C_3 plants; Prentice et al. (2011) and differences in microclimate (e.g., rainfall and soil depth), as well as potential sampling variation. Nevertheless, the systematic enrichment across taxa and ecosystem compartments supports the role of seabird inputs in elevating baseline $\delta^{13}C$ through physiological mechanisms. Other studies have shown elevated $\delta^{13}C$ values in consumers in seabird-influenced ecosystems for example, in lizards (Barrett et al., 2005); in invertebrates (Hawke & Clark, 2010); and in mice (Bicknell et al., 2020), likely resulting from direct assimilation of marine-derived carbon via feeding on seabirds, their guano, prey spills, or associated carrion.

The mean foliar $\delta^{15}N$ value in plants sampled on Rangitāhua in 2023 (7.33‰ ± 4.88‰) exceeded a global mean (0.9‰) but did not exceed its upper 95% CI (i.e., 8.7‰; Craine et al., 2015). However, the mean foliar $\delta^{15}N$ value for the same species sampled on the Meyer Islands in the same year (11.40‰ ± 4.87‰) exceeded both the global mean and its upper 95% CI (Craine et al., 2015). These results are consistent with those from other islands, where seabirds can elevate $\delta^{15}N$ values of

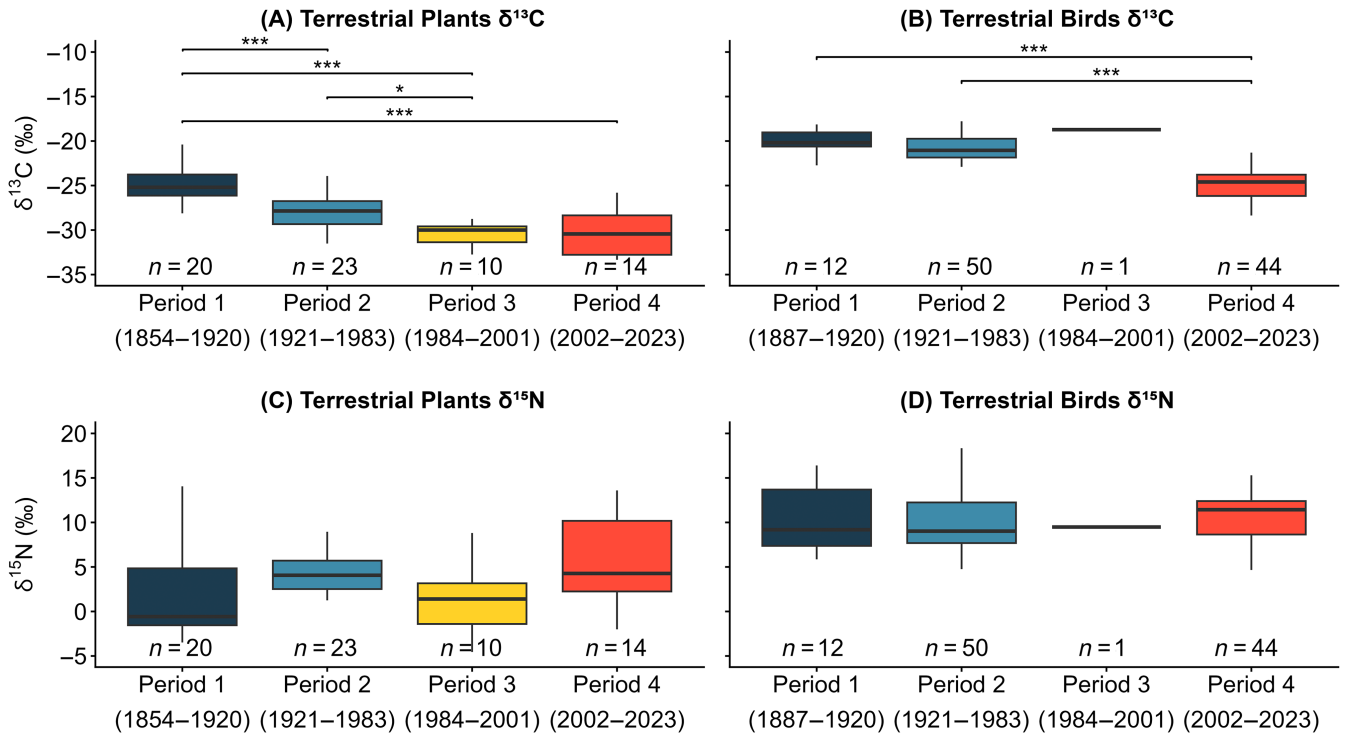

FIGURE 6 Temporal variation in (A), (B) $\delta^{13}C$ and (C), (D) $\delta^{15}N$ values for terrestrial plants (1854–2023) and forest birds (1887–2023) on Rangitāhua across historical collection periods. The $\delta^{13}C$ and $\delta^{15}N$ values are shown as boxplots grouped by time period; the midline indicates the median, box limits represent the first and third quartiles (interquartile range), and whiskers extend to the smallest/largest values up to 1.5 times the interquartile range. Sample sizes per group are indicated below each box. Statistical significance between periods was tested using pairwise Wilcoxon rank-sum tests with Bonferroni correction for multiple comparisons. Significance codes: ***$p < 0.001$; *$p < 0.05$.

island soils and vegetation by 10‰–20‰, with $\delta^{13}C$ values responding indirectly through nutrient-mediated plant physiological changes (Anderson & Polis, 1998; Barrett et al., 2005; Bokhorst et al., 2019; Estupiñán-Montaño et al., 2022; Graham et al., 2018). Increased $\delta^{15}N$ values in the terrestrial biota of rat-free, seabird-dominated islands such as the Meyer Islands has also been noted for temperate Aotearoa New Zealand islands (Jones, 2010; Markwell & Daugherty, 2003) and tropical Indian Ocean islands (Benkwitt et al., 2021). Higher $\delta^{13}C$ and $\delta^{15}N$ values in soils and biota on the Meyer Islands were significant only at the base of the terrestrial food web, but not at higher trophic levels (omnivores and detritivores). This aligns with evidence that primary producers and baseline consumers best reflect nutrient enrichment, while omnivores and predators show greater isotopic variability due to dietary generalism (Bicknell et al., 2020; Caut et al., 2012). However, the absence of enrichment in higher trophic levels on the Meyer Islands contrasts with findings from other rat-free Aotearoa New Zealand islands where beetles, spiders, lizards, and birds all showed elevated $\delta^{15}N$ values (Hawke & Miskelly, 2009; Jones, 2010; Markwell & Daugherty, 2002).

