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To cite this article: D. J. Hawke & J. Newman (2007) Carbon-13 and nitrogen-15 enrichment in coastal forest foliage from nutrient-poor and seabird-enriched sites in southern New Zealand, New Zealand Journal of Botany, 45:2, 309-315, DOI: [10.1080/00288250709509719](https://doi.org/10.1080/00288250709509719)

To link to this article: <http://dx.doi.org/10.1080/00288250709509719>



Published online: 18 Feb 2010.



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Carbon-13 and nitrogen-15 enrichment in coastal forest foliage from nutrient-poor and seabird-enriched sites in southern New Zealand

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Abstract To assess the effect of nutrient inputs from breeding seabirds on forest foliage $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, we collected foliage samples from two contrasting locations. *Olearia lyallii* forest on North East Island at The Snares hosts large numbers of (in particular) breeding sooty shearwaters (*Puffinus griseus*). At Mason Bay (Rakiura/Stewart Island), samples of *Brachyglottis rotundifolia*, *Griselinia littoralis*, and *Dracophyllum longifolium* were collected from two strata within diverse dune forest and one stratum from the open dunes. The $\delta^{13}\text{C}$ results were typical of C_3 plants and did not differ significantly between Mason Bay and North East Island. In contrast, the $\delta^{15}\text{N}$ results from Mason Bay (mean \pm standard deviation, $-6.1 \pm 1.7\text{‰}$) were significantly lower than expected for temperate forest (95% confidence interval of difference, 2.7–3.9‰), and dramatically lower ($19.1\text{--}21.5\text{‰}$) than North East Island where enrichments ($+14.2 \pm 3.1\text{‰}$) were among the highest ever reported for vegetation.

Keywords *Brachyglottis*; *Dracophyllum*; *Griselinia*; *Olearia*; Snares; sooty shearwater; Stewart Island

INTRODUCTION

Although much reduced from pre-human times, many coastal areas around New Zealand and elsewhere serve as breeding and resting habitat for seabirds and seals. The effect of the ensuing disturbance on plant communities is well known (Warham 1996; Bancroft et al. 2005), with the likelihood that plants such as *Lepidium* depend on the extreme nutrient status and repeated disturbance (Norton et al. 1997).

Unlike most traditional ecological methods, stable isotope analysis can be used to trace nutrient flows directly. Most elements have more than one stable (non-radioactive) isotope, with the lighter isotope predominating. The isotopes of a given element differ in their physical properties and reaction rates. Consequently, ratios of isotopes such as carbon-13/carbon-12 ($\delta^{13}\text{C}$) and nitrogen-15/nitrogen-14 ($\delta^{15}\text{N}$) change as the elements concerned move through ecosystems. Applications to plant science encompass both ecology and physiology and include exploring responses to water stress (Edwards et al. 2000), elucidating nutrient sources (Tozer et al. 2005), and developing predictive models for soil processes that affect plant-available nutrients (Vervaeet et al. 2002).

Values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in vegetation can be affected by environmental factors operating over many spatial scales. Tropical forest foliage $\delta^{15}\text{N}$ increases toward the tropics, related to the greater availability of N in (and losses from) tropical forests (Martinelli et al. 1999). At smaller spatial scales, animal breeding and resting sites have high soil $\delta^{15}\text{N}$ arising primarily from ammonia volatilisation (Mizutani et al. 1986; Hawke 2001). Forest vegetation $\delta^{13}\text{C}$ is affected by light (the canopy effect; Heaton 1999), nutrient stress (Clay et al. 2001), and moisture stress due to temperature and humidity (Edwards et al. 2000) and salt (van Groenigen & van Kessel 2002). Within this context, the aim of our study was to evaluate the response of foliage $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ to extreme differences in nutrient status arising from seabird breeding.

MATERIALS AND METHODS

Study area

We sampled forest supporting a high density of breeding seabirds (probable nutrient excess) and forest growing on sand dunes (probable nutrient stress), at sites with similar rainfall. Samples were collected from Mason Bay on Rakiura/Stewart Island, and North East Island at The Snares. North East Island is the largest (280 ha) of the islands which make up The Snares, 105 km SSW of Rakiura at 48°07'S. Mason Bay is a 10 km long sandy beach on the western side of Rakiura, and is backed by extensive sand dunes. Peat soils dominate at The Snares (Marshall 1909 in Fineran 1969), while at Mason Bay the forest grows in poorly developed soil on granitic sand (Johnson 1992; pers. obs.). Annual rainfall at The Snares is poorly known; Flint & Fineran (1969) recorded a daily mean of 5.7 mm (2100 mm year⁻¹) from measurements over 19 days in 1961. No data exist for Mason Bay, but on nearby Whenua Hou (Codfish Island) annual rainfall is 1546 mm (mean for 1992–2002; G. Harper pers. comm.).

