

## REVIEW

## The biogeochemistry and ecological impact of Westland petrels (*Procellaria westlandica*) on terrestrial ecosystems

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**Abstract:** The Westland petrel (*Procellaria westlandica*) is a 1200 g medium-sized seabird whose breeding colonies are dispersed across 700 ha of forest on the western coast of South Island, New Zealand. These birds represent the sole landscape-scale lowland remnant of formerly widespread petrel and shearwater colonies in mainland New Zealand and provide an opportunity to investigate maritime species' impact on terrestrial ecosystems characteristic of pre-human New Zealand. This review develops a conceptual model of biogeochemical processes influenced by Westland petrels from a single burrow to individual colonies and thence to a catchment scale. Results show the distinctiveness of the Westland petrel system, with colonies moving around the landscape in response to local damage by earthquakes and storms. Based on monitored streams in forested landscapes elsewhere, storms also control N and P fluxes to streams. Non-seabird temperate forests are dominated by mycorrhizal plant-soil interactions, but the high N and P status of Westland petrel colony soils minimises the role of fungi in soil processes, including trace element (Se) uptake. The more N-rich C:N ratio in tree foliage within habitat occupied by the colony may provide nutritional support for terrestrial herbivorous animals, including those whose ranges extend beyond the colony. Overall, the review emphasises the spatial and temporal dynamics of the Westland petrel terrestrial ecosystem, and highlights potential ecological linkages that connect colonies to the wider landscape.

**Keywords:** allochthonous, biodiversity, conservation, nutrient cycling, Procellariidae, stable isotope, trace element

### Introduction

#### Westland petrel life history

The Westland petrel is a medium-sized (1200 g) burrow-nesting petrel that comes ashore only on the western coast of New Zealand's South Island, where it is one of two landscape-scale remnants of the petrel and shearwater colonies that occupied mainland New Zealand in pre-human times. Based on a combination of evidence from fossil deposits (summarised in Worthy & Holdaway 2002), soil chemistry (Hawke & Wu 2012), Māori oral history recorded by early ethnologists (Cowan 1923 pp. 19, 64, 68), and records from early European naturalists (Stead 1927), these colonies were widespread but the birds' impact on biogeochemical processes in soils and plants is poorly understood. Studies of Westland petrel breeding colonies therefore provide an opportunity to investigate the functioning of a major component of pre-human New Zealand.

Unlike most seabirds from temperate climates, Westland petrels breed in winter, inhabiting their breeding colonies from March to November or December (Baker & Coleman 1977). During the breeding season, both breeding and non-breeding adults range across northern South Island continental shelf waters along both eastern and western coasts north of 44° S, especially in areas of steep bathymetry near major underwater

canyons (Waugh et al. 2018). Juveniles, fledglings and post-breeding adults then migrate in 6 days directly to South American waters, where they remain until next breeding season (Landers et al. 2011). The Westland petrel population of 4000 pairs breeds in lowland podocarp rainforest (Fig. 1) at 50–200 m altitude in 29 colonies dispersed across 700 ha of deeply dissected hill country south of the Punakaiki River (Wood & Otley 2013). This hill country abuts a 1 km wide alluvial coastal plain, and the small order streams draining the petrel colonies either enter the sea directly or terminate in coastal lagoons.

#### Study site history, and colony lifetime

Westland petrel research on land has mostly used a sub-colony in Scotsman's Creek (formerly Scotchman's Creek), hereafter the Study Colony. This site is 1.6 km from the coast at 120 m altitude and consists of a flattish ridge with steep (c. 25°) SSE-facing side slopes, the ridge (and the Study Colony) terminating at the seaward end in a cliff; an aerial photograph is given in Hawke (2004).

Seabirds have bred continuously at the Study Colony since at least 1765 (tree ring  $\delta^{15}\text{N}$  data; Holdaway et al. 2007) but were absent at 1040–1260 CE (radiocarbon and  $\delta^{15}\text{N}$  of soil; Hawke 2004), consistent with Westland petrel colonies moving around the steep, unstable landscape in response to



**Figure 1.** Westland petrel flight take-off tree and associated guano streaks; an active burrow showing penetration of both A (high organic content, dark colour) and B (low organic content, pale colour) soil horizons (both transparencies 10 June 2004).

major storms and earthquakes (Hawke 2004). Burrow density is approximately  $0.24 \text{ m}^{-2}$  (Waugh et al. 2003); most burrows lie near the top of the side slopes close to access to take-off sites (Best & Owen 1976; Fig. 1), although some burrows occur at lower density downslope to the valley floor.

The Study Colony occupies the upper section of a concave erosion surface immediately below the ridgeline. Soil at the site is an Orthic Brown Soil (New Zealand Soil Classification; Hewitt 1998) with silt loam or silty clay loam texture developed on blue-grey muddy sandstone (P. Tonkin, quoted in Hawke 2010b). Depth of this mineral soil to lithic contact is typically 30–40 cm. There is strong horizon development, with an A horizon of 15–20 cm overlying a Bw or BC horizon. Soil pH is acidic (mean  $\pm$  SD,  $4.1 \pm 0.3$ ; Hawke & Wu 2012), but no more so than similar non-seabird sites nearby (Hawke & Powell 1995). Many burrows penetrate both horizons (Fig. 1).

Burrow construction by burrowing seabirds typically extends over several seasons (Furness 1991), and burrows at the Study Colony are long-lived (decades–century) structures (Hawke 2010b). Nevertheless, the terrain across the entire region is steep and comparatively unstable, experiencing frequent high-rainfall storms and recurrent earthquakes. Consequently, the area occupied by Westland petrels is susceptible to landslip and colonies subject to partial or complete destruction.

Two examples exemplify the potential for destruction. In November 2004, a fresh landslip approximately 3 m wide just below the ridgeline behind the Study Colony had carried away burrows. At the next visit, in April 2005, the landslip was still very visible. Nevertheless, revegetation was occurring, a 1 m high poroporo (*Solanum laciniatum* / *S. aviculare*) dominating the remaining open ground.

A more extreme event came from the remnants of Cyclone Ita in April 2014, which yielded heavy rain alongside the strongest wind gusts ever recorded locally (Waugh et al. 2015a). The consequences for six of the largest Westland petrel colonies, in terms of vegetation destruction and landslips, ranged from minimal (two colonies) to landslips removing a substantial proportion of the burrows and accompanying toppling of canopy trees. At the Study Colony, Waugh et al. (2015a) reported “ $\frac{1}{4}$  to  $\frac{1}{2}$  of canopy trees fallen...[and] large landslips encroaching on [the] lower margins of the colony”, leading to the loss of 27% of the colony’s burrows.

Although this level of destruction superficially suggests serious consequences for the Westland petrel population, 20–50% of burrows are unoccupied each breeding season and approximately half of adult birds do not breed every year (Waugh et al. 2003, 2015b). Consequently, the current demographics of Westland petrels afford some degree of protection to both colony, and regional, scale catastrophes. Nevertheless, any loss of breeding habitat can have at least short- or medium-term effects on the number of birds and their susceptibility to other, unrelated threats (Waugh et al. 2015b; Burger 2018).

These descriptions of the impact of major storms (Waugh et al. 2015a) fit well with the nature of the side-slope of the Study Colony as a concave erosion surface, a caesium-137 depth profile consistent with minor post-1963 soil movement (Hawke 2010b), and reports of localised land slips carrying away burrows (Hawke & Powell 1995). Conversely, lead-210 depth profiles indicate overall slope stability on a decades–century timescale (Hawke 2010b). These studies suggest that Westland petrels breeding colonies are not permanent features but move around the landscape at least partly in response to colony damage and burrow destruction. The timescale of this movement is likely in the order of centuries (Holdaway et al. 2007).

### Review aims and structure

Westland petrel breeding biology and foraging ecology have been described elsewhere (Wood & Ottley 2013, Waugh et al. 2015b, 2018). This review focuses on the effects of Westland petrel breeding activities on the biogeochemistry and ecology of terrestrial soil and freshwater environments in the context of other areas (primarily islands) occupied by colonial seabirds and draws comparisons with processes in non-seabird breeding sites. As such, the review takes its inspiration from the landscape scale approach to ecological processes across the marine–terrestrial boundary pioneered by Gary Polis and co-workers (Polis et al. 2004).

The major part of the review comprises the construction and discussion of a box model that brings together the various ecosystem compartments (forest soils, plants, streams etc) affected by Westland petrels on land and their principal connecting pathways. The review then concludes with a discussion of the box model’s conservation and management



implications that emphasise the importance of taking a landscape approach to Westland petrels (and other seabirds) on land.

