



Minimal ecosystem uptake of selenium from Westland petrels, a forest-breeding seabird



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HIGHLIGHTS

- Seabirds boost Se in breeding colony soil, but subsequent uptake is unknown.
- Plant foliage from seabird and non-seabird sites had equally low Se contents.
- Seabird and non-seabird stream biota had indistinguishable Se status.
- Incorporation of trace elements brought ashore by seabirds cannot be assumed.

GRAPHICAL ABSTRACT



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ABSTRACT

Endemic Westland petrels (*Procellaria westlandica*) are a remnant of extensive seabird populations that occupied the forested hill country of prehuman New Zealand. Because seabird guano is rich in Se, an often-deficient essential element, we proposed that Westland petrels enhance Se concentrations in ecosystems associated with their breeding grounds. We sampled terrestrial (soil, plants, riparian spiders) and freshwater (benthic invertebrates, fish) components from Westland petrel-enriched and non-seabird forests on the western coast of New Zealand's South Island, an area characterised by highly leached, nutrient-poor soils. Median seabird soil Se was an order of magnitude higher than soil from non-seabird sites (2.2 mg kg^{-1} compared to 0.2 mg kg^{-1}), but corresponding plant foliage concentrations (0.06 mg kg^{-1} ; 0.05 mg kg^{-1}) showed no difference between seabird and non-seabird sites. In streams, Se ranged from 0.05 mg kg^{-1} (riparian foliage) to 3.1 mg kg^{-1} (riparian spiders and freshwater mussels). However, there was no difference between seabird and non-seabird streams. Stoichiometric ratios (N:Se, P:Se) showed Se loss across all ecosystem components relative to seabird guano, except in seabird colony soil where N was lost preferentially. Seabirds therefore did not enrich the terrestrial plants and associated stream ecosystems in Se. We conclude that incorporation of trace elements brought ashore by seabirds cannot be assumed, even though seabirds are a significant source of marine-derived nutrients and trace elements to coastal ecosystems world-wide.

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1. Introduction

Selenium (Se) is an essential trace element found in antioxidant and regulatory proteins (Brown and Arthur, 2001), the best known being the glutathione peroxidases. Although comparatively little is known of the importance of Se deficiencies to individual species in natural habitats unaffected by human activities (Araie and Shairaiwa, 2009), Se deficiency in humans is associated with remarkably diverse health effects. These range from diabetes mellitus to mental illness (Rayman, 2012; Conner et al., 2015), and individuals prioritise biosynthesis of the various selenoproteins in response to their Se status (Howard et al., 2013; Lin et al., 2015). Industrial activities and enriched soil parent material enhance Se in some aquatic systems and terrestrial soils and biota to toxic levels, but low concentrations bordering on deficiency are more common (Fordyce, 2013). In such places, Se from outside sources can be particularly important.

The comparatively high Se concentrations found in marine vertebrates probably assist mercury and cadmium detoxification (Ikemoto et al., 2004; Lovvorn et al., 2013; Siscar et al., 2014). Before global human expansion the marine-terrestrial interface was more porous, with many rivers seasonally occupied by anadromous fish and seabirds breeding considerable distances inland (Doughty et al., 2015). Numerous studies in the systems that still host these marine visitors have shown uptake by terrestrial and stream systems of marine-derived nutrient elements, particularly nitrogen (N). As well as nutrients, seabirds enrich the soils of their breeding and roosting sites with a suite of trace elements, including Se (Xu et al., 2011; Mallory et al., 2015).

Although organic selenides (Se(II)) are particularly important in marine systems, soil solution and freshwater Se is mostly divided between Se(IV) and Se(VI) (Cutter and Cutter, 1995; Baines et al., 2001; Miller et al., 2013). Of the inorganic forms of the higher oxidation states, selenite (Se(IV)) is the more useful to terrestrial plants, but its affinity for soil colloids is stronger than selenate (Se(VI)) thereby decreasing its availability. In turn, the affinity for soil colloids is affected by competing ions sulphate (affecting selenate) and phosphate (affecting selenite) (Hopper and Parker, 1999). Plant uptake of soil Se is controlled by a combination of soil concentration, mineralogy, redox potential, pH and microbial activity, and plant physiology (Fordyce, 2013; Durán et al., 2013). Furthermore, redox speciation and adsorption by soil colloids is highly dynamic under typical soil conditions, so predicting plant response to changes in total Se concentration is problematic.