Seabird-derived nutrient enrichment on the Meyer Islands extended offshore, with higher $\delta^{15}N$ values across three trophic levels compared with organisms near Rangitāhua. Such land–sea coupling has been documented, with allochthonous inputs enhancing nearshore productivity close to seabird islands (Graham et al., 2018; Healing et al., 2024; Hentati-Sundberg et al., 2020; McCauley et al., 2012; Young et al., 2011). Other studies have shown elevated $\delta^{15}N$ across trophic levels in nearshore habitats around islands never invaded by rats and with dense seabird communities compared with those near islands from which rats have been eradicated. For example, six species of macroalgae all had higher $\delta^{15}N$ values around warm temperate islands in Aotearoa New Zealand that had never been invaded by rats (Rankin & Jones, 2021), while turf algae, macroalgae, and herbivorous reef fish in the Chagos Archipelago showed the same pattern (Benkwitt et al., 2021; Graham et al., 2018). In contrast, $\delta^{13}C$ values in marine taxa in our study did not differ between islands, likely because marine producers assimilate carbon from a variety of carbon sources in seawater, which are not strongly influenced by seabirds. Overall, our study suggests $\delta^{15}N$ is a more sensitive tracer of land–sea nutrient coupling in marine systems.

Change in the Rangitāhua ecosystem over time

Carbon isotope responses: A physiological proxy for nutrient loss

Carbon isotope values ($\delta^{13}C$) in land plants and birds on Rangitāhua declined over 169 and 136 years respectively. The combined consequences of loss of seabirds and mammal invasions may have contributed to the decline. The loss of direct sources of marine C as seabird colonies were extirpated is unlikely to have had a strong influence on $\delta^{13}C$ values in land plants and birds, since the contribution of marine-derived CO_2 for local photosynthesis (c. −18‰ in petrel guano), even from high rates of guano input (e.g., c. 100 kg C ha^{-1} $year^{-1}$ on Rottnest island, Australia; Bancroft et al., 2005) is negligible relative to ambient atmospheric CO_2. On the other hand, loss of N inputs from guano may have slowed CO_2 release from the remineralization of soil organic matter (c. −25‰; Hawke & Vallance, 2015), and this, coupled with loss of soil organic matter due to trampling and erosion caused by high abundance of goats prior to 1981, may have driven the decline in $\delta^{13}C$ in terrestrial plants and birds. The legacy effects of loss of soil organic matter and that recolonization by seabirds has only begun in the last 20 years are likely reasons that there has been no reversal of the decline in $\delta^{13}C$ values in the most recent period.

Light availability determines $\delta^{13}C$ in leaves, with forest canopy leaves typically higher than those in understories (5‰–10‰ less negative) (Ehleringer et al., 1986; Ometto et al., 2006). The decline in $\delta^{13}C$ values in Rangitāhua plants over 169 years could have been a consequence of changing vegetation structure; denser canopies could have resulted in more shaded leaves among the species sampled, especially of understory woody species such as *Coprosma acutifolia* and *Piper excelsum*. The loss of seabird colonies, especially after Norway rat invasion in 1921, could have resulted in denser canopies and greater understory biomass because of the cessation of the intense disturbance regime seabirds cause around their colonies (Ellis, 2005). However, at the same time the seabird disturbance regime ceased, goats denuded understories on Rangitāhua and even browsed the canopies of trees (Gentry, 2013; Parkes, 1984). Invasive rats are likely to have further reduced understory biomass through consumption of seeds and seedlings (Shiels & Drake, 2015). The negative influences of invasive mammals on forest biomass would have increased light availability, probably more than counteracting any decline in light resulting from loss of seabird disturbances, in which case a long-term increase in $\delta^{13}C$ values might be expected—the opposite of what our study shows. A long-term decline in $\delta^{13}C$ values could also have been a consequence of reduced moisture stress in plants (e.g., Fessenden and Ehleringer, 2003), in turn affecting higher trophic levels. As with light, any alleviation of moisture stress that attended increased understory biomass after loss of seabird disturbance would have probably been more than counteracted by effects of goats causing loss of understory and canopy biomass, coupled with their trampling and erosion of litter, increasing moisture stress. If this was so, a long-term increase in $\delta^{13}C$ values might be expected, the opposite of what we found. We cannot exclude the possibility that biases in sampling could have resulted in the decline of $\delta^{13}C$ values with respect to both light and moisture stress as drivers, that is, if earlier collections were biased toward canopy leaves or drier sites and later collections to shaded leaves or moister sites.

Variations in emissions of volcanic or hydrothermal CO_2 are another potential driver of changes in $\delta^{13}C$ values on Rangitāhua. Fluctuations in volcanic activity on Mount Usu, Japan, resulted in soil CO_2 $\delta^{13}C$ values varying between −0.9‰ and −30.9‰ (Hernández et al., 2006) and volcanically derived CO_2 can influence vegetation $\delta^{13}C$ values (Holdaway et al., 2018). Volcanic activity on Rangitāhua has declined over the last c. 200 years, that is, two intense eruptions in the 19th century (1814, 1870) and two less intense eruptions since (1964, 2006; Shane & Wright, 2011) and the decline in $\delta^{13}C$ values in land plants and birds may have been influenced by declining volcanic activity on the island.

Global climate change affected the study site throughout the periods for which we have sample specimens. Although we controlled for the Seuss effect, increasing concentrations of atmospheric CO_2 could have reduced water-use efficiency and increased isotopic discrimination in the C_3 plants we sampled, leading to more negative $\delta^{13}C$ values (Beerling & Woodward, 1995; Farquhar et al., 1982; Farquhar & Lloyd, 1993). However, the expected magnitude of impact (~0.5‰–1‰; Schubert & Jahren, 2012) is much less than the decline in plant $\delta^{13}C$ values we found. Climate change-driven reductions in rainfall or humidity can reduce stomatal conductance and reduce discrimination against ^{13}C, resulting in less negative $\delta^{13}C$ values (Farquhar et al., 1989) but on Rangitāhua Island $\delta^{13}C$ values in plants became more negative over time, even though post-1930 rainfall records from the island show that periods of reduced rainfall have become more common, especially since 2000 (NIWA Data Portal). Hence, we conclude that climate change is unlikely to be a major driver of the changes we found in $\delta^{13}C$ in terrestrial plants.

The decline in $\delta^{13}C$ values in terrestrial birds on Rangitāhua over 136 years shows that change in $\delta^{13}C$

values is not limited to primary producers. It is possible that species such as the kākāriki (*Cyanoramphus novaezelandiae*) included in our study could assimilate marine-derived carbon through opportunistic consumption of seabird guano, carrion, or spilt prey (Hobson & Clark, 1992), as observed in *Cyanoramphus unicolor* on the Antipodes Islands (Green, 1999). However, such feeding is likely limited, making this pathway an unlikely explanation for the multi-species $\delta^{13}C$ decline observed in our study.