## Box model construction

Box models provide a simple but rigorous visual framework for understanding the movement of material or energy through a system (Bormann & Likens 1967; Burton & Likens 1975), and are widely used in ecology (e.g. Kaye et al. 2006). They divide the system concerned into a series of compartments (or reservoirs) containing a particular substance of interest, connected by the processes that transfer the substance from one compartment to another. Model construction is an iterative process, with field measurements or laboratory experiments informing the addition or elimination of connecting pathways and providing estimates of compartment sizes and fluxes.

### Definitions and terminology

Ecological studies at seabird breeding sites often use natural abundance stable isotope ratios of carbon (C) and nitrogen (N) to discriminate between marine and terrestrial sources of these elements, and to establish trophic relationships (Wainwright et al. 1998). The isotopic number ratios ( $^{13}\text{C}/^{12}\text{C}$ ;  $^{15}\text{N}/^{14}\text{N}$ ) are expressed on the delta scale as  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  according to  $\delta X = 1000 \times \{[\text{isotope ratio (sample)} - \text{isotope ratio (primary standard)}] / \text{isotope ratio (primary standard)}\}$  (Coplen 2011). The primary standard for  $\delta^{13}\text{C}$  is the limestone Vienna PeeDee Belemnite (VPDB); the primary standard for  $\delta^{15}\text{N}$  is atmospheric  $\text{N}_2$ .

### Information sources

The box model compartments for this review were informed by those widely used in catchment-scale forest ecology. For the Westland petrel system, model construction is at an early stage with few direct measurements available. Exceptions are the soil N, phosphorus (P) and selenium (Se) compartments, for which residence times are of the order of decades (Hawke 2005; Hawke & Wu 2012).

In terms of connecting pathways, Westland petrels have  $\delta^{13}\text{C}$  values of  $-19\text{‰}$  (feathers, representative of living tissue) and  $-22\text{‰}$  (guano) compared with typical foliage and soil values away from petrel influence of  $-33\text{‰}$  and  $-28\text{‰}$ . Delta- $^{15}\text{N}$  values are similarly enhanced, at  $17\text{‰}$  (petrel feathers) and  $12\text{‰}$  (guano) compared with  $-8\text{‰}$  and  $+2\text{‰}$  for foliage and soil (Hawke 2005; Hawke & Holdaway 2005; Hawke & Vallance 2015; Hawke et al. 2017a). The dominance of petrel inputs to forest and streams comes from the enhancement in both  $\delta^{15}\text{N}$  values and (for forest biota) C:N ratios, as discussed below. Movement of petrel-derived N and P into estuarine lagoons and the sea can be expected on mass balance grounds. This involves petrel N transfer to streams (Harding et al. 2004), the maintenance of guano-like N:P ratios in petrel colony soil (Hawke 2005), and regular flushing of stream beds during rainstorms.

Confinement of most ammonia loss to burrow soils is based on measurements by Riddick et al. (2012). Plant uptake of N will be primarily inorganic; both inorganic and organic P are plant available (Hawke & Condron 2014). Foliar uptake of gaseous N will not include  $\text{N}_2$ , as legumes are absent and the abundance of petrel-derived N will suppress soil microbe  $\text{N}_2$  fixation. The predominance of inorganic N over organic

N loss to streams predicted in the model comes from Phillips et al. (2013).

## Box model compartment: Petrel colony forest

### Sub-compartment: Petrel colony soil–nutrient enrichment

In many climates globally, N and P availability in soils regulate terrestrial plant productivity, biomass, decomposition and foliar chemistry (Cleveland et al. 2006; Elser et al. 2007; Ostertag & DiManno 2016), typically mediated through biologically available soil fractions. Superimposed on soil parent material sources of N and P is landscape – scale physical or biological transport, often from the sea (Polis et al. 2004). Seabirds contribute to global N and P cycling at a level comparable to other, non-industrial sources (Otero et al. 2018), and this contribution would have been proportionately larger in pre-industrial times when seabirds were more widely distributed (Doughty et al. 2015). This contribution would have been more important in the pre-human New Zealand landscape, when seabirds were abundant in an environment without mammalian predators able to exert predation at levels beyond that of the primarily avian suite of indigenous predators (Worthy & Holdaway 2002).

Soil nutrient enhancement by seabirds occurs primarily via guano deposition, although other detritus such as dead nestlings, broken eggs, and adults killed by predation, in territorial disputes or (rarely) in landing accidents also contribute (Gillham 1960; Ward 1961; Warham 1990, 1996). Consequently, colony soil is enriched by guano and other detritus both within burrows and on the colony forest floor. The temporal and spatial structure of this enrichment is poorly understood, especially within burrows. However, any detritus deposited within burrows that remains at the end of each breeding season is likely to be returned, along with its associated soil, to the forest floor during burrow cleaning at the start of the following season (Fig. 1). Although no measurements have been made of the amounts involved, this loosely associated soil is then likely to be more erodible in storms.

The annual level of seabird nutrient input at breeding colonies globally ( $100\text{--}300\text{ g N m}^{-2}$ ,  $8\text{--}29\text{ g P m}^{-2}$ ) is an order of magnitude higher than typical annual fertiliser application rates in intensive agriculture ( $9\text{--}59\text{ g N m}^{-2}$ ,  $1.4\text{--}9.2\text{ g P m}^{-2}$ ) and much higher than other external nutrient sources (Furness 1991; Vitousek et al. 2009). For Westland petrels, their comparatively low burrow density ( $0.24\text{ m}^{-2}$ ; Waugh et al. 2003) probably places nutrient inputs toward the lower end of the range of seabird inputs estimated by Furness (1991). Even so, the likely inputs at both individual colonies and across the 700 ha currently occupied by Westland petrel colonies will be substantial in an environment usually considered nutrient poor (e.g. Brunn et al. 2016; Hawke et al. 2017a).

Given the intensity of N and P inputs at petrel colonies, one might expect extraordinarily high total N and total P concentrations in soil. However, demonstrating such an enrichment is problematic because a valid comparison should involve control sites with otherwise identical soil parent material and climate. This is especially difficult in New Zealand because of the diversity of soil parent materials and climate, and because of potential legacy effects from former seabird breeding. These legacy effects could be especially important because a diverse regional seabird fauna lived where Westland petrels are now found (Worthy & Holdaway 1993), and because Westland petrel colonies themselves move around the landscape.

Notwithstanding these limitations, informative comparisons can be made. Firstly, median Westland petrel surface soil N concentrations (0.77%; Hawke et al. 2013, 2017) fall within the range of means from 98 seabird islands across 9 non-polar island systems worldwide (0.30–0.97%; Mulder et al. 2011). Similarly, total P in Westland petrel colony surface soils (mean  $\pm$  SD, 1390  $\pm$  460 mg kg<sup>-1</sup>; Hawke 2005) is well within the range of surface soil total P concentrations (150–2700 mg kg<sup>-1</sup>) reported by Mulder et al. (2011) across the four island systems for which they had data. Secondly, although median soil N concentrations at the Westland petrel colony are higher than climatically and floristically similar non-seabird sites 130 km away at Ōkārito and Saltwater and a drier but floristically similar site on the South Island east coast at Pūtarīngamotu Riccarton Bush, the data overlapped considerably (Fig. 3). Despite this similarity in soil nutrients, foliar N concentrations at the Westland petrel colony were much higher than floristically and climatically similar non-seabird sites at Ōkārito and Saltwater (Fig. 3); the conundrum posed by this enrichment is discussed in further detail below.

Mulder et al. (2011) found no seabird density effect on soil N and a relatively small effect on soil P that they attributed to legacy effects driven by the strong affinity of both organic and inorganic phosphorus for soil colloids. However, much of the total soil P inventory at the Westland petrel colony (41–87%, 0–60 cm; Hawke 2005) can be explained by soil parent material weathering which was not considered by Mulder et al. (2011). Furthermore, the range of global seabird soil P concentrations falls within the range of those from non-seabird natural systems (Porder & Ramachandran 2012). In contrast, significant contributions from N in parent material (cf. Houlton et al. 2018) are unlikely in Westland petrel soils because the muddy sandstone parent material has an extremely N-poor molar N:P ratio of 1.1 (Hawke 2005). Consequently, saturation of soil binding sites by N and P from seabirds and potential parent material contributions need to be considered alongside potential legacy effects in explaining the absence of seabird density effects on soil nutrient concentrations.

Elemental ratios are useful indicators of limitation and saturation in soil systems. Carbon: N, N:P and C:P ratios (Fig. 4; data from Hawke 2005) are remarkably similar at the Westland petrel study colony to non-seabird forest soil systems (0–10 cm data compiled by Cleveland and Liptzin 2007). Reiterating that Westland petrel colony soils are mineral soils, soil C:N ratios are constant with depth at the Westland petrel site (mean  $\pm$  SD, 15.8  $\pm$  1.8 by mass), and are at the C-rich end of the global distribution for forest soils (mean  $\pm$  SD, 12.4  $\pm$  7.1). In contrast, the N:P ratio was slightly P-rich, declining from 5.4 near the surface to 2.6 at 40–60 cm depth, compared to other forest soils (6.6  $\pm$  5.6). The C:P ratio declined from 84.6 near the surface to 43.3 at 40–60 cm; the Westland petrel surface soil values are almost identical to the global mean of 82.1. This overall similarity to non-seabird forest soils despite guano inputs points to a saturation of soil with N and P and implies high loss rates that match guano inputs (Hawke 2005).