Although the enrichment of seabird roosting and breeding soils with nutrients and trace elements (including Se) is well known, effects on the wider environment have been largely ignored. The holding capacity of soil for any added element is limited by the availability of binding sites. Once this capacity is exceeded in contexts with unusually high input fluxes, inputs must inevitably be balanced by outputs (Hawke, 2005). Neither Se(IV) nor Se(VI) has a significant gas phase under natural conditions. Consequently, Se inputs from seabirds should ultimately be released into any nearby streams leading to potential Se enhancement of stream biota.

The western coast of New Zealand's South Island (the "West Coast") has localised seabird breeding in forests with strongly leached, infertile soils. Our previous work found unexceptional Se concentrations in seabird colony plant foliage from the West Coast (Hawke and Wu, 2012). In our current study, we hypothesised that even lower concentrations would be found in West Coast soils and plants away from the influence of seabirds, and that stream biota downstream of seabird colonies would be enriched in Se. We also applied a stoichiometric approach (N:Se; phosphorus: Se, P:Se) to determine accumulation patterns within seabird-affected streams.

2. Materials and methods

2.1. Experimental design

Westland petrels are one of the few substantive remnants of the formerly extensive seabird populations in New Zealand. The species is

restricted to the West Coast, with 4000 breeding pairs spread across four forested catchments 1–2 km from the coast (Wood and Otley, 2013). The conservation status of the species is "Vulnerable" (IUCN, 2013), and access to breeding sites and the associated landscape is restricted by conservation authorities to a single colony of 200–400 breeding pairs (Vaugh et al., 2015). The seaward boundary of the area set aside for Westland petrel protection lies just inland of a coastal highway. Access to streams between the protected area and the highway is unrestricted.

In our first comparison we added soil and terrestrial plant sampling from a control location to data from the only accessible West Coast seabird colony site (Hawke and Wu, 2012). Because different plant taxa grow at the control and seabird sites, we included some archival samples from another control site which has a plant taxon (tree ferns *Cyathea* spp.) in common with the seabird site. In our second comparison we sampled streams (including riparian plants and soil) draining all four seabird catchments alongside five control streams.

The other constraint we addressed in our study design was the minimum sample size for Se analysis of 200–500 mg. Given the small sample mass of individual stream invertebrates and the small size of available streams, we needed to allow for the possibility that no stream would yield sufficient material across all functional feeding groups even with pooled samples. We therefore set up sampling to provide paired comparisons between seabird and non-seabird streams across as many functional feeding groups as possible, and sampled all available streams. The small size of the streams, with their highly mobile pebble and cobble substrates, combined with frequent intense rain events to make periphyton sampling impractical.

2.2. Study sites

Samples came from two native forests 175 km apart, Punakaiki (seabird and non-seabird soil, plant and stream samples) and Okarito (non-seabird soil and plant samples) (Fig. 1; Table 1). Both have a mild, humid climate typical of the West Coast, with a mean annual temperature of approximately 11 °C and 2500–3000 mm annual rainfall. Away from areas affected by seabirds, West Coast soils are typically P limited (Parfitt et al., 2005). There were no significant human land uses (e.g. urbanisation or farming) at the localities we sampled.

Okarito Forest is a multi-tiered podocarp rainforest as close to its pre-human state as any in New Zealand, and was included in the study for this reason and to provide a well-characterised locality with highly leached, nutrient-poor soils. The area we sampled (Johnston, 2014) has acidic (pH 4) silt loam soils developed on locally steep glacial outwash moraines. The landscape at Punakaiki comprises deeply dissected hill-country bounded by a narrow coastal plain. The hill-country seabird site we sampled has been occupied by seabirds since at least 1750 (Holdaway et al., 2007) and has acidic (pH 3.5–4.0) silt loam soils developed on Late Miocene – early Pliocene blue-grey muddy sandstone. Soils on the coastal plain adjoining the stream sampling sites are developed on Tertiary gravels (Nathan et al., 2002).