Instead, for most species, the $\delta^{13}C$ values in bird feathers reflects an integration of C sources from across the food web across the geographic range of the bird at the time feathers are regrown; for omnivorous terrestrial birds, this includes plant material and invertebrate prey across several trophic levels (Bearhop et al., 2002; Quillfeldt et al., 2008). Although more mobile species in our time series, such as tūī (*Prosthemadera novaeseelandiae*) and kākāriki could potentially visit and forage on the heavily seabird-influenced Meyer Islands in any period, their inclusion alongside more sedentary taxa (e.g., Eurasian blackbird, *Turdus merula* and song thrush, *Turdus philomelos*) did not obscure the declining trend. Declining $\delta^{13}C$ values in terrestrial birds therefore most likely reflect ecosystem-wide influences, such as either a decline in allochthonous nutrient subsidies or reduced volcanic activity on the island, rather than species-specific foraging behaviors or sampling artifacts.

Nitrogen isotope responses: Degradation and shifting baselines

We predicted that $\delta^{15}N$ values in the same plant species on Rangitāhua sampled over four periods between 1854 and the present would be high in the earliest period (Period 1) when seabirds were abundant, as they are in contemporary samples from the Meyer Islands, which have had continuously high seabird populations. Instead, $\delta^{15}N$ in plants from Rangitāhua in Period 1 was much lower than contemporary samples from the Meyer Islands with no significant change across any periods of differing seabird abundances and periods when goats were abundant on the island. The lack of an increase in $\delta^{15}N$ values in plants between the period of most extreme alteration of the island (extirpation of most seabirds and high goat abundance; Period 2, 1922–1981) and the present (c. 40 years after goat eradication and with seabird abundance growing 20 years after rat eradication) was not necessarily expected because $\delta^{15}N$ in plants on islands can increase within decades of rat eradication and subsequent recolonization by seabirds (Jones, 2010).

Several non-mutually exclusive explanations may account for the lack of change in Rangitāhua plant $\delta^{15}N$ values despite 169 years of drastic environmental change. Long-term goat impacts could explain the lack of difference in plant $\delta^{15}N$ values between Period 2, when goats were abundant, and the present. Goats alter N cycling directly, through feces and urine (enriching ^{15}N −3‰ to 10‰; Sutoh et al., 1987) and indirectly through selective browsing that reduces litter quality, trampling, and erosion of organic layers that disrupts soil mutualisms (Bardgett & Wardle, 2003; Kardol et al., 2014). The legacy of these effects can persist for decades (Bardgett & Wardle, 2003). Although plant $\delta^{15}N$ declined after goat removal from Hawaiian forest (Soper et al., 2024), the very high densities of goats on Rangitāhua (>1 ha^{-1}; Parkes, 1984) and their long residence time (187 years) may have resulted in stronger, enduring effects.

The lack of difference in plant $\delta^{15}N$ values between Periods 2–3 and the present, 20 years after rat and cat eradication and during seabird recovery, mirrors results from temperate New Zealand islands (13–217 ha) where plant, soil, and spider $\delta^{15}N$ values showed no significant increases 7–32 years after mammal eradication and seabird recolonization (Pascoe et al., 2025). In contrast, warm temperate islands in New Zealand showed significant plant $\delta^{15}N$ enrichment 12–22 years after rat eradication (Jones, 2010). On Rangitāhua, recolonizing seabirds could still be too sparse and patchy to yet strongly influence plant $\delta^{15}N$ (the area of Rangitāhua is an order of magnitude greater than the largest island in the study of Jones, 2010). Island size is a critical factor: stronger $\delta^{15}N$ enrichment has been documented on smaller tropical Indian Ocean islands (Benkwitt et al., 2021) and cool temperate islands in British Columbia (Obrist et al., 2022), where higher perimeter-to-area ratios facilitate nutrient penetration. This also explains why plant $\delta^{15}N$ values on Rangitāhua in period 1, despite high seabird numbers, were lower than in contemporary Meyer Islands plants.

The absence of plant $\delta^{15}N$ differences between Period 1 (1854–1920), when seabirds were abundant on Rangitāhua, and later periods, when seabirds were extirpated or beginning to recolonize, is difficult to explain. Early collections (Period 1) were primarily taxonomic, so samples may have been biased toward sites less influenced by seabirds, but this is uncertain. Herbarium storage could also have altered $\delta^{15}N$ through contamination or chemical treatments (Barrow et al., 2008), although such processes typically elevate rather than depress values, particularly in older specimens (Nielsen et al., 2017). Alternatively, plant $\delta^{15}N$ values in Period 1 may simply reflect weaker seabird influence on Rangitāhua ecosystems compared with the Meyer

Islands, which may therefore not be analogues of past or future Rangitāhua states. The lack of differences in plant $\delta^{15}N$ values in subsequent periods, especially when the island was heavily influenced by mammals, could be because of legacies of a lower-level seabird influence on Rangitāhua over millennia before invasions. In the early 1950s, when nearly all seabird colonies were extirpated, soil total N concentrations across Rangitāhua were 0.44% (mean among 30 samples <30 cm depth; Wright & Metson, 1959), hence they may not have been appreciably depleted during Periods 2 and 3 of our study. Moreover, even if seabird-enriched total N concentrations in soils had declined, plant $\delta^{15}N$ values increase with time as soil N is depleted and more recalcitrant forms of N are accessed from soil N pools (Hawke & Condron, 2014).

At higher trophic levels, there were no significant differences in terrestrial bird $\delta^{15}N$ values across the periods of our study. Our results support a view that ecosystem $\delta^{15}N$ values are an insufficiently sensitive indicator of response to the eradication of invasive mammals (Pascoe et al., 2025) and indeed may also be an inadequate indicator of the effects of mammal invasion on islands and resulting seabird extinctions.

CONCLUSIONS AND IMPLICATIONS

Our study provides new insights into the long-term ecological consequences of seabird loss and invasive mammal impacts on oceanic islands by integrating stable isotopes, chemical, and ecological data across space and time. Results support the hypothesis that seabird colonies drive nutrient enrichment of both terrestrial and nearshore marine ecosystems. On the Meyer Islands, with dense seabird populations, elevated $\delta^{15}N$ and $\delta^{13}C$ values across multiple trophic levels, along with high soil N and P concentrations, underscore the critical role of seabird-derived marine subsidies and the utility of stable isotopes—particularly $\delta^{15}N$—as tracers of sea–land nutrient coupling.