The Snares hosts a high density of breeding seabirds, particularly sooty shearwaters (titi; *Puffinus griseus*) which number in the millions (Miskelly et al. 2001). No colonial seabirds breed at Mason Bay, although New Zealand dotterels (*Charadrius obscurus*) use sand flats behind the dunes for roosting. Mason Bay was formerly home to a breeding population of South Georgian diving petrels *Pelecanoides georgicus* (Holdaway et al. 2003), but this population has been extinct for hundreds of years.

The majority of North East Island is almost exclusively tupare (*Olearia lyallii*) forest (Fineran 1969). Vegetation at Mason Bay was described by Johnson (1992). In the central sector of Mason Bay, dune forest of moderate slope immediately south of Big Sandhill consists of rata (*Metrosideros umbellata*) and rimu (*Dacrydium cupressinum*) with an understorey primarily of inaka (*Dracophyllum longifolium*), broadleaf (*Griselinia littoralis*), and muttonbird scrub (*Brachyglottis rotundifolia*). On gentle slopes either side of Duck Creek, immediately behind the beach proper, is a diverse low forest of *Coprosma* spp., *G. littoralis*, *D. longifolium*, *B. rotundifolia*, and cabbage tree (*Cordyline australis*) with patches of manuka (*Leptospermum scoparium*) grading to introduced marram grass (*Ammophila arenaria*) and scattered *B. rotundifolia*. The canopy in the Duck Creek forest is more wind-shorn than forest on Big Sandhill.

Sample collection and analysis

Samples were collected in April 2001 and December 2002 (Mason Bay), and January–February 2002 (North East Island). At Mason Bay, three strata were selected. Samples from individual trees (11 *B. rotundifolia*, 10 *D. longifolium*, 10 *G. littoralis*) in forest on moderate slopes on Big Sandhill were collected from 9 transects 100 m apart, running into the forest from its northern edge. Thirteen *B. rotundifolia*, 11 *D. longifolium*, and 11 *G. littoralis* samples from forest on gentle slopes at Duck Creek were collected from 8 transects 100 m apart across the valley. Twelve *B. rotundifolia* samples were collected from 4 open sites with marram grass as the dominant plant in sand dunes behind the beach. Two sites were 200 m apart, immediately adjacent to the beach; the other 2 were 50 m inland of the beach sites. At each site, 3–5 trees at least 10 m apart were sampled. On North East Island 7 *O. lyallii* samples came from randomly established transects set up for studies of *P. griseus* breeding ecology. All vegetation samples consisted of 50–200 g foliage from a single tree, 1.5–2.5 m above the ground. No attempt was made to differentiate between leaves grown in different years. Samples were stored in sealed polythene bags in a cool, dark place. In the laboratory, leaves were removed from supporting branchlets then dried in an oven at 60°C.

Total N, $\delta^{15}\text{N}$, total C, and $\delta^{13}\text{C}$ were determined in duplicate using a Europa Geo 20/20 elemental analyser – isotope ratio mass spectrometer at GNS Science Ltd (Lower Hutt, New Zealand). The isotope ratios were calculated as a per mil (‰) deviation from atmospheric N ($\delta^{15}\text{N}$) and the international limestone standard VPDB ($\delta^{13}\text{C}$):

$$\delta (\text{‰}) = 1000 \times (R_{\text{sample}} - R_{\text{standard}}) / R_{\text{standard}}$$

where R_{sample} is the ratio of the heavy to the light isotope and R_{standard} is the corresponding ratio for the standard. Results were validated during each analytical run by replicated comparisons with NBS-22 and ANU sucrose ($\delta^{13}\text{C}$), and N-1 ($\delta^{15}\text{N}$) standards. The standard error of repeated analysis of isotope standards for was 0.1‰ ($\delta^{13}\text{C}$) and 0.2‰ ($\delta^{15}\text{N}$). The means \pm 95% confidence intervals of the absolute differences between the 85 analysis duplicates in the study were $0.14 \pm 0.03\text{‰}$ ($\delta^{13}\text{C}$), $0.26 \pm 0.04\text{‰}$ ($\delta^{15}\text{N}$), $0.8 \pm 0.2\%$ (total C), and $0.04 \pm 0.01\%$ (total N). The total C and total N data were used to calculate C:N ratios for checking assumed site nutrient status; a higher C:N ratio is expected in forest growing on sand dunes.