The seabird and non-seabird streams near Punakaiki (Fig. 1; Table 1) are 1st or 2nd order streams in regenerating forest following logging many decades ago. One of the four non-seabird streams, Canoe Creek, is a larger 4th order stream. The streams are slightly acidic (pH 6.4–6.7); with the exception of calcium, major component composition is dominated by sea salt inputs (RG-G and DL, unpub. data). Calcium in seabird streams is enhanced relative to non-seabird streams, potentially either co-leached with nitrate (Likens et al., 1998) or directly from seabird guano. The seabird status of McMillans Creek is unclear, with the valley being used as a petrel flyway to a breeding site just over the catchment boundary. The $^{15}\text{N}/^{14}\text{N}$ (expressed as $\delta^{15}\text{N}$) of stream biota is a useful indicator of seabird inputs (Harding et al., 2004), and $\delta^{15}\text{N}$ of benthic algae from McMillans Creek was lower than three of the four seabird creeks (Scotchmans, Hibernia and Liddys creeks) but higher than Waiwhero Creek (RG-G, unpub. data).

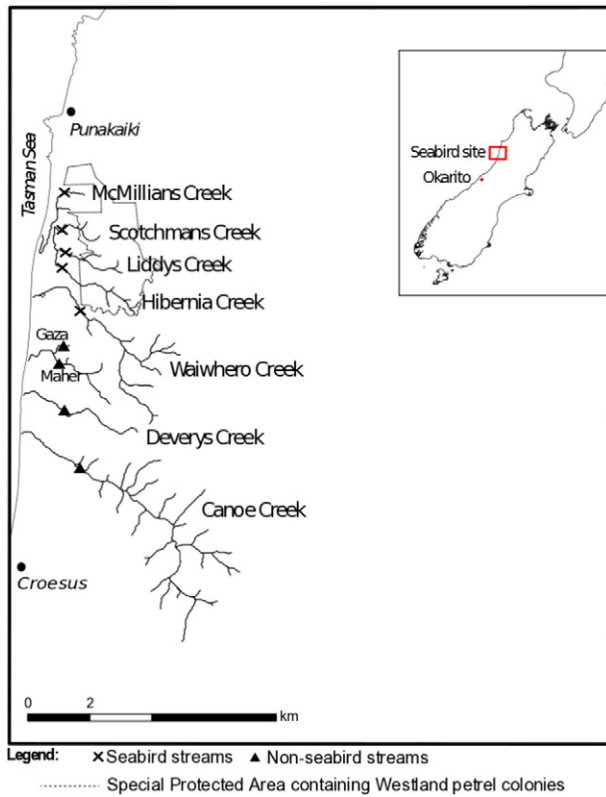


Fig. 1. Location of the study sites on the West Coast of the South Island of New Zealand. Seabird status and samples collected at each site are listed in Table 1.

Given the lack of Se enhancement we found in seabird-affected systems, we used a stoichiometric analysis to investigate patterns of retention and dispersal in two of the seabird streams. We combined results from the two streams with the least human impact (Scotchmans and Hibernia creeks) as demonstrated by the presence of the disturbance-sensitive freshwater mussel *Echyridella*. Scotchmans Creek is also the catchment with the highest Westland petrel population (Wood and Otley, 2013).