Although the effects of Westland petrels (and other burrowing seabirds) on total soil N and P concentrations are less than might be expected from their level of input, plant-available (bicarbonate extractable) P in Westland petrel soils is extremely high (56  $\pm$  28 mg kg<sup>-1</sup>) and much higher than a control site (12.1  $\pm$  1.8 mg kg<sup>-1</sup>; Hawke & Powell 1995). Field and laboratory studies suggest that these high bicarbonate-extractable P concentrations in Westland petrel soils are continuously replenished from other non-marine soil P pools.

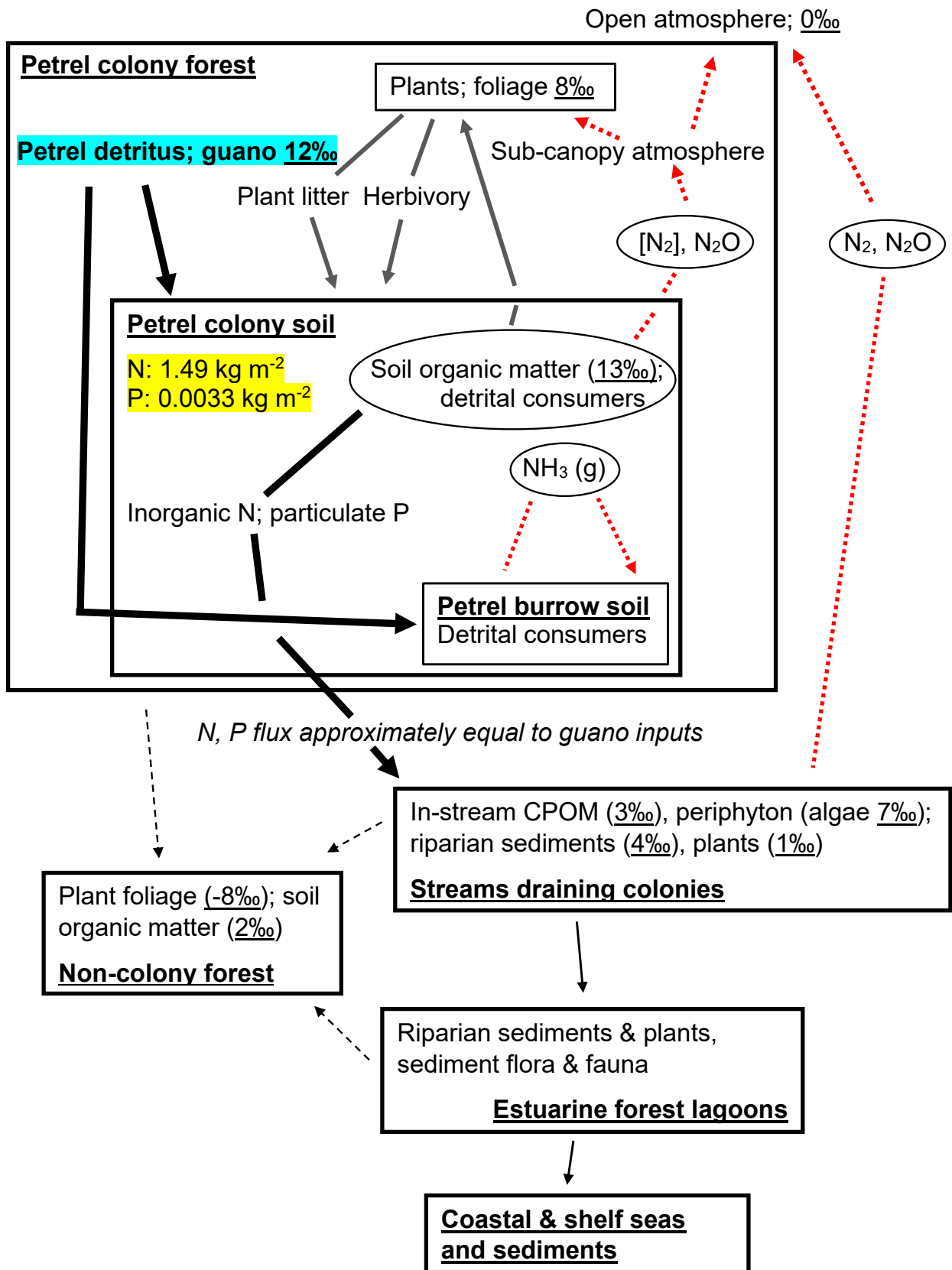
Bicarbonate extractable P values from a portion of a colony destroyed by slumping downslope 12 months before sampling (range, 26–88 mg kg<sup>-1</sup>; mean 50  $\pm$  28 mg kg<sup>-1</sup>) entirely overlapped with values from an undamaged section of a colony (range, 25–107 mg kg<sup>-1</sup>; median 65  $\pm$  27 mg kg<sup>-1</sup>;  $t = 0.9836$ , d.f. = 5,  $P = 0.370$ ; Hawke & Powell 1995). In a glass house pot trial using soil from the Study Colony to grow *Pinus radiata* and wheat (*Triticum aestivum*) and designed to progressively deplete soil N and P, bicarbonate extractable P remained constant at 65–70 mg kg<sup>-1</sup>. This occurred even as total soil P declined by c. 100 mg kg<sup>-1</sup>, from 800 to 700 mg kg<sup>-1</sup> (Hawke & Condron 2014). These plants accessed highly refractory fractions of soil P to maintain a consistent foliar stoichiometry as soil nutrients were progressively depleted. However, this is not necessarily unique to Westland petrel colony soils, with studies in other systems showing mobilisation of refractory soil P fractions (Brandtberg et al. 2010; Nash et al. 2014). These refractory soil P fractions typically limit P availability to plants and, in the absence of an external P source such as breeding seabirds, become a larger proportion of soil P as a soil ages (Walker & Syers 1976; Vitousek et al. 2010).

In summary, total concentrations of N and P respond poorly to seabird presence due to saturation of soil binding sites. Instead, Westland petrels (and other seabirds) primarily affect the forms in which nutrients are found, with extraordinarily high values of bicarbonate-extractable P. However, nothing is known of the size distribution of inorganic and organic forms of P within seabird soils. Studies in non-seabird soils emphasise the importance of the clay size fraction for retaining organic P (Spohn 2020), and it would be interesting to see if the same applies in Westland petrel colony soils given its silt loam texture.

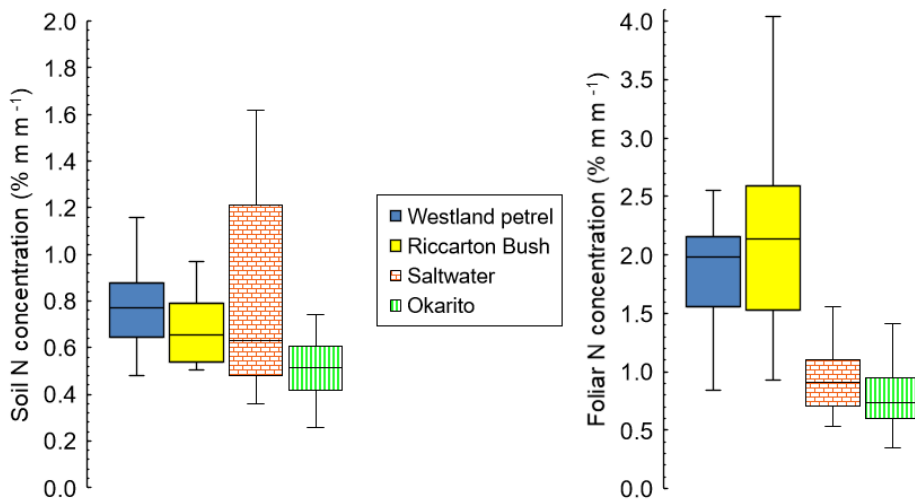
#### Sub-compartment: Petrel colony soil—carbon and nitrogen isotope ratios

The previous section addressed seabirds as an external P source by estimating the soil parent material contribution to total soil P, noting that Westland petrel guano (1.7% P) has nearly 30 times the P content of Study Colony soil parent material (0.061%) (Hawke 2005). In contrast, seabird derived N is differentiated from terrestrial fixed atmospheric N in its higher  $\delta^{15}\text{N}$  (12‰ for Westland petrel guano; Fig. 2). Various studies have reported enhanced surface soil  $\delta^{15}\text{N}$  values of up to 28‰ due to seabird presence (Mulder et al. 2011). Although there are few published depth distributions, Hawke (2005) obtained depth data from five soil profiles at the Westland colony extending to 35–60 cm.