The usefulness of stable isotopes as proxies to track loss of these inputs over time was limited. Although $\delta^{15}N$ values in plants did not change, the consistent chronological decline of $\delta^{13}C$ values in Rangitāhua terrestrial plants and birds could be due to sustained loss of seabird-derived nutrients, also influenced by volcanic activity. This trend has not reversed following eradication of goats in 1984 and cats and rodents by 2004.

Two major disruptions shaped Rangitāhua: seabird extirpation by predators, and vegetation and soil degradation by goats. Although these mammals are gone, seabirds have yet to reach population sizes that restore ecosystem-scale nutrient flows. Studies on small islands show $\delta^{15}N$ recovery within as little as a decade of eradication of predatory mammals (e.g., Jones, 2010) but others document persistent suppression 16 years after eradication (Pascoe et al., 2025). Our data from 41 years after goats were eradicated and 21 years after predatory mammals were eradicated from a large oceanic island underscore that recovery is neither rapid nor uniform.

Whether Rangitāhua will return to a pre-invasion state or shift to a novel one remains unclear. Pre-invasion plant $\delta^{15}N$ values differed from those of the contemporary Meyer Islands, suggesting these small islands may be an unsuitable analogue or baseline for the much larger Rangitāhua, either in the past or in the future. Differences could reflect specimen preservation or sampling bias, but more likely reflect intrinsic ecological contrasts between the archipelago's small islets and its main island.

The slow process of recovery of ecosystem functions after mammal eradication on Rangitāhua likely reflects its size, its degraded habitats, the disturbance regimes (volcanic and seismic events, cyclones), climate change, and the life history traits of seabirds that formerly bred there. After successful mammal eradications on isolated, oceanic islands, re-establishing seabird-mediated nutrient flows may take much longer than 20 years. Restoring seabird-driven ecosystem functions on these islands may require not only eradicating invasive mammals but also actively facilitating recolonization of some seabird species.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data in this research were collected under Ngāti Kuri leadership from islands over which they hold customary authority. The authors recognize Ngāti Kuri sovereignty and authority to control data about their lands under the CARE Principles for Indigenous Data Governance (https://www.gida-global.org/care). Accordingly, the underlying data are considered sensitive and are not publicly available. Qualified researchers may request access through Te Ara Whānui Research Centre (Ngāti Kuri Trust Board), where requests will be evaluated in accordance with Ngāti Kuri governance processes and all researchers involved. All scripts used for data processing and analysis (Klemm, 2026) are available from Zenodo: https://doi.org/10.5281/zenodo.20788131.

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REFERENCES

Anderson, A. 1980. "The Archaeology of Raoul Island (Kermadecs) and Its Place in the Settlement History of Polynesia." *Archaeology & Physical Anthropology in Oceania* 15: 131–141.

Anderson, W. B., and G. A. Polis. 1998. "Marine Subsidies of Island Communities in the Gulf of California: Evidence from Stable Carbon and Nitrogen Isotopes." *Oikos* 81: 75–80.

Anderson, W. B., and G. A. Polis. 1999. "Nutrient Fluxes from Water to Land: Seabirds Affect Plant Nutrient Status on Gulf of California Islands." *Oecologia* 118: 324–332.

Bancroft, W. J., M. J. Garkaklis, and D. Roberts. 2005. "Burrow Building in Seabird Colonies: A Soil-Forming Process in Island Ecosystems." *Pedobiologia* 49(2): 149–165.

Bardgett, R. D., and D. A. Wardle. 2003. "Herbivore-Mediated Linkages Between Above Ground and Below Ground Communities." *Ecology* 84: 2258–68.

Barrett, K., W. B. Anderson, D. A. Wait, L. L. Grimser, G. A. Polis, and M. D. Rose. 2005. "Marine Subsidies Alter the Diet and Abundance of Insular and Coastal Lizard Populations." *Oikos* 109: 145–153.

Barrow, L. M., K. A. Bjorndal, and K. J. Reich. 2008. "Effects of Preservation Method on Stable Carbon and Nitrogen Isotope Values." *Physiological and Biochemical Zoology* 81: 688–693.

Bearhop, S., S. Waldron, S. C. Votier, and R. W. Furness. 2002. "Factors that Influence Assimilation Rates and Fractionation of Nitrogen and Carbon Stable Isotopes in Avian Blood and Feathers." *Physiological and Biochemical Zoology* 75: 451–58.

Beerling, D. J., and F. I. Woodward. 1995. "Leaf Stable Carbon Isotope Composition Records Increased Water-Use Efficiency of C3 Plants in Response to Atmospheric CO_2 Enrichment." *Functional Ecology* 9: 394–401.

Bellingham, P. J., D. R. Towns, E. K. Cameron, J. J. Davis, D. A. Wardle, J. M. Wilmshurst, and C. P. Mulder. 2010. "New Zealand Island Restoration: Seabirds, Predators, and the Importance of History." *New Zealand Journal of Ecology* 34: 115–136.

Bellingham, P. J., S. K. Wiser, A. E. Wright, E. K. Cameron, and L. J. Forester. 2010. "Disperser Communities and Legacies of Goat Grazing Determine Forest Succession on the Remote Three Kings Islands, New Zealand." *Biological Conservation* 143: 926–938.

Benkwitt, C. E., A. Zora, A. Ebrahim, R. Govinden, I. D. Lange, S. Evans, M. Schulze, E. Cotton, L. Bennett, and N. A. J. Graham. 2025. "Nutrient Connectivity Via Seabirds Enhances Dynamic Measures of Coral Reef Ecosystem Function." *PLoS Biology* 23: e3003222.

Benkwitt, C. E., R. L. Gunn, M. Le Corre, P. Carr, and N. A. J. Graham. 2021. "Rat Eradication Restores Nutrient Subsidies from Seabirds Across Terrestrial and Marine Ecosystems." *Current Biology* 31: 2704–11.

Berry, S. C., G. T. Varney, and L. B. Flanagan. 1997. "Leaf δ13C in *Pinus resinosa* Trees and Understory Plants: Variation Associated with Light and CO_2 Gradients." *Oecologia* 109: 499–506.

Bicknell, A. W. J., B. W. Walker, T. Black, J. Newton, J. M. Pemberton, R. Luxmoore, R. Inger, and S. C. Votier. 2020. "Stable Isotopes Reveal the Importance of Seabirds and Marine Foods in the Diet of St Kilda Field Mice." *Scientific Reports* 10: 6088.

Bokhorst, S., P. Convey, and R. Aerts. 2019. "Nitrogen Inputs by Marine Vertebrates Drive Abundance and Richness in Antarctic Terrestrial Ecosystems." *Current Biology* 29: 1721–27.