2.3. Sample collection

Stream sampling was carried out at single points 0.3–2 km from the coast and 0.8–2.2 km downstream from seabird colonies (if present). A single composite soil sample comprised three cores (15 × 4 cm) 5 m apart either side of each stream, and approximately 1 m from the stream wetted edge. Approximately 50 g (dry weight) of riparian vegetation (live leaves and twigs) representing a selection of plant species was collected within 1 m of the wetted edge. Individual stream benthic

invertebrates, fish, and riparian spiders were collected between December 2013 and March 2014 by kick-net (0.5 mm mesh) and hand-picking for invertebrates and by fish trap. Stream biota samples were assigned to functional feeding groups (grazer, filter feeder, invertebrate predator, fish predator) (Cummins and Klug, 1979). The minimum sample size requirements for the chemical analysis and the small size of the available streams precluded a comprehensive taxon-based collection strategy. Only a single fish species was found across multiple sites (redfin bullies *Gobiomorphus huttoni*). Coarse particulate organic matter (>0.5 mm, CPOM; approximately 50 g dry weight) came from stream bed debris.

Foliage sampling from Okarito Forest involved 4–5 sampling points along each of two 150–250 m transects. Within each sampling point, we collected a foliage sample from each plant within a 2 m radius at 0.1, 1.5 and 3.5 m height; samples were pooled by taxon (tawheowheo *Quintinia serrata*, silver pine *Manoao colensoi*, rimu *Dacrydium cupressinum*, kamahi *Weinmannia racemosa*, kanuka *Kunzea ericoides*, and celery pine *Phyllocladus alpinus*) at each sampling height. Scotchmans Creek seabird forest data (tree fern, $n = 10$; nikau palm *Rhopalostylis sapida*, $n = 10$) came from Hawke and Wu (2012). Scotchmans Creek soil samples were collected from a transect running 50 m downslope through an altitude range of 118–141 m, measured by calibrated barometric altimeter; microbial carbon and isotopic data from these samples have been reported elsewhere (Hawke and Vallance, 2015). Archived non-seabird foliage samples (tree fern, $n = 7$; April 2006) came from the site used as a control by Hawke and Holdaway (2005), and were included to provide a comparison with Scotchmans Creek tree fern. Supporting Scotchmans Creek seabird forest data (soil parent material and Westland petrel guano) came from Hawke (2005) and Hawke and Wu (2012).

2.4. Sample analysis for total Se, total P and total N

Samples for analysis were pooled from 2 to 6 individual animals, except the common stream mayfly *Deleatidium* spp. for which 60 individuals were needed to meet the analytical sample mass requirement. Samples were dried (60 °C) within 48 h of collection, and stored in the dark at room temperature until analysis. Stream invertebrates were degutted before analysis and all instars and body sizes were used; the shell was excluded from mussel analysis. Abdominal muscle was used for fish analysis, muscle being the dominant tissue mass-wise. Plant material (including CPOM) was extracted with tetramethyl ammonium hydroxide (90 °C for 1 h; Fecher et al., 1998) or microwave-assisted nitric acid/hydrogen peroxide (CEM MARS 5 Express; Araújo et al., 2002). Soil was extracted with nitric acid/hydrochloric acid (US EPA Method 200.2). Analysis of sample digests for Se and P used inductively coupled plasma-mass spectrometry (ICP-MS; Perkin Elmer ELAN DRC Plus, Perkin Elmer ELAN DRC II, or Agilent 7700). Analysis of foliage and soil samples for N used continuous flow isotope ratio mass spectrometry; the concentration data were collected as part of a stable isotope study to be reported elsewhere.

Table 1
Sampling design, according to the locations in Fig. 1.

Region	Location	Seabirds present	Terrestrial soil and foliage samples	Stream biota, riparian plants and soil samples
Punakaiki	Scotchmans Creek	Yes	Yes ^a	Yes
	Liddys Creek	Yes	No	Yes
	Waiwhero Creek	Yes	No	Yes
	Hibernia Creek	Yes	No	Yes
	McMillans Creek ^b	?	No	Yes
	Gaza Creek	No	No	Yes
	Maher Creek	No	No	Yes
	Deverys Creek	No	No	Yes
	Canoe Creek	No	No	Yes
Okarito	Croesus	No	Plant foliage only	No
	Okarito Forest	No	Yes	No

^a Hawke and Wu (2012).

^b Used by Westland petrels as a flight path to a colony just outside the catchment boundary in its upper reaches (G.C. Wood, conversation with DJH 13 August 2015).