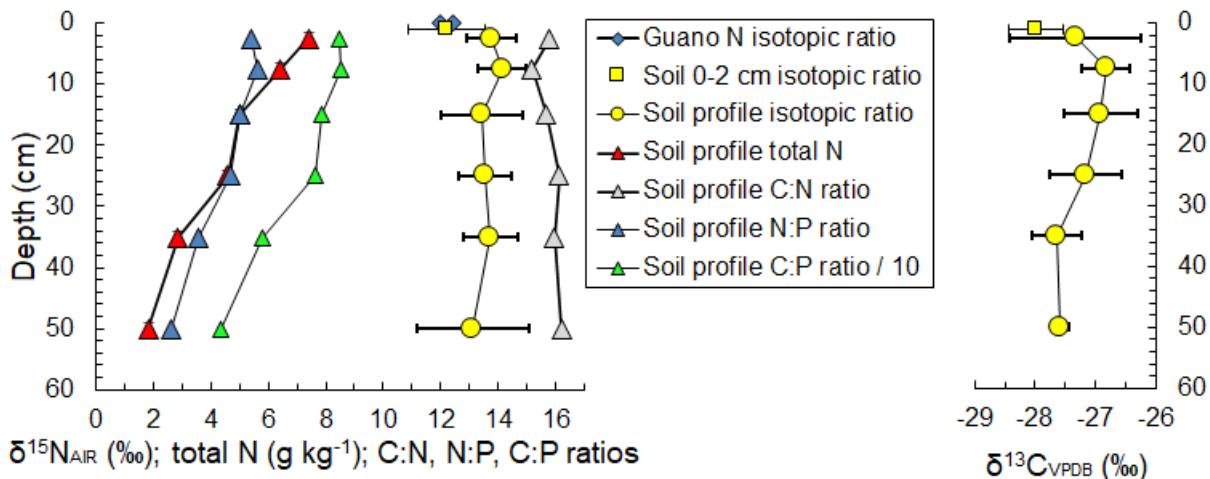
In temperate forests globally, soil nutrient status reflects both the balance between organic and inorganic N pool sizes and the rate of organic material turnover (Phillips et al. 2013). In turn, the  $\delta^{15}\text{N}$  distribution with soil depth is a useful way of characterising N processing within the soil profile (Hobbie & Ouimette 2009). In nutrient-poor non-seabird soils globally where organic forms dominate N cycling, soil  $\delta^{15}\text{N}$  values almost always increase steadily with depth (Hobbie & Ouimette 2009). Conversely, higher N status soils characterised by arbuscular mycorrhizal symbioses display a sub-surface  $\delta^{15}\text{N}$  maximum followed by decreasing soil  $\delta^{15}\text{N}$  values; in these soils inorganic forms dominate N cycling and N is lost primarily as nitrate (Hobbie & Ouimette 2009; Phillips et al. 2013). From a microbial ecology viewpoint, high nutrient forest systems are dominated by bacteria rather than fungi and the microbes are typically C-limited (Kopáček et al. 2013). As well as nutrient effects on the relative biomass of bacteria



**Figure 2.** Westland petrel impact on the terrestrial landscape showing major potential retention and loss pathways for N and P; pathways shown by red dashed arrows are for N only. As explained in the text, petrel detritus (primarily guano) is added to both the colony forest floor and within petrel burrows (bold black arrows), and soil is exchanged between the two (Fig. 1). Nitrogen isotopic enrichment is shown where known, as an indicator of marine N movement; N and P compartment sizes in colony soil (yellow highlight) are 0–60 cm inventories. Petrel nutrient transfer to non-petrel forest (black dashed arrows) is geochemically insignificant, but petrel nutrients may be ecologically important for mobile species such as kererū that range between petrel and non-petrel forest (see text). Data sources: Hawke (2005), Gamlen-Greene et al. (2017), Hawke et al (2017a). CPOM: coarse particulate organic matter.



**Figure 3:** Soil and foliar N concentrations at the Westland petrel colony compared with nearby non-seabird sites (Ōkārīto, Saltwater) and a non-seabird site on the drier east coast (Pūtaringamotu Riccarton Bush). Data are from Hawke et al. (2013, 2017a).



**Figure 4:** Soil  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  depth distributions (mean  $\pm$  SD, from twelve 0–2 cm samples and from five soil profiles) showing the unexpected independence in  $\delta^{15}\text{N}$  values with depth, alongside Westland petrel guano values from June and November 2004. The large SD for the deepest  $\delta^{15}\text{N}$  comes from a particularly low value from one soil profile (10.4‰). Westland petrel guano  $\delta^{13}\text{C}$  values ranged from  $-20$  to  $-24$ ‰, and are omitted for clarity. Also shown are total N concentration and C:N, N:P and C:P ratios (by mass) depth profile data for comparison. Data collected for Hawke (2005) and Hawke and Vallance (2015; 0–2 cm data only). Plots of the individual  $\delta^{15}\text{N}$  profiles are shown in Appendix S1, alongside profiles from subantarctic Adams Island.

and fungi, nutrients also affect the structure of soil bacterial communities (Goldford et al. 2018).

Although foliar N concentrations and C:N ratios show that Westland petrel colony soils are well endowed with N (Figs 3, 4), there was no soil  $\delta^{15}\text{N}$  depth dependence in Westland petrel soils to 30 cm and no significant difference between profiles (two-way ANOVA; test for equal  $\delta^{15}\text{N}$  with depth,  $F = 0.471$ ,  $df = 3$ ,  $P = 0.708$ ; test for equal means between profiles,  $F = 1.439$ ,  $df = 4$ ,  $P = 0.281$ ; Fig. 4). The four profiles that extended to 60 cm depth yielded a similar result (test for equal  $\delta^{15}\text{N}$  with depth,  $F = 0.3949$ ,  $df = 5$ ,  $P = 0.845$ ; test for equal means between profiles,  $F = 3.232$ ,  $df = 3$ ,  $P = 0.052$ ). This absence of a depth dependence contrasts with a 2‰ increase in the top 12 cm of coastal podocarp forest soil at a site 250 km to the south (Brunn et al. 2016).

Total N concentrations in Westland petrel soils decreased significantly with depth (linear correlation and Spearman's

Rank, both  $P = 0.0001$ ;  $r^2 = 0.46$ ) and differed significantly with both depth and between profiles to 30 cm (two-way ANOVA; test for equal total N with depth,  $F = 0.4.167$ ,  $df = 3$ ,  $P = 0.031$ ; test for equal means between profiles,  $F = 9.23$ ,  $df = 4$ ,  $P = 0.0012$ ; Fig. 4); the significance increased dramatically when the four profiles to 60 cm were analysed (test for equal total N with depth,  $F = 12.85$ ,  $df = 5$ ,  $P < 0.0001$ ; test for equal means between profiles,  $F = 12.81$ ,  $df = 3$ ,  $P = 0.0002$ ; Fig. 4).

The soil  $\delta^{15}\text{N}$  depth profiles (Fig. 4) demonstrate a 1–2‰ enhancement over guano  $\delta^{15}\text{N}$  values. Hawke and Vallance (2015) used 0–2 cm surface soil samples rather than 0–5 cm zone sampled by Hawke (2005). These shallower values were intermediate between guano and 0–5 cm values (Fig. 4), so that the mineralisation processes driving this isotopic fractionation occur at or near the soil surface.

The mean depth-weighted soil  $\delta^{13}\text{C}$  value from Hawke (2005) is  $-27.3$ ‰, and typical of temperate forest soils and



much lower than the mean guano value ( $-21.9\%$ ). As with  $\delta^{15}\text{N}$ ,  $\delta^{13}\text{C}$  values were similarly independent of depth, and varied between profiles (test for equal  $\delta^{13}\text{C}$  with depth to 30 cm,  $F = 0.471$ ,  $df = 3$ ,  $P = 0.708$ ; test for equal means between profiles,  $F = 0.696$ ,  $df = 4$ ,  $P = 0.609$ ). The difference between guano and soil  $\delta^{13}\text{C}$  values indicates that the mineralisation driving C isotopic fractionation occurs at the soil surface as with  $\delta^{15}\text{N}$ , that guano C is entirely mineralised to  $\text{CO}_2$ , or that the guano signal is diluted out by photosynthetic C input.