Brook, F. J. 1998. "Stratigraphy and Paleontology of Pleistocene Submarine Volcanic-Sedimentary Sequences at the Northern Kermadec Islands." *Journal of the Royal Society of New Zealand* 28: 235–257.

Brothers, R. N., and E. J. Searle. 1970. "The Geology of Raoul Island, Kermadec Group, Southwest Pacific." *Bulletin Volcanologique* 34: 7–37.

Brown, D., and L. Baker. 2009. "The Lord Howe Island Biodiversity Management Plan: An Integrated Approach to Recovery Planning." *Ecological Management & Restoration* 10: 70–78.

Bury, S. J., K. J. Peters, A. J. M. Sabadel, G. K. St John, C. Trueman, M. B. Wunder, M. R. D. Cobain, et al. 2024. "Southern Ocean Humpback Whale Trophic Ecology. I. Combining Multiple Stable Isotope Methods Elucidates Diet, Trophic Position and Foraging Areas." *Marine Ecology Progress Series* 734: 123–155.

Caut, S., E. Angulo, B. Pisanu, L. Ruffino, L. Faulquier, O. Lorvelec, J.-L. Chapuis, M. Pascal, E. Vidal, and F. Courchamp. 2012. "Seabird Modulations of Isotopic Nitrogen on Islands." *PLoS One* 7: e39125.

Cheeseman, T. F. 1887. "Kermadec Islands 1887." Auckland. Auckland Museum Manuscripts Collection 58-20-2.

Chinn, W. G. H. 2011. "The Kermadec Islands Terrestrial Invertebrate Fauna: Observations on the Taxonomic Distribution and Island Biogeography." *Bulletin of the Auckland Museum* 20: 443–462.

Chynoweth, M. W., C. M. Litton, C. A. Lepczyk, S. C. Hess, and S. Cordell. 2013. "Biology and Impacts of Pacific Island Invasive Species. 9. *Capra hircus*, the Feral Goat (Mammalia: Bovidae)." *Pacific Science* 67: 141–156.

Coblentz, B. E. 1978. "The Effects of Feral Goats (*Capra hircus*) on Island Ecosystems." *Biological Conservation* 13: 279–286.

Courchamp, F., J. L. Chapius, and M. Pascal. 2003. "Mammal Invaders on Islands: Impact, Control and Control Impact." *Biological Reviews* 78: 347–383.

Craine, J. M., E. N. J. Brookshire, M. D. Cramer, N. J. Hasselquist, K. Koba, E. Marin-Spiotta, and L. Wang. 2015. "Ecological Interpretations of Nitrogen Isotope Ratios of Terrestrial Plants and Soils." *Plant and Soil* 396: 1–26.

Croxall, J. P., S. H. M. Butchart, B. Lascalles, A. J. Stattersfield, B. Sullivan, A. Symes, and P. Taylor. 2012. "Seabird Conservation Status, Threats and Priority Actions: A Global Assessment." *Bird Conservation International* 22: 1–34.

de la Luz, J. L. L., J. P. Rebman, and T. Oberbauer. 2003. "On the Urgency of Conservation on Guadalupe Island, Mexico: Is It a Lost Paradise?" *Biodiversity and Conservation* 12: 1073–82.

de Lange, P. 2011. "Kermadec Biodiscovery Expedition 2011 (Part II – The Meyers)." *Newsletter of the New Zealand Plant Conservation Network* 93: 3–8.

de Lima Martins, G. S., E. M. Rodrigues, M. D. Costa, A. N. da Rocha Campos, and M. R. Tótola. 2021. "A Not So Cool Harlley's Legacy: The Catastrophic Human-Made Trindade Island Devastation and its Recovery." *Applied Soil Ecology* 167: 104105.

Dercon, G., E. Clymans, J. Diels, R. Merckx, and J. Deckers. 2006. "Differential 13C Isotopic Discrimination in Maize at Varying Water Stress and at Low to High Nitrogen Availability." *Plant and Soil* 282: 313–326.

Duda, M. P., J. R. Glew, N. Michelutti, G. J. Robertson, W. A. Montevecchi, J. A. Kissinger, D. C. Eickmeyer, J. M. Blais, and J. P. Smol. 2020. "Long-Term Changes in Terrestrial Vegetation Linked to Shifts in a Colonial Seabird Population." *Ecosystems* 23: 1643–56.

Duffy, C., and S. T. Ahyong. 2015. "Annotated Checklist of the Marine Flora and Fauna of the Kermadec Islands Marine Reserve and Northern Kermadec Ridge, New Zealand." *Bulletin of the Auckland Museum* 20: 19–124.

Edgar, G. J., R. D. Stuart-Smith, T. J. Willis, S. Kininmonth, S. C. Baker, S. Banks, N. S. Barrett, et al. 2014. "Global Conservation Outcomes Depend on Marine Protected Areas with Five Key Features." *Nature* 506: 216–220.

Edwards, M. S., T. F. Turner, and Z. D. Sharp. 2002. "Short- and Long-Term Effects of Fixation and Preservation on Stable Isotope Values (δ13C, δ15N, δ34S) of Fluid-Preserved Museum Specimens." *Copeia* 4: 1106–12.

Ehleringer, J. R., C. B. Field, Z.-F. Lin, and C.-Y. Kuo. 1986. "Leaf Carbon Isotope and Mineral Composition in Subtropical Plants Along an Irradiance Cline." *Oecologia* 70: 520–26.

Ellis, J. C. 2005. "Marine Birds on Land: A Review of Plant Biomass, Species Richness, and Community Composition in Seabird Colonies." *Plant Ecology* 181: 227–241.

Erskine, P. D., D. M. Bergstrom, S. Schmidt, G. R. Stewart, C. E. Tweedie, and J. D. Shaw. 1998. "Subantarctic Macquarie Island: A Model Ecosystem for Studying Animal-Derived Nitrogen Sources Using 15N Natural Abundance." *Oecologia* 117: 187–193.

Estupiñán-Montaño, C., M. J. Zetina-Rejón, F. Galván-Magaña, A. Delgado-Huertas, F. R. Elorriaga-Verplancken, C. J. Polo-Silva, J. Rojas-Cundumí, D. J. Villalobos-Ramírez, and A. Sánchez-González. 2022. "Trophic Connectivity Between the Terrestrial and Marine Ecosystems of Malpelo Island, Colombia, Evaluated Through Stable Isotope Analysis." *Marine Biology* 170: 11.

Farquhar, G. D., and J. Lloyd. 1993. "Carbon and Oxygen Isotope Effects in the Exchange of Carbon Dioxide Between Terrestrial Plants and the Atmosphere." In *Stable Isotopes and Plant Carbon Water Relations*, edited by J. R. Ehleringer, A. E. Hall, and G. D. Farquhar, 47–70. New York: Academic Press.