2.5. Data analysis

Because a small number of samples had Se concentrations below the analytical limit of detection, we used medians and quartiles for summary statistics where there was a sufficient sample size. In the stream comparisons we used standard deviation rather than quartiles, because of the small number of streams. Homogeneity of the terrestrial foliage data was assessed using a chi-squared test. Comparison of seabird and non-seabird soil and tree fern results used the non-parametric Mann-Whitney *U*. The comparison between seabird and non-seabird stream food web components included a wide range of Se concentrations, so we used the paired non-parametric Wilcoxon test after log transforming the data. Statistical analysis used the software package PAST (University of Oslo, Norway).

3. Results

3.1. Seabird and non-seabird forest soil and plants

Okarito non-seabird forest soil concentrations (median, 0.2 mg kg^{-1} ; LQ, $<0.2 \text{ mg kg}^{-1}$; UQ, 0.3 mg kg^{-1} ; $n = 8$) were an order of magnitude lower than Hawke and Wu's (2012) Scotchmans Creek seabird forest data ($2.2, 1.8, 2.3 \text{ mg kg}^{-1}$; $n = 10$) (Mann Whitney $U = 0$; $p < 0.001$). In contrast, Okarito forest foliage concentrations ($0.03\text{--}0.06 \text{ mg kg}^{-1}$) were remarkably similar to the published results from Scotchmans Creek seabird forest (Fig. 2), even though the nikau palm data from Hawke and Wu (2012) were somewhat variable. Tree fern species were the only plant taxon in common between seabird and non-seabird forest sites ($n = 10$; $n = 7$, respectively) and foliage concentrations overlapped (Mann Whitney $U = 20.5$, $p = 0.17$) (Fig. 2). Across the seven terrestrial plant taxa sampled (including tree ferns), foliar Se concentrations fitted a chi-squared distribution ($\chi^2 = 0.031$; $df = 7$, $p > 0.995$).

3.2. Stream biota (including riparian plants and soil)

Within streams, Se concentrations increased from 0.1 mg kg^{-1} at the base of the food web (CPOM) to $1\text{--}3 \text{ mg kg}^{-1}$ for predators (fish; riparian spiders; and toebiters) (Fig. 3). Redfin bully data came from all 5 seabird streams and 3 of the non-seabird streams; *Paranephrops* (an omnivorous freshwater crayfish), *Dolomedes* (an aquatic spider) and *Archichauliodes diversus* (a megalopteran or toebiter) came from 1 seabird and 1 non-seabird stream; and the common mayfly (*Deleatidium* spp.) came from 1 seabird stream. Filter-feeding mussels (*Echyridella*) contained a Se concentration comparable to stream predators but live animals were found only in a single seabird stream (Hibernia Creek)

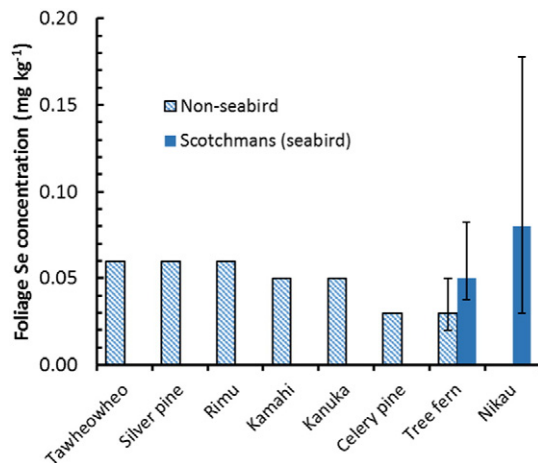


Fig. 2. Terrestrial foliage data by taxon; taxa with individual samples are plotted as medians with upper and lower quartiles. Systematic plant names are given in the Materials and methods section.