The concept of a third category of N cycling, where there is no depth dependence in soil  $\delta^{15}\text{N}$  values, is supported by data from a mixed species petrel colony on Adams Island, Auckland Islands group, New Zealand sub-Antarctic. The soil involved is peat, which is in a different soil order (Organic Soil) from Westland petrel colony soils (Brown Soil) in the New Zealand Soil Classification (Hewitt 1998). On Adams Island, soil  $\delta^{15}\text{N}$  values in four profiles to 75 cm depth showed no depth dependence (two-way ANOVA; test for equal  $\delta^{15}\text{N}$  with depth,  $F = 0.230$ ,  $df = 4$ ,  $P = 0.916$ ; test for equal means between profiles,  $F = 23.66$ ,  $df = 3$ ,  $P < 0.0001$ ; Appendix S1 in Supplementary Materials) notwithstanding a significant difference between profiles.

In summary, the high plant-available N and P status of seabird soils accompanied by the independence in soil  $\delta^{15}\text{N}$  values with depth (and exemplified by the Westland petrel system) indicates that seabird forest soils may provide an additional nutrient cycling category beyond those identified by Phillips et al. (2013). As such, this additional category is not merely an outlier of their “high nutrient economy” category of forest soils. This additional category most likely occurs where the nutrient supply is such that mycorrhizal symbioses are no longer necessary for plants to obtain their nutrients and is characterised by the disappearance (at a colony scale) of any depth dependence in soil  $\delta^{15}\text{N}$  values. This inhibition of soil fungi was used by Hawke et al. (2017) to explain the minimal seabird effect on Se uptake by Westland petrel colony plants; what is needed now is direct determination of mycorrhizal infection of plants growing in Westland petrel colony soils.

This new depth dependence category for soil  $\delta^{15}\text{N}$  values enables a picture of the dynamics of the wider landscape occupied by Westland petrels. In an active colony, the high concentrations of plant-available N and P along with the low pH suggests minimal mycorrhizal involvement (Frater et al. 2018) and guano and litter N are nitrified at the soil surface. This limited role for mycorrhizae may affect plant responses to stress, herbivores and soil pathogens, and regulate competition between plants growing in the petrel colony (Tedersoo et al. 2020). Once the colony is abandoned or destroyed and seabird nutrient inputs cease, plant-available N and P concentrations and stoichiometry may change as nitrate and other labile forms are leached and arbuscular mycorrhizal involvement increases. Although N is still lost as nitrate, organic N cycling becomes increasingly important as time goes by. At some point, petrels may reoccupy the site and the cycle begins again. Although tentative, this picture is built on an extensive and long-standing literature on the effects of the soil environment on mycorrhizal interactions with plants, albeit in non-seabird systems. As just noted, a good place to start on exploring the validity of this picture is to determine the factors affecting mycorrhizal infection of plants within the Westland petrel colony.

### Sub-compartment: Petrel colony soil—nutrient retention and loss

Total N and P concentrations in Westland petrel colony soils are typical of seabird soils elsewhere, and C:N, N:P and C:P ratios are similar to forest soils globally that are without seabird colonies. The minimal effects on total N and P soil concentrations due to Westland petrels and the absence of seabird density effects in the Mulder et al. (2011) cross-island comparison can both be explained by saturation of soil binding sites for N and P, and the inability to retain the extra nutrients continuously supplied by breeding petrels. Hawke (2005) investigated the binding saturation of soil nutrients and calculated an extraordinarily short residence time for P of 4–41 years. This calculation assumes that soil P fractions are in equilibrium with each other so that preferential loss of one fraction (e.g. P dissolved in soil drainage) is replaced from other, less reactive fractions (e.g. by P desorption from soil particle surfaces). The mobility of P between soil fractions found experimentally by Hawke and Condon (2014) and the buffering of bicarbonate-extractable P found both experimentally and in the field (Hawke & Powell 1995; Hawke & Condon 2014) support this assumption.

Potential differences between N and P retention in colony soils can be identified by comparing soil and guano N:P stoichiometries. Guano stoichiometry for Westland petrels has a strong seasonal dependence driven by changes in diet, N:P ratios ranging from 4.1 (June, during egg laying) to 16.4 (November, immediately pre-fledging; both stoichiometries on a molar basis) (Hawke 2005). Hawke (2005) measured soil N:P stoichiometries from 0–60 cm depth, finding  $9.5 \pm 2.2$  (mean  $\pm$  SD; based on total soil P) and  $15.0 \pm 6.3$  (P in excess of parent material contributions), which overlaps with guano stoichiometry. The similarity of soil and guano N:P ratios implies that the two elements are lost from the soil system at comparable rates, which is surprising because P has no gas phase environmental chemistry and its inorganic salts are less soluble and more strongly retained by soil colloids than N. This similarity between soil and guano N:P ratios in Westland petrel colony soil contrasts with seabird islands with peat soil, where N:P ratios are much more N-rich because of the absence of minerals to bind P (Hawke & Newman 2004; Hawke 2010a).

Evaluating potential loss pathways (Fig. 2), the multiple pathways for N loss from soil include both gaseous losses ( $\text{NH}_3$ , NO,  $\text{N}_2\text{O}$ ,  $\text{N}_2$ ) and leaching to streams (nitrate, organic N) (Galloway et al. 2003; Taylor et al. 2015; Isobe et al. 2018) as well as uptake by plants. However, as already noted the actual picture in Westland petrel colony soils is probably much simpler, with leaching to streams dominated by inorganic forms (Phillips et al. 2013) and minimal net losses of gaseous N. Minimal net gaseous N loss is consistent with the small  $\delta^{15}\text{N}$  enhancement in soil (Fig. 4), isotopic fractionation during gaseous losses usually being large. Although some gaseous  $\text{NH}_3$  losses are reported from seabird colonies, Riddick et al. (2012) found that these losses are significant only for surface nesting species. Combined with this, reactive N emissions (such as  $\text{NH}_3$  and  $\text{N}_2\text{O}$ ) from soil in a forested system such as that occupied by Westland petrels have the potential for capture by the forest canopy (Sparks 2009) and return to the soil via litterfall. The slightly higher N:P ratios found in the upper portion of the soil profile by Hawke (2005) are consistent with the importance of high N:P leaf litter input rather than low N:P guano.

Notwithstanding this rather simple picture,  $\text{N}_2\text{O}$  emissions

are highest in silty soils (Balaine et al. 2016), and (as noted earlier) Westland petrel soils have a silt loam or silty clay loam texture. Recent research (Zistl-Schlingmann et al. 2019) has also demonstrated high levels of  $N_2$  loss in soils subject to manure application, amounting to 30–40% of applied N. Resolving the disparate lines of evidence as to the significance of gaseous N loss from Westland petrel colony soils will require measurements of the fluxes of the various components of N and P in soil drainage (including overland flow), concurrent with measurement of the fluxes of gaseous N and internal cycling through litter fall. Unfortunately, performing these measurements without hampering petrel breeding activities will be difficult.

Although the similarity of guano and Westland petrel colony N:P ratios shows that the loss of both elements is similar on a decadal scale, shorter time scale processes are almost certainly decoupled. The only documented example of short-term changes in N:P stoichiometry is the seasonal pattern found in guano addition, which (as noted above) is more P-rich early in the breeding season. However, other processes leading to decoupling of N from P loss are likely. For example, high intensity rainfall events could mobilise particulate loss pathways for P, lead to high leaching of nitrate and, by saturating the soil with water, enhance denitrification (Balaine et al. 2016). In contrast, low intensity rainfall is unlikely to mobilise P loss via particulate loss but may lead to nitrate leaching and enhance either complete or partial denitrification.

Although there are few measurements, the high N loading of soil by petrel guano (typically 110–310 kg N m<sup>-2</sup> on an annual basis; Furness 1991) has the potential to enhance nitrate leaching. In turn, this may lead to calcium (Ca) co-leaching because positively charged ions will be co-leached with nitrate to maintain electrical neutrality (Perakis et al. 2014); Ca is the most abundant cation in most soils and is relatively soluble. A single sampling in April 2014 of stream waters draining Scotsman's and Hibernia creeks supported this, yielding Ca concentrations of c. 20 mg L<sup>-1</sup> compared with 4 mg L<sup>-1</sup> in petrel-free Maher and Deverys creeks (DJ Hawke; unpublished data).

#### Sub-compartment: Petrel colony soil—trace element enhancement, retention and loss

The three trace elements studied to date in the Westland petrel system are aluminium (Al), cadmium (Cd) and selenium (Se); Al because of its toxicity to plants and stream biota, Cd because of its toxicity to animals, and Se because it is an essential element for animal nutrition often deficient in New Zealand soils. Furthermore, both Cd and Se are typically enriched in marine vertebrates.