Farquhar, G. D., J. R. Ehleringer, and K. T. Hubick. 1989. "Carbon Isotope Discrimination and Photosynthesis." *Annual Review of Plant Biology* 40: 503–537.

Farquhar, G. D., M. H. O'Leary, and J. A. Berry. 1982. "On the Relationship Between Carbon Isotope Discrimination and the Intercellular Carbon Dioxide Concentration in Leaves." *Functional Plant Biology* 9: 121–137.

Fessenden, J. E., and J. R. Ehleringer. 2003. "Temporal Variation in δ13C of Ecosystem Respiration in the Pacific Northwest: Links to Moisture Stress." *Oecologia* 136: 129–136.

Fry, B., D. M. Baltz, M. C. Benfield, J. W. Fleeger, A. Gace, H. L. Hass, and Z. J. Quiñones-Rivera. 2003. "Stable Isotope Indicators of Movement and Residency for Brown Shrimp (*Farfantepenaeus aztecus*) in Coastal Louisiana Marshscapes." *Estuaries* 26: 82–97.

Fukami, T., D. A. Wardle, P. J. Bellingham, C. P. H. Mulder, D. R. Towns, G. W. Yeates, K. I. Bonner, M. S. Durrett, M. N. Grant-Hoffman, and W. M. Williamson. 2006. "Above- and Below-Ground Impacts of Introduced Predators in Seabird-Dominated Island Ecosystems." *Ecology Letters* 9: 1299–1307.

Furey, L., C. Ross-Sheppard, and K. E. Prickett. 2015. "Obsidian from Macauley Island: A New Zealand Connection." *Bulletin of the Auckland Musuem* 20: 511–18.

Gaskin, C. P. 2011. "Seabirds of the Kermadec Region: Their Natural History and Conservation." In *Science for Conservation*, Vol. 316. Wellington: Department of Conservation.

Gentry, S. 2013. *Raoul and the Kermadec Islands*. Wellington: Steele Roberts Publishers.

Graham, N. A., S. K. Wilson, P. Carr, A. S. Hoey, S. Jennings, and M. A. MacNeil. 2018. "Seabirds Enhance Coral Reef Productivity and Functioning in the Absence of Invasive Rats." *Nature* 559: 250–53.

Green, T. C. 1999. "Aspects of the Ecology of Antipodes Island Parakeet (*Cyanoramphus unicolor*) and Reischek's Parakeet (*C. novaezelandiae hochstetteri*) on Antipodes Island, October – November 1995." *Notornis* 46: 301–310.

Hamann, O. 1993. "On Vegetation Recovery, Goats and Giant Tortoises on Pinta Island, Galápagos, Ecuador." *Biodiversity and Conservation* 2: 138–151.

Hata, K., M. Kohri, S. Morita, S. Hiradate, and N. Kachi. 2014. "Complex Interrelationships Among Aboveground Biomass, Soil Chemical Properties, and Events Caused by Feral Goats and Their Eradication in a Grassland Ecosystem of an Island." *Ecosystems* 17: 1082–94.

Hawke, D. J. 2004. "Maximum Possible Age of a Petrel Breeding Colony near Punakaiki (South Island, New Zealand) from Radiocarbon and Stable Isotope Analysis of Soil." *Journal of the Royal Society of New Zealand* 34: 1–7.

Hawke, D. J., and C. M. Miskelly. 2009. "13C and 15N Enrichment in Snipe (*Coenocorypha* spp.) from Islands Across the New Zealand Biogeographic Region." *Journal of the Royal Society of New Zealand* 39: 35–42.

Hawke, D. J., and J. M. Clark. 2010. "Isotopic Signatures (13C/12C; 15N/14N) of Blue Penguin Burrow Soil Invertebrates: Carbon Sources and Trophic Relationships." *New Zealand Journal of Zoology* 37: 313–321.

Hawke, D. J., and J. R. Vallance. 2015. "Microbial Carbon Concentration in Samples of Seabird and Non-Seabirdforest Soil: Implications for Leaf Litter Cycling." *Pedobiologia* 58(1): 33–39.

Hawke, D. J., and L. M. Condron. 2014. "Mobilisation of Recalcitrant Soil Nutrient Fractions Supports Foliar Nitrogen to Phosphorus Homeostasis in a Seabird Soil." *Plant and Soil* 385: 77–86.

Healing, S., C. E. Benkwitt, R. E. Dunn, and N. A. J. Graham. 2024. "Seabird-Vectored Pelagic Nutrients Integrated Into Temperate Intertidal Rocky Shores." *Frontiers in Marine Science* 11: 1343966.

Hentati-Sundberg, J., C. Raymond, M. Sköld, O. Svensson, B. Gustafsson, and S. Bonaglia. 2020. "Fueling of a Marine-Terrestrial Ecosystem by a Major Seabird Colony." *Scientific Reports* 10: 15455.

Hernández, P. A., K. Notsu, H. Okada, T. Mori, M. Sato, F. Barahona, and N. M. Pérez. 2006. "Diffuse Emission of CO_2 from Showa-Shinzan, Hokkaido, Japan: A Sign of Volcanic Dome Degassing." *Pure and Applied Geophysics* 163: 869–881.

Hilderbrand, G. V., T. A. Hanley, C. T. Robbins, and C. C. Schwartz. 1999. "Role of Brown Bears (*Ursus arctos*) in the Flow of Marine Nitrogen Into a Terrestrial Ecosystem." *Oecologia* 121: 546–550.

Hilton, M. G., D. R. Thompson, P. M. Sagar, R. J. Cuthbert, Y. Cherel, and S. J. Bury. 2006. "A Stable Isotopic Investigation Into the Causes of Decline in a Sub-Antarctic Predator, the Rockhopper Penguin *Eudyptes chrysocome*." *Global Change Biology* 12: 611–625.

Hipfner, J. M., M. J. F. Lemon, and M. S. Rodway. 2010. "Introduced Mammals, Vegetation Changes and Seabird Conservation on the Scott Islands, British Columbia, Canada." *Bird Conservation International* 20: 295–305.

Hobson, K. A., and R. G. Clark. 1992. "Assessing Avian Diets Using Stable Isotopes 1: Turnover of 13C in Tissues." *Condor* 94: 181–88.

Holdaway, R. N., B. Duffy, and B. Kennedy. 2018. "Evidence for Magmatic Carbon Bias in 14C Dating of the Taupo and Other Major Eruptions." *Nature Communications* 9: 4110.

Iredale, T. 1910. "Birdlife on the Kermadec Islands." *Emu* 10: 2–16.