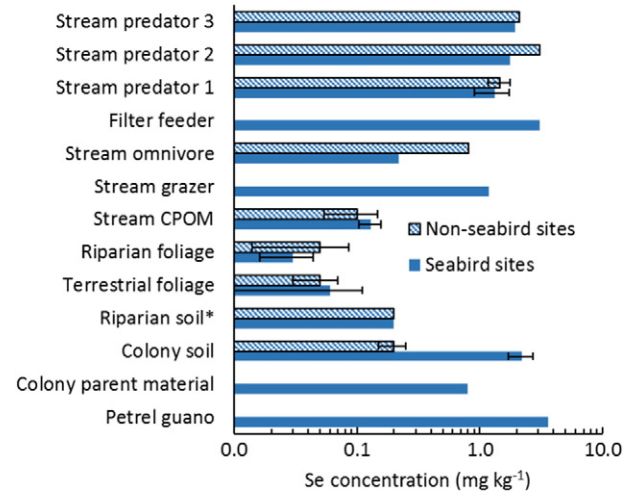


Fig. 3. Combined terrestrial and stream Se medians; riparian soil results were all less than the limit of detection (0.2 mg kg^{-1}) and are shown by an asterisk. Error bars for replicated samples are standard deviations. Key to feeding groups: stream predator 1, redfin bully; 2, *Dolomedes* spider; 3, megalopteran *Archichauliodes*; filter feeder, mussel *Echyridella*; stream omnivore, crayfish *Paranephrops*; stream grazer, mayfly *Deleatidium*.

despite extensive searches; a few fresh shells were found in Scotchmans Creek.

3.3. Whole-ecosystem comparisons

Concentrations of Se were not affected by the presence of Westland petrels (Wilcoxon paired sample test; $n = 8$, $W = 21$, $p = 0.74$; Fig. 3). This result at an ecosystem level occurred despite concentrations ranging across $1\frac{1}{2}$ orders of magnitude and high concentrations in petrel colony soil.

Stoichiometric plots using the Scotchmans and Hibernia creek samples (Fig. 4) showed that Westland petrel guano was more Se-enriched relative to both N and P than any of the stream components measured (riparian vegetation, CPOM, invertebrate grazer, invertebrate filter feeder, and predatory fish) except riparian soil. Furthermore, riparian soil P concentrations were low (Scotchmans Creek, 310 mg kg^{-1} ; Hibernia Creek, 350 mg kg^{-1}) and Se concentrations were below the analytical detection limit (0.2 mg kg^{-1}), driving a low P:Se ratio (Fig. 4). Even the filter feeding mussel *Echyridella* did not approach the level of Se enhancement relative to N and P found in petrel guano. Colony soil had a N:Se ratio intermediate between petrel guano and soil parent material, but the colony soil P:Se ratio was higher than both guano and parent material. However, colony vegetation assimilated Se much more weakly than either N or P.

4. Discussion

The absence of a seabird effect on the Se content of forest plant foliage from the petrel colony was surprising, given an extensive literature showing plant Se enhancement from either Se addition or seleniferous soils (Hu et al., 2014; Yasin et al., 2015). Although terrestrial plants do not appear to require Se for their own metabolism, uptake varies widely (Munier-Lamy et al., 2007). Uptake of soil Se by terrestrial plants is greatest in the presence of selenobacteria and/or mycorrhiza (Larsen et al., 2006; Durán et al., 2013), when competing ions such as sulphate (selenate) or phosphate (selenite) are present in low concentrations (Hopper and Parker, 1999; Liu et al., 2015), and when the Se is present as selenate rather than selenite (Hopper and Parker, 1999; Yu et al., 2011). Redox speciation is the least likely of these explanations because selenite-Se rather than selenate-Se controls Se distribution in Scotchmans Creek seabird colony soil (Hawke and Wu, 2012). The