The box model used to frame this review (Fig. 2) focuses on plant macro-nutrients N and P rather than trace elements. Although Al is a major component of soil aluminosilicate minerals, acidic conditions solubilise Al to reach micromolar concentrations in soil solution. Even though concentrations in soil solution are low compared to the Al held in soil minerals, their toxicity is an important control on the composition of forest plant communities (Godbold et al. 1988). Aluminium in dissolved (non-colloidal) form in soil solution comprises highly toxic uncomplexed Al<sup>3+</sup> and its various hydrolysis species (free Al), and nontoxic Al<sup>3+</sup>-organic complexes. The toxicity of Al is exerted in soil solution rather than bulk soil and Hawke and Powell (1995) found that dissolved free Al concentrations in soil solution were similar in an active colony

site (mean ± SD, 4.6 ± 3.3 μmol L<sup>-1</sup>), a former colony site (1.7 ± 0.7 μmol L<sup>-1</sup>), and a non-colony control (1.7 ± 0.2 μmol L<sup>-1</sup>); however, total Al concentrations in soil solution were almost an order of magnitude higher at the control site (13.5 ± 4.0, 8.0 ± 2.0 and 62.8 ± 5.3 μmol L<sup>-1</sup> respectively). Consequently, the proportion of uncomplexed (i.e. toxic) Al is much greater in Westland petrel soils, which Hawke and Powell (1995) attributed to the formation of organic-Al-P complexes. This supports results showing that soil organic matter cycling is substantially affected by the presence of Westland petrels (Hawke & Vallance 2015).

Cadmium accumulates in marine food webs (Øverjordet et al. 2015), and this is reflected in enhanced Cd concentrations in seabird-affected soils globally (Liu et al. 2012, 2013). Approximately 50% of soil Cd at both the Westland petrel site and at a Hutton's shearwater (*Puffinus huttoni*) breeding colony in the Seaward Kaikoura Ranges come from soil parent material (Harrow et al. 2006). In the absence of direct measurements of any Westland petrel-derived material loss, ratios provide a basis for comparison. Soil Cd:P ratios for different seabird soil types are 0.0024 and 0.0039 for two seabird island peat soils where there are no inorganic surfaces to adsorb either Cd or P (Hawke & Newman 2004), compared with mineral soil results of 1.8 × 10<sup>-4</sup> (Westland petrel site; Harrow et al. 2006), 1.2 × 10<sup>-4</sup> (Hutton's shearwater site; Harrow et al. 2006), or tropical islands from which seabirds had recently been extirpated (3.8 × 10<sup>-4</sup>; Liu et al. 2012). The enhancement in Cd:P ratio in the peat soils occurred despite a lower pH (3.0–3.8 vs. 3.6–4.7 at the Westland petrel site; Hawke & Powell 1995), Cd retention in soils being greater at higher pH (Elbana & Selim 2019). Consequently, the low Cd:P ratio in Westland petrel colony soil provides evidence that petrel-derived Cd, like N and P, disperses to the wider environment.

As with Cd, Se accumulates in marine food webs but functions to ameliorate mercury (Hg), Cd and other trace metal toxicity in animals (Ikemoto et al. 2004; Lovvorn et al. 2013). Given the enrichment of Cd in seabird colony soils, the dynamics of Se enrichment are especially relevant. In Westland petrel soils, Se concentrations are an order of magnitude higher than similar non-seabird soils (2.2 mg kg<sup>-1</sup> compared to 0.2 mg kg<sup>-1</sup>) and intermediate between petrel guano (3.8 mg kg<sup>-1</sup>) and soil parent material (0.8 mg kg<sup>-1</sup>) (Hawke & Wu 2012). As with P and Cd, a substantial proportion of Westland petrel colony soil Se comes from soil parent material weathering with 64% of soil Se being from guano. This guano derived Se correlates with both δ<sup>15</sup>N (consistent with petrel guano input) and decreasing pH. The pH effect is consistent with adsorption on soil colloids, Se being an anion in most soils and anion adsorption being strongest at low pH.

#### Sub-compartment: Petrel colony forest plants—N concentration and δ<sup>15</sup>N enhancement

Enhanced foliar N and lower C:N ratios are widely reported from seabird breeding sites (Mulder et al. 2011). Consistent with these results, foliar N concentrations for all individual plants with foliage at 0.5–2.5 m along a transect through the Westland petrel Study Colony (median ± SD: 1.99 ± 0.68%; n = 18) are double those at nearby climatically similar non-seabird sites Ōkārito (0.72 ± 0.26%; n = 49) and Saltwater (0.95 ± 0.31%; n = 37) (Fig. 1; Hawke et al. 2017a). The foliar N effect carried over into foliar C:N ratios (Westland petrel, 21.6 ± 11.3; Ōkārito, 66.4 ± 21.2; Saltwater, 57.6 ± 21.3). Although different plant species were sampled, the foliar enhancements in nutrient content and stoichiometry are



entirely consistent with the global plant fertilisation literature (Ostertag & DiManno 2016), whereby concurrent addition of N and P fertilisers enhance foliar concentrations in virtually all ecosystem types (Ostertag & DiManno 2016).

The Westland petrel colony understorey foliar N concentrations and C:N ratios are similar to those at Pūtaringamotu Riccarton Bush on the much drier east coast (median foliar N,  $2.14 \pm 0.77\%$ ; C:N,  $26.8 \pm 9.3$ ; Hawke et al. 2017). The Westland petrel colony results are also similar to those reported for *Olearia lyalli* forest on North East I. (Snares Islands group, New Zealand sub-Antarctic) supporting nearly four times the density of sooty shearwater *Ardenna grisea* (formerly *Puffinus griseus*) burrows ( $0.90 \text{ m}^{-2}$ ; Charleton et al. 2009) (foliar N,  $1.30 \pm 0.12\%$ ; C:N,  $33 \pm 3$ ; Hawke & Newman 2007). Seabird-derived foliar enhancements are therefore not exceptional and can be achieved by vegetation on alluvial mineral soils elsewhere.

### Sub-compartment: Petrel colony forest plants—Se concentrations

Selenium concentrations showed no enhancement in colony plant foliage even though the presence of Westland petrels enhanced soil Se concentrations by an order of magnitude (Hawke & Wu 2012; Hawke et al. 2017b). The absence of a soil Se effect is unusual, a foliar Se response typically accompanying soil Se concentration changes (Fordyce 2013).

As already discussed, the absence of depth dependence in soil  $\delta^{15}\text{N}$  values in the petrel colony indicates that mycorrhizal symbioses are no longer necessary for plants to obtain N and P. If field measurements of mycorrhizal infection support this view, the absence of a Se enhancement in Westland petrel colony plants could be a consequence of the suppression of mycorrhizal symbioses (Hawke et al. 2017b). Mycorrhizal symbioses are important in driving zinc uptake (Watts-Williams et al. 2015), whereas enhancing the Se status of wheat requires mycorrhizae and/or selenobacteria (Durán et al. 2013).

### Trophic relationships within the colony

Living at an interface between marine and terrestrial environments, seabird colony biota may source C from either system. However, the C in burrowing petrel colonies is compartmentalised with vascular plant C showing no sign of marine origin even in the comparatively dense petrel colonies described above for Snares Islands (Hawke & Newman 2007). Marine C appears only in colony food chains based on the petrels, whether predators consuming live seabirds, necrovores consuming seabird corpses, or detritivores consuming seabird discards. Each of these categories may in turn support higher-order predators, which may be either indigenous or introduced.

For burrow-nesting seabirds such as Westland petrels, animal detritus is deposited inside the burrow and on the surface of the adjacent soil and vegetation. This labile, nutrient rich detritus within and outside the burrow environment provides diverse habitats for unusual invertebrates (Orwin et al. 2016). On the Chathams group of islands almost due east of the Westland petrel site, Emberson (1998) listed two species of the genus *Saprinus* (Histeridae) “commonly associated with petrel burrows and carcasses”; two species from the family Leiodidae (one a Chathams endemic) found on a dead broad-billed prion (*Pachyptila vittata*); *Opedius antipodurn* and a new species of *Creophilus* (both Staphylinidae) from petrel burrows but also found on the forest floor; and *Zeonidicola chathamensis* (Cavognathidae), a species endemic to the Chathams and

associated with petrel burrows. Clark described a predatory mesostigmatic mite *Ayersacarus woodi* from Westland petrel burrows (Clark & Hawke 2011). The genus is endemic to seabird environments on mainland New Zealand and associated islands (Clark & Hawke 2012), and its nine described species exhibit a substantial degree of endemism between locations. Furthermore, the nesting area within burrows contains “many beetles and some chernetine pseudoscorpions” (Jackson 1958), at least during the breeding season. A similar array of invertebrates has been documented with blue penguins *Eudyptula minor* on Motunau Island (off the South Island east coast), where histerid beetles and pseudoscorpions occupy similar isotopic niches but are spatially separated within burrow soil (Hawke & Clark 2010a). Conversely, the higher N content of colony foliage may exclude some herbivores adapted to low nutrient environments (Kurze et al. 2018) while favouring others.