Jones, H. P. 2010. "Seabird Islands Take Mere Decades to Recover Following Rat Eradication." *Ecological Applications* 20: 2075–80.

Jones, H. P., J. Appoo, C. E. Benkwitt, S. B. Borrelle, R. E. Dunn, H. E. Epstein, L. A. Fowlke, et al. 2025. "The Circular Seabird Economy Is Critical for Oceans, Islands and People." *Nature Reviews Biodiversity* 1: 689–702.

Kardol, P., I. A. Dickie, M. G. St. John, S. W. Husheer, K. I. Bonner, P. J. Bellingham, and D. A. Wardle. 2014. "Soil-Mediated Effects of Invasive Ungulates on Native Tree Seedlings." *Journal of Ecology* 102: 622–631.

Keeling, C. D. 1979. "The Suess Effect: 13Carbon-14Carbon Interrelations." *Environment International* 2: 229–300.

Klemm, M. 2026. "Marina-Klemm/StableIsotopesAnalysis_Rangitahua: SIAAnalysis (Version SIAAnalysis)." Computer Software. Zenodo. https://doi.org/10.5281/zenodo.20788131.

Kolb, G. S., H. S. Young, and W. B. Anderson. 2011. "Effects of Seabirds on Island Consumers." In *Seabird Islands: Ecology Invasions, and Restoration*, edited by C. P. H. Mulder, W. B. Anderson, D. R. Towns, and P. J. Bellingham, 212–241. New York: Oxford University Press.

Lorrain, A., H. Pethybridge, N. Cassar, A. Receveur, V. Allain, N. Bodin, L. Bopp, et al. 2020. "Trends in Tuna Carbon

Isotopes Suggest Global Changes in Pelagic Phytoplankton Communities." *Global Change Biology* 26: 458–470.

MacGillivray, J. 1854. *Journal of the Voyage of HMS Herald*. Kew, London: The National Archives (formerly Public Record Office).

Markwell, T. J., and C. H. Daugherty. 2002. "Invertebrate and Lizard Abundance Is Greater on Seabird-Inhabited Islands than on Seabird-Free Islands in the Marlborough Sounds, New Zealand." *Ecoscience* 9: 293–99.

Markwell, T. J., and C. H. Daugherty. 2003. "Variability in N, C and Kjeldahl Nitrogen of Soils from Islands with and Without Seabirds in the Marlborough Sounds, New Zealand." *New Zealand Journal of Ecology* 27: 25–30.

Matisoo-Smith, E., D. G. Sutton, T. N. Ladefoged, D. M. Lambert, and J. S. Allen. 1999. "Prehistoric Mobility in Polynesia: mtDNA Variation in *Rattus exulans* from the Chatham and Kermadec Islands." *Asian Perspectives* 38: 186–199.

McCauley, D. J., P. A. DeSalles, H. S. Young, R. B. Dunbar, R. Dirzo, M. M. Mills, and F. Micheli. 2012. "From Wing to Wing: The Persistence of Long Ecological Interaction Chains in less-Disturbed Ecosystems." *Scientific Reports* 2: 409.

Merton, D. V. 1970. "Kermadec Islands Expedition Reports: A General Account of Birdlife." *Notornis* 17: 147–199.

Minagawa, M., and E. Wada. 1984. "Stepwise Enrichment of 15N Along Food Chains: Further Evidence and the Relation Between δ15N and Animal Age." *Geochimica et Cosmochimica Acta* 48: 1135–40.

Moss, B. 2017. "Marine Reptiles, Birds and Mammals and Nutrient Transfers Among the Seas and the Land: An Appraisal of Current Knowledge." *Journal of Experimental Marine Biology and Ecology* 492: 63–80.

Mulder, C. P. H., H. Jones, K. Kameda, C. Palmborg, S. Schmidt, J. Ellis, J. Orrock, et al. 2011. "Impacts of Seabirds on Plant and Soil Properties." In *Seabird Islands: Ecology Invasions, and Restoration*, edited by C. P. H. Mulder, W. B. Anderson, D. R. Towns, and P. J. Bellingham, 135–176. New York: Oxford University Press.

Mulder, C. P. H., W. B. Anderson, D. R. Towns, and P. J. Bellingham. 2011. *Seabird Islands: Ecology, Invasion and Restoration*. New York: Oxford University Press.

Nielsen, T. F., J. R. Larsen, A. Michelsen, and H. H. Bruun. 2017. "Are Herbarium Mosses Reliable Indicators of Historical Nitrogen Deposition?" *Environmental Pollution* 231: 1201–7.

Obrist, D. S., O. T. Fitzpatrick, N. E. M. Brown, P. J. Hanly, W. Nijland, L. Y. Reshitnyk, S. B. Wickham, C. T. Darimont, J. D. Reynolds, and B. M. Starzomski. 2022. "Scale-Dependent Effects of Marine Subsidies on the Island Biogeographic Patterns of Plants." *Ecology and Evolution* 12: e9270.

Ohashi, H., H. Kato, M. Murao, H. Kato, K. Kawakami, H. Kurokawa, M. Oguro, et al. 2024. "Historic Deforestation and Non-Native Plant Invasions Determine Vegetation Trajectories Across an Oceanic Archipelago." *Applied Vegetation Science* 27: e12767.

Oliver, W. R. B. 1910. "The Vegetation of the Kermadec Islands." *Transactions and Proceedings of the New Zealand Institute* 42: 112–175.

Ometto, J. P. H. B., J. R. Ehleringer, T. F. Domingues, J. A. Berry, F. Y. Ishida, E. Mazzi, N. Higuchi, L. B. Flanagan, G. B. Nardoto, and L. A. Martinelli. 2006. "The Stable Carbon and Nitrogen Isotopic Composition of Vegetation in Tropical Forests of the Amazon Basin, Brazil." *Biogeochemistry* 79: 251–274.

Ortiz-Catedral, L., S. M. H. Ismar, K. Baird, D. H. Brunton, and M. E. Haubner. 2009. "Recolonization of Raoul Island by Kermadec Red-Crowned Parakeets *Cyanoramphus novaezelandiae cyanurus* after Eradication of Invasive Predators, Kermadec Islands Archipelago, New Zealand." *Conservation Evidence Journal* 6: 26–30.

Parkes, J. P. 1984. "Feral Goats on Raoul Island. I: Effect of Control Methods on Their Density, Distribution, and Productivity." *New Zealand Journal of Ecology* 7: 85–93.

Pascoe, P. P., M. Bartlett, J. Shaw, T. Rowan, C. K. Weldrick, and H. P. Jones. 2025. "Decadal Change in Seabird-Driven Isotopes on Islands with Differing Invasion Histories." *Ecological Applications* 35(4): e70030.