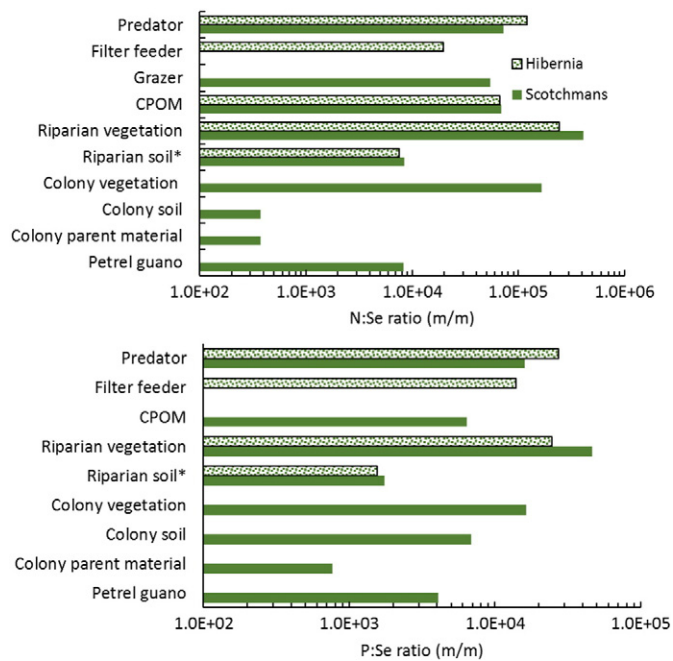


Fig. 4. Nitrogen: Se and phosphorus: Se for two seabird streams (Hibernia and Scotchmans creeks). Descriptors: Predator, redfin bully; Filter feeder, freshwater mussel *Echyridella*; Grazer, mayfly *Deleatidium*. Riparian soil Se was below detection limit so the ratios (denoted by asterisks) are minimum values. Parent material data sources: Hawke (2005; N, P); Hawke and Wu (2012; Se).

acidic soil pH, humid climate and silty soil texture suggest a similar speciation at Okarito Forest.

Turning to a possible microbial explanation for the similarity between seabird and non-seabird forest foliage Se, microbial biomass is carbon-limited in Scotchmans Creek seabird soil and much lower than at Okarito Forest (Hawke and Vallance, 2015). Alongside the likely favouring of bacteria over fungi (Treseder, 2008; Wright et al., 2010), the high soil nutrient status of seabird soil potentially inhibits the mycorrhizal contribution to plant nutrition (Treseder, 2004). A similar effect was reported by Kardol et al. (2014), where exclusion of ungulates (and their excreta) drove higher levels of mycorrhizal colonisation of forest plants. A recent study of zinc uptake found that the mycorrhizal contribution to plant zinc status decreased as soil zinc concentration increased (Watts-Williams et al., 2015). Furthermore, Ova et al. (2015) were able to directly link decreased zinc uptake to the inhibition of mycorrhiza by high soil P concentrations.

The combination of the carbon limitation of soil microbes in nutrient-saturated seabird soil and the likely inhibition of mycorrhizal nutrient uptake suggests that the mycorrhizal contribution to plant Se status in our seabird soil was correspondingly low. Furthermore, the abundance of P accessible by plants growing in seabird soil (Hawke and Condon, 2014) is also likely to inhibit selenite-Se uptake by roots (Hopper and Parker, 1999). Conversely, the low nutrient status of Okarito Forest soil and the plants it supports (DJH, unpub. data) potentially increased the mycorrhizal contribution to plant nutrition, and removed potential competition from soil phosphate.

Effects at the base of the food web may also underlie the absence of a seabird effect we found within streams. The Se distribution within stream food webs depends on the concentration and speciation of dissolved Se, its uptake by primary producers, and subsequent transfer to higher trophic levels (Stewart et al., 2010). Although Se uptake by aquatic primary producers in culture follows a log-linear relationship with Se concentration (Conley et al., 2011), these measurements are often performed at the micromolar levels found in highly degraded systems such as mining sites. In contrast, uptake at the nanomolar concentrations typical of more natural systems is independent of Se

concentration (Baines and Fisher, 2001). This difference in concentration dependence is due to two different transport systems, a high-affinity and easily saturated Se-specific transport system operating at low concentration and a non-specific system at higher concentration (Araie and Shairaiwa, 2009; Gojkovic et al., 2015). Although we did not measure either dissolved Se or algal Se, our inability to detect enhanced Se enhancement in seabird stream invertebrates and fish is consistent with the absence of a concentration response at the base of the food web reported elsewhere (Baines and Fisher, 2001). However, both the proposed saturation of Se uptake systems in seabird streams and the role of seabird nutrients in soil mycorrhiza inhibition both need to be confirmed.