Consumers may specialise in marine or terrestrial C, or depend on a combination of the two. In the Westland petrel system, kererū (*Hemiphaga novaeseelandiae*) depends on terrestrial C, while the mesostigmatic mite *A. woodi* is a burrow-dwelling predator that depends on petrel detritus (Hawke & Holdaway 2005; Clark & Hawke 2011). Conversely, weka (*Gallirallus australis*) is an omnivorous rail that in seabird colonies consumes a mixture of marine and terrestrial C (Hawke & Holdaway 2005; Harper 2007). Outside the breeding season they feed on petrel detritus or petrel detritivores, while chicks are probably predated during breeding.

Hawke et al. (2013) tested the hypothesis that burrow-dwelling invertebrates would be more dependent on marine C than those from the adjacent soil surfaces, but instead found that invertebrates from both environments were utilising mainly terrestrial C. Opportunistic predators such as *Maoriella* (a centipede) are likely to use both terrestrial and marine derived C, but disentangling the contributions from the different sources is challenging given the wide range in foliage  $\delta^{13}\text{C}$ .

Modification of the seabird-colony biota has occurred with the pervasive impacts of introduced mice and rats throughout mainland New Zealand forests (Emberson 1998; Marris 2000; Innes 2005; Ruscoe & Murphy 2005). Emberson’s (1998) survey of the beetle fauna of the Chatham Islands group noted a “relatively large number of species from Rangatira [also known as South East Island] ... [reflecting] its lack of introduced predators (particularly rodents), its areas of relatively intact forest, and the nutrient-rich habitats associated with burrowing seabirds”. He then highlighted the greater diversity and abundance of beetles on Rangatira compared with much larger Pitt Island, which has introduced rodents. The species found on Rangatira but not Pitt Island “fall into three main groups: relatively large, ground inhabiting species, that might be vulnerable to mouse predation...; forest litter inhabiting species...; and species often associated with burrow nesting birds and bird carrion” (Emberson 1998; p. 59).

Rodent abundance and dynamics in Westland petrel colonies are unknown but Jackson (1958) reported that rats were common, and mice are ubiquitous within mainland New Zealand forests (Ruscoe & Murphy 2005). Rats are omnivores, although their dependence on different sources of C within the Westland petrel system is unknown. Other introduced animals known to frequent the colony include goats and dogs, and their effects on the petrels are similarly unknown.

Studies at other sites indicate that lizards would have been more abundant, larger and with faster growth rates at sea-bird colony sites (Markwell & Daugherty 2002; Barratt

et al. 2005, Wright et al. 2013, Briggs et al. 2012; Richardson et al. 2019). Similarly, indigenous bird biodiversity is much reduced in the Westland petrel landscape and guilds such as avian herbivore, aerial insectivore and avian predator either diminished or eliminated (Worthy & Holdaway 2002; Hawke & Holdaway 2005; Lee et al. 2010).

### Implications for plant productivity in petrel colony forest

Few studies have linked the biogeochemistry at seabird colonies to local plant productivity and biomass accumulation. Holdaway et al. (2007) found similar tree growth rates in rimu (*Dacrydium cupressinum*) and matai (*Prumnopitys taxifolia*) at the Westland petrel site and at non-seabird sites in South Westland and Fiordland. However, inter-annual variances between individual trees at the Westland petrel colony were asynchronous, unlike those at the two control sites, perhaps indicating that some other, non-biogeochemical factor limits Westland petrel colony tree growth between years.

The relatively high N (> 1.5%) levels in petrel colony woody foliage (Hawke et al. 2017a) may periodically increase insect herbivory (Onuf et al. 1977), although suppression by rats and mice is likely nowadays. Effects of higher nutrient levels on herbivores include greater abundance, higher body growth rates and a more N-rich stoichiometry (Hawke & Holdaway 2005; Kerpel et al. 2006; Kendrick & Benstead 2013; Welti et al. 2020). These measures are mostly hypothetical for the Westland petrel system, although detritivorous amphipods within the Westland petrel colony have a C:N body stoichiometry enriched in N by 15% (Hawke & Holdaway 2005). Improved nutrient supply in foliage at seabird colonies can also impact vertebrates. A near doubling of foliage N increased the length and mass (the latter by a factor of six) of herbivorous iguanas occupying seabird sites in the Bahamas (Richardson et al. 2019).

Although purely herbivorous indigenous reptiles are absent, kererū, an herbivorous bird, remain common in West Coast forests (including the Westland petrel site). They prefer high nutrient foliage, flowers and fruit (O'Donnell & Dilks 1994), and may potentially benefit (e.g. laying dates, time to fledging, clutches per season, or adult and juvenile survival) from enhanced foliar nutrition found at the Westland petrel site.

Litter fall measurements are difficult in petrel colonies because birds typically tumble through the forest canopy as they return to their burrows. High nutrient forest environments typically have short-lived (Ludovick Achat et al. 2018), rapidly decomposing (Phillips et al. 2013) leaves.

### Box model compartment: Streams draining petrel colonies

#### Nitrogen concentrations and $\delta^{15}\text{N}$ values in stream biota

There is evidence that petrel-derived marine N from colony soils is transferred into streams and taken up by stream biota. These processes are evident in  $\delta^{15}\text{N}$  values, as those in stream biota downstream of Westland petrel colonies are intermediate between streams in the same area without petrels, and plant foliage and soil from the petrel colony (Harding et al. 2004; Gamlen-Greene et al. 2018). However, Gamlen-Greene et al. (2018) found no petrel effect on adjacent stream biota C:N ratios. Consequently, the N from petrels replaces rather than enhances N from riparian or in-stream sources. This most likely reflects an important role for light co-limitation of plants in densely forested streams (Gamlen-Greene et al. 2018).

#### Selenium concentrations in stream biota

As already discussed, Se concentrations showed no enhancement in colony plant foliage, and this absence of enhancement also occurred in stream biota (Hawke & Wu 2012; Hawke et al. 2017b). The absence of a petrel effect on stream biota occurred despite substantial transfer from colony soils to streams inferred from N:Se and P:Se stoichiometry and mass balance considerations (Hawke et al. 2017b).

Hawke et al. (2017) cited literature reports of two Se uptake systems in natural waters; a high affinity system operating at low Se concentrations and a comparatively low affinity system affecting high concentrations. In streams draining Westland petrel colonies the absence of a petrel effect on Se in stream biota could involve saturation of the high affinity Se transport system operating at low concentrations (Hawke et al. 2017b). Alternatively, Se uptake may be affected by interactions with other trace elements. For example, Se detoxifies excessive concentrations of Hg and other toxic trace elements. In this scenario, high Se concentrations often reflect a substantial trace element burden. A good example of this phenomenon in fresh waters is the study by López-Perea et al. (2019), on wetlands affected by wastewater and other human activities. Here, substantial uptake by high trophic level birds was accompanied by significant Hg contamination; sediment Se concentrations were similar to those in Westland petrel colony soils. Finally, the high trophic level vertebrate sampled by Hawke et al. (2017) was an insectivorous fish (the red-finned bully *Gobiomorphus huttoni*), but muscle rather than liver was analysed; muscle has a somewhat lower Se concentration (Li et al. 2019).

#### Implications of an unstable petrel colony history for nutrient and trace element dynamics

The consequences of landslips, erosion and subsequent seabird colony destruction on sediment, nutrient and trace element fluxes to the streams draining Westland petrel colonies are unknown, as are the effects on biogeochemical processes both in-stream and in the riparian zone. However, the consequences of individual extreme storm events have been investigated elsewhere, and the results indicate what might happen in the Westland petrel landscape given that it experiences storms of a wide range of severity. Hurricane Irene and Tropical Storm Lee struck an area of temperate NE USA in late August–early September 2011 while hurricanes Harvey and Irma struck subtropical SE USA in late August–early September 2017. Both events affected streams with a comprehensive range of monitoring instrumentation in place (Irene & Lee; Vidon et al. 2018) or were sampled during and immediately following the storm events (Harvey and Irma; Chen et al. 2019). This area has broadly similar climate (900–2000 mm annual precipitation; mean annual temperature 10–18°C), topography (the affected area included a large segment of the Appalachian Mountains, which reach up to 2000 m) and plant community type (mixed broadleaf-conifer forest) to the area occupied by Westland petrels.

In areas affected by Hurricane Irene and Tropical Storm Lee, stream total N and particulate P exports in reached 15–40 % and 10–125 % respectively of the annual fluxes; total suspended solids often exceeded annual exports (Vidon et al. 2018). In steeper areas affected by the storms, large-scale slope failure and erosion occurred. As might be expected, the infiltration of oxygen-saturated water into the riparian zone lifted the water table in riparian soils and increased the dissolved oxygen content, redox potential, and  $\text{N}_2\text{O}$  and  $\text{CH}_4$

fluxes (Vidon et al. 2017, cited in Vidon et al. 2018).