Post, D. M. 2002. "Using Stable Isotopes to Estimate Trophic Position: Models, Methods, and Assumptions." *Ecology* 83(3): 703–718.

Prentice, I. C., T. Meng, H. Wang, S. P. Harrison, J. Ni, and G. Wang. 2011. "Evidence of a Universal Scaling Relationship for Leaf CO_2 Drawdown Along an Aridity Gradient." *New Phytologist* 190: 169–180.

Quillfeldt, P., R. A. R. McGill, J. F. Masello, F. Weiss, I. J. Strange, P. Brickle, and R. W. Furness. 2008. "Stable Isotope Analysis Reveals Sexual and Environmental Variability and Individual Consistency in Foraging of Thin-Billed Prions." *Marine Ecology Progress Series* 373: 137–148.

Rankin, L. L., and H. P. Jones. 2021. "Nearshore Ecosystems on Seabird Islands Are Potentially Influenced by Invasive Predator Eradications and Environmental Conditions: A Case Study at the Mercury Islands, New Zealand." *Marine Ecology Progress Series* 661: 83–96.

Schubert, B. A., and A. H. Jahren. 2012. "The Effect of Atmospheric CO_2 Concentration on Carbon Isotope Fractionation in C3 Land Plants." *Geochimica et Cosmochimica Acta* 96: 29–43.

Shane, P., and I. C. Wright. 2011. "Late Quaternary Tephra Layers Around Raoul and Macauley Islands, Kermadec Arc: Implications for Volcanic Sources, Explosive Volcanism and Tephrochronology." *Journal of Quaternary Science* 26: 422–432.

Shapiro, S. S., and M. B. Wilk. 1968. "Approximations for the Null Distribution of the w Statistic." *Technometrics* 10: 861–66.

Shiels, A. B., and D. R. Drake. 2015. "Barriers to Seed and Seedling Survival of Once-Common Hawaiian Palms: The Role of Invasive Rats and Ungulates." *AoB Plants* 7: plv057.

Soper, F. M., K. S. Sparks, R. J. Cole, C. P. Giardina, C. M. Litton, and J. P. Sparks. 2024. "Inconsistent Recovery of Nitrogen Cycling after Feral Ungulate Removal Across Three Tropical Island Ecosystems." *Biogeochemistry* 167: 651–663.

Spriggs, M., and A. Anderson. 1993. "Late Colonization of East Polynesia." *Antiquity* 67: 200–217.

Sutoh, M., T. Koyama, and T. Yoneyama. 1987. "Variations of Natural 15N Abundances in the Tissues and Digesta of Domestic Animals." *Radioisotopes* 36: 74–77.

Swift, J. A., P. Roberts, N. Boivin, and P. V. Kirch. 2018. "Restructuring of Nutrient Flows in Island Ecosystems Following Human Colonization Evidenced by Isotopic Analysis of Commensal Rats." *Proceedings of the National Academy of Sciences* 115: 6392–97.

Sykes, W. R. 1977. *Kermadec Islands Flora – An Annotated Check List*. Department of Scientific and Industrial Research Bulletin No. 219. Wellington: Department of Scientific and Industrial Research.

Szpak, P., F. J. Longstaffe, J.-F. Millaire, and C. D. White. 2012. "Stable Isotope Biogeochemistry of Seabird Guano Fertilization: Results from Growth Chamber Studies with Maize (*Zea mays*)." *PLoS One* 7: e33741.

Taylor, G. 2000. *Action Plan for Seabird Conservation in New Zealand. Part A: Threatened Seabirds*. Threatened Species Occasional Publication, Vol. 16. Wellington: Department of Conservation.

Towns, D. R., D. A. Wardle, C. P. H. Mulder, G. W. Yeates, B. M. Fitzgerald, G. R. Parrish, P. J. Bellingham, and K. I. Bonner. 2009. "Predation of Seabirds by Invasive Rats: Multiple Indirect Consequences for Invertebrate Communities." *Oikos* 118: 420–430.

Trnski, T., and P. J. de Lange. 2015. "Introduction to the Kermadec Biodiscovery Expedition 2011." *Bulletin of the Auckland Museum* 20: 1–18.

Veitch, C. R. 2004. "Birds of the Kermadec Islands, South-West Pacific." *Notornis* 51: 61–90.

Veitch, C. R., C. G. Gaskin, K. Baird, and S. M. H. Ismar. 2011. "Changes in Bird Numbers on Raoul Island, Kermadec Islands, New Zealand, Following the Eradication of Goats, Rats, and Cats." In *Island Invasives: Eradication and Management*, edited by C. R. Veitch, M. N. Clout, and D. R. Towns, 372–76. Gland, Switzerland: IUCN.

Vitousek, P. M. 1988. "Diversity and Biological Invasions of Oceanic Islands." In *Biodiversity*, edited by E. O. Wilson and F. M. Peter. Washington, DC: National Academy Press.

Wardle, D. A., P. J. Bellingham, T. Fukami, and K. I. Bonner. 2012. "Soil-Mediated Indirect Impacts of an Invasive Predator on Plant Growth." *Biology Letters* 8: 574–77.

Wardle, P. 1991. *Vegetation of New Zealand*. Cambridge: Cambridge University Press.

Warren, B. H., D. Simberloff, R. E. Ricklefs, R. Aguilée, F. L. Condamine, D. Gravel, H. Morlon, et al. 2015. "Islands as Model Systems in Ecology and Evolution: Prospects Fifty Years After MacArthur-Wilson." *Ecology Letters* 18: 200–217.

Wilder, B. T., A. T. Becker, and D. L. Dettman. 2022. "Marine Subsidies Produce Cactus Forests on Desert Islands." *Scientific Reports* 12: 17110.

Willis, T. J., C. J. Sweeting, S. J. Bury, S. J. Handley, J. C. Brown, D. J. Freeman, D. G. Cairney, and M. J. Page. 2013. "Matching and Mismatching Stable Isotope (δ 13 C and δ 15 N) Ratios in Fin and Muscle Tissue Among Fish Species: A Critical Review." *Marine Biology* 160: 1633–44.

Wright, A. C. S., and A. J. Metson. 1959. "Soils of Raoul Island (Sunday) Island, Kermadec Group." *New Zealand Soil Bureau. Bulletin* 10: 49.

Young, H. S., L. Hurrey, and G. S. Kolb. 2011. "Effects of Seabird-Derived Nutrients on Aquatic Systems." In *Seabird Islands: Ecology Invasions, and Restoration*, edited by C. P. H. Mulder, W. B. Anderson, D. R. Towns, and P. J. Bellingham, 242–260. New York: Oxford University Press.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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