The N:Se and P:Se stoichiometric data from the two seabird streams were greater than that for petrel guano and therefore also consistent with a system essentially saturated with Se. Furthermore, the enhanced N:Se and P:Se implies that the entire stream system was preferentially losing Se. The extra Se from seabirds may simply not be required, perhaps because stream biota do not need to accumulate Se to detoxify the high levels of mercury and cadmium often found in pelagic seabirds. Although we have no mercury data, the cadmium concentrations in our redfin bully samples ($n = 7$; range, 0.014–0.070 mg kg⁻¹; median, 0.031 mg kg⁻¹; RG-G and DJH, unpub. data) showed no relationship with Se (Spearman's rank $p = 0.92$).

Freshwater mussel *Echyridella* shells are abundant in prehistoric Māori midden deposits (Smith, 2013), indicating that they were a common source of food for the early settlers of New Zealand. Like other mussels, their mode of feeding leads to accumulation of trace metals (Roper and Hickey, 1995). We were unable to compare the Se status of seabird stream and non-seabird stream *Echyridella*. Despite thorough searching, the only sign of *Echyridella* was in Scotchmans and Hibernia creeks; shells, and no live animals were found in Scotchmans Creek. Although formerly widely distributed in streams (Winterbourn, 2004) and lakes (Rowe and Schallenberg, 2004), the genus is “in decline” (Hitchmough et al., 2007). Seabirds contribute substantially to the trace element status of terrestrial environment (Xu et al., 2011) and they produce large quantities of ammonia (Riddick et al., 2012). The mussel's glochidia larvae are susceptible to ammonia and various metals (Clearwater et al., 2014), so finding *Echyridella* only in seabird streams was a surprise; all the creeks we sampled have abundant native fish as potential larval hosts (Walker et al., 2001). However, the comparative abundance of calcium in seabird streams may have assisted shell formation in an otherwise low-calcium environment.

Detritus transport across ecosystem boundaries is a well-known driver of processes in recipient systems (Vanni et al., 2004). Attention is now focusing on the elemental stoichiometries of these flows as they affect food web dynamics (Sitters et al., 2015). The emphasis in the ecological stoichiometry literature has typically been on nutrient elements (carbon, N, P; Sterner and Elser, 2002). The ecological stoichiometric argument should also apply to trace elements, since trace elements are just as necessary for biological function as the traditional nutrient elements. Expressed in stoichiometric terms, the active discrimination against Se for P but not N relative to petrel guano in our seabird colony soil data most likely came from the high environmental mobility of N. Although soil N:Se was intermediate between parent material and guano, a substantial contribution to soil N from parent material (sensu Morford et al., 2016) seems unlikely given the overwhelming guano N inputs to seabird soils (Furness, 1991).

The combination of sensitivity to disturbance, high conservation status, and the often small area of individual roosting and breeding sites is particularly challenging for studying the biogeochemistry of seabirds ashore. As already noted, these were fundamental factors in our study design and in general they limit the replication available to a researcher. To compensate, conclusions must be tested at multiple sites especially when results from a particular study are unexpected. The minimal effect of seabird Se in our study contradicts results from highly modified aquatic and agricultural systems, so we recommend that researchers

test our findings at further seabird sites as well as exploring Se uptake by both soil and stream primary producers.

5. Conclusions

We had expected that the order of magnitude difference in soil Se concentrations between otherwise similar seabird and non-seabird systems would translate to higher seabird colony plant foliage concentrations, but surprisingly we did not find this. Similarly, the Se status acquired by Westland petrels in the marine environment was not transferred to stream biota. Despite an abundance of marine-derived Se from seabirds, our results consequently showed that incorporation of trace elements brought ashore by seabirds cannot be assumed. Seabirds may therefore not have been an ecologically-significant historic source of Se to terrestrial and stream ecosystems in New Zealand. However, study at further sites is warranted.

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