In the lower-order forest streams affected by hurricanes Harvey and Irma, the storms disproportionately mobilised less bioreactive soil-derived organic material (Chen et al. 2019). Within streams, highly bioreactive organic material was shunted downstream from shaded, light-limited headwater areas (Chen et al. 2019). Infiltration of storm-derived waters carrying both dissolved and colloidal N into the riparian zone would provide a mechanism for the elevated  $\delta^{15}\text{N}$  values of found in riparian plants (2.4 ‰) and soil (2.1 ‰) of streams hosting Westland petrel colonies (Gamlen-Greene et al. 2018).

Combining these observations, the high nutrient and trace element inputs to Westland petrel streams inferred by mass balance calculations (Harding et al. 2004; Hawke 2005) are probably concentrated and mobilised downstream during storm events into the estuarine lagoons that lie along the coastal fringe in the region. One such extreme storm event affecting Westland petrel colonies was Cyclone Ita, and as with the watersheds reported by Vidon et al. (2018), some colonies were more affected than others (Waught et al. 2015a). However, there have been no measurements of plant or sediment nutrient or trace element concentrations in these estuarine lagoons; this remains a major challenge for future research.

### Productivity and biomass accumulation in streams

In terms of petrel colony effects on biomass accumulation and productivity within streams draining petrel colonies, freshwater mussel shells typically record growth conditions in their growth rings and shell mass (Gröcke & Gillikin 2008). The freshwater mussels occasionally found in the study area (kāhahi *Echyridella* sp.) have a decades-century life span, making these shells an important potential environmental record. However, there have been no studies to date.

### Box model compartments across the wider landscape

These compartments (Fig. 2) encompass forest in former colonies within the Westland petrel landscape, forest never occupied by petrels, and estuarine and coastal waters and their riparian and littoral zones.

Transport of seabird-derived nutrients away from nesting colonies may occur via highly mobile animals, of which kererū is an obvious example (Hawke & Holdaway 2005). Both the timing of this mobility and the number of individuals are important. Individual kererū reside locally for days to weeks before moving elsewhere in response to food availability (Powlesland et al. 2011). Based on seed dispersal measurements, virtually all excretion by kererū is within 100 m of the source plant (Wotton & Kelly 2012), implying that nutrient dispersal beyond a petrel colony is minimal (Hawke & Holdaway 2005). More likely, however, are ecological effects where the more nutritious foliage or more abundant herbivores inside the petrel colony lead to consumers exerting stronger top-down effects when they move beyond the colony (Holt 2004). However, measuring or modelling these effects is challenging (Earl & Zollner 2017).

Avian consumers facilitating nutrient transfer across the landscape were potentially greater in prehuman New Zealand. For example, subantarctic Adams Island, an essentially unmodified and mammal-free 10 000 ha island in the Auckland Islands group, hosts several avian taxa that move

between seabird and non-seabird areas. These include snipe (*Coenocorypha aucklandica aucklandica*, an insectivore), red-crowned parakeets (kākārīki; *Cyanoramphus novaezelandiae novaezelandiae*, a herbivore), and bellbirds (korimako; *Anthornis melanura*, an omnivore) (Hawke & Holdaway 2009; Hawke & Miskelly 2009). Bellbirds on Adams Island are especially interesting in that they forage beyond the forest into the littoral zone, and generally live much closer to the ground than in mainland New Zealand (Hawke & Holdaway 2009; Elliott et al. 2020). However, all three of these species are either extinct or much reduced nowadays thus weakening the potential influence of Westland petrel colonies on the surrounding landscape.

### Conservation and management implications

Westland petrel colonies are a remarkable landscape-scale remnant of pre-human New Zealand, even though additional petrel species were almost certainly sympatric in pre-human times. Adams Island again provides a useful analogy, with colonies of white-chinned petrels (*P. aequinoctialis*; a species of similar size to Westland petrels) patchily dispersed within the forested landscape interspersed with colonies of smaller species (especially white-headed petrels *Pterodroma lessonii*) (Elliott et al. 2020; Rexer-Huber et al. 2020). Within the landscape occupied by Westland petrels, the extinct Scarlett's shearwater (*Puffinus spelaesus*) was especially abundant (Worthy & Holdaway 1993). Consequently, the insights into pre-human New Zealand biogeochemistry and ecology provided by present day Westland petrels are important but incomplete.

Although many individual petrel colonies remain on headlands, rock stacks and islands around the New Zealand coast, the Westland petrel system is unusual in that it occupies an entire forested landscape through which colonies move over long time scales. This use of landscape is analogous to salmon in Alaska, where a “shifting habitat mosaic” (Brennan et al. 2019) is fundamental to maintaining the species' landscape-scale productivity. The importance of a landscape-scale seabird colony system was recently demonstrated in the Kaikoura Range following local habitat destruction caused by the 2016 earthquake. Hutton's shearwater (*Puffinus huttoni*) occupy parts of the alpine zone and many colonies were destroyed. Resilience to major disasters is an important feature of landscape – scale colony occupation by Westland petrels, and conservation at this scale is essential in preserving the species and its associated terrestrial and aquatic ecosystems.

Although islands around New Zealand hosting seabirds have been steadily freed of mammalian predators, invasive species affect many others. Motunau Island, which lies off the South Island east coast at a similar latitude to the area occupied by Westland petrels, has a plant community almost completely comprised of invasive weeds but is mammal-free with an abundant reptile and invertebrate fauna (Hawke and Clark 2010b). Conversely, the Westland petrel colonies on mainland New Zealand retain their indigenous vegetation but with a much-diminished reptile, invertebrate and land bird fauna (Hawke & Holdaway 2005).

Any objective of returning the landscape occupied by Westland petrels to some primeval state requires clear definition. Jones et al. (2011) applied Simberloff (1990)'s pioneering work on island restoration into a seabird island context, highlighting the difference between restoration (in comparison with an undisturbed reference site) and passive



recovery (the removal of particular introduced species, such as mammalian predators). Furthermore, ecosystem restoration involves more than simple biodiversity to include nutrient cycling and trophic restoration (Benayas et al. 2009; Kollmann et al. 2016) alongside engagement with indigenous peoples (Peltzer et al. 2019). In terms of nutrient cycling, petrels are ecosystem engineers (Smith et al. 2011) and have a foundational role in the conservation of New Zealand's coastal forest ecosystems.

In terms of biodiversity, a full restoration is impossible because of the post-human extinction of numerous bird and reptile taxa, and, using Simberloff's (1990) categorisation, there is no undisturbed reference site against which to make comparisons. Nevertheless, a large degree of trophic recovery that returns at least some of the formerly present indigenous reptiles, large invertebrates and a greater diversity of birds should be possible through removal of all mammalian predators and grazers.

## Conclusions

Seabird colonies in New Zealand represent the rich diversity of coastal and pelagic seabirds, and are hotspots of intense nutrient and trace element cycling that provide examples of natural nutrient enrichment in terrestrial and stream ecosystems. Using a conceptual box model (Fig. 2) to guide the discussion, this review has highlighted biogeochemical, ecological and biodiversity effects of Westland petrels on land. These effects include loss to waterways as the primary mechanism balancing N, P and trace element inputs from petrel breeding activities, the profound effect of major storms and earthquakes, and the hosting in their burrows of unique invertebrate taxa.

The proposed model remains largely qualitative. Consequently, it would benefit from more estimates of compartment sizes and fluxes that link to ecological effects on the plants and animals living in and near petrel colonies. Furthermore, we have little understanding of the effects of Westland petrels on primary and secondary productivity within colonies (both above- and below-ground) and associated streams, and the mechanisms by which the guano-like stoichiometry of colony soil N and P is maintained. Direct estimation of these quantities in a petrel colony environment is challenging, requiring a broader approach including modelling that incorporates studies in non-seabird systems and glasshouse or mesocosm laboratory experiments. The ecological consequences of Westland petrel-derived foliar nutrient enrichment for life history parameters of more terrestrial herbivorous avian species such as kererū are also completely unknown and difficult to determine. Finally, research on the Westland petrel system has yet to include downstream estuarine and nearshore waters, noting that seabird colonies on islands influence the productivity and biogeochemistry of surrounding waters (Wing et al. 2014; Shatova et al. 2016).

Westland petrel colonies exert their biogeochemical and ecological effects across a temperate forest landscape, and it is this landscape as much as the individual colonies that is unique. Petrel and shearwater colonies occupied broad swathes of suitable habitat across pre-human New Zealand. The Westland petrel landscape therefore provides an opportunity to assess the ecological and biogeochemical processes that applied in those times notwithstanding the effects of mice, rats, mustelids, goats and other introduced mammals. This assessment could contribute to an integrated natural and social history of the

region, which places petrel biogeochemistry and ecology alongside the activities of people past and present.

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### Supplementary material

Additional supporting information may be found in the supplementary material file for this article:

**Appendix S1.** Individual soil profile  $\delta^{15}\text{N}$  values with depth at the Westland petrel colony and at Adams Island; data from Hawke (2005) and Hawke and Holdaway (2009).

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