Statistical methods

Differences in isotopic enrichments and C:N ratios were determined using one-way ANOVA with Island, Strata, and Species pooled into groups and post hoc planned contrasts used to test for differences between factors; significance was accepted at $P = 0.05$. Comparison of $\delta^{15}\text{N}$ results with the temperate forest foliage data set of Martinelli et al. (1999) used a t -test with Welch's correction for potentially unequal variances.

RESULTS

The two islands differed significantly for all analyses except $\delta^{13}\text{C}$ (Table 1), the $\delta^{13}\text{C}$ results being typical of terrestrial C_3 plants (range -32.7‰ to -24.6‰ ; Fig. 1). Bearing in mind that atmospheric N_2 is the reference for the $\delta^{15}\text{N}$ scale, *O. lyallii* from the seabird breeding island was highly enriched in ^{15}N (range $+8.3$ to $+17.6\text{‰}$; mean $+14.2\text{‰}$; standard deviation 3.1‰ ; $n = 7$) while all samples from Mason Bay were depleted (range -1.0 to -9.1‰ ; mean -6.1‰ ; standard deviation 1.7‰ ; $n = 78$). Mason Bay $\delta^{15}\text{N}$ results were significantly lower than data collated by Martinelli et al. (1999) for temperate forest foliage ($P < 0.0001$; $t = 11.454$; d.f. = 165; 95% confidence interval of difference, 2.7 – 3.9‰) but North East Island $\delta^{15}\text{N}$ results were significantly higher ($P < 0.0001$; $t = 14.280$; d.f. = 6; 95% confidence interval of difference, 14.1 – 19.9‰). We recognise that our sampling was somewhat unbalanced, with fewer samples from North East Island. However, the differences we observed for $\delta^{15}\text{N}$ were

so large that we believe the interpretation of the results to be reliable.

The site contrasts in $\delta^{15}\text{N}$ at Mason Bay between Big Sandhill and the two locations on gentler terrain were both significant whereas the contrast between dune and Duck Creek was not. The species effects involving *B. rotundifolia* were comparatively small but significant, but the contrast between *D. longifolium* and *G. littoralis* was insignificant. The difference between Mason Bay and North East Island data (c. 20‰) was much larger than the differences between individual species or sites at Mason Bay (both c. 2‰). All $\delta^{13}\text{C}$ site contrasts at Mason Bay were significant with Big Sandhill data being most depleted and data from dune trees being least depleted. Two of the three $\delta^{13}\text{C}$ species contrasts at Mason Bay were significant, the exception being *D. longifolium* and *G. littoralis*.

Foliage from North East Island had much higher total N and lower C:N than that from Mason Bay (Tables 1 and 2). The three sites at Mason Bay did not differ in either total N or C:N. Although we did not measure soil nutrient availability, nitrate and ammonia concentrations are high in the peat soils of active seabird colonies (Hawke & Newman 2004) while soil N is low in many sandy soils (Batjes 1996). The substantially lower C:N ratio in the North East Island samples is consistent with a higher nutrient status than at Mason Bay. The abundance of *O. lyallii* is also consistent with our nutrient availability assumptions. While *O. lyallii* is dominant on North East Island (Fineran 1969) and absent from Mason Bay (Johnson 1992), it is found in forest elsewhere on Rakiura (Wilson 1994).

Table 1 Results of statistical analysis using one-way ANOVA of $\delta^{13}\text{C}$ (‰), $\delta^{15}\text{N}$ (‰), N concentration (% m/m), and C:N ratio (m:m) data, presented as difference \pm 95% confidence interval. Only contrasts which yielded ≥ 1 significant difference are shown; all significant contrasts were significant at $P < 0.001$. NS, $P > 0.05$; NEI, North East Island; BSH, Big Sandhill; DC, Duck Creek; DI, *Dracophyllum longifolium*; GI, *Griselinia littoralis*; Br, *Brachyglottis rotundifolia*.

Type of Contrast	Contrast	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	Total N	C:N
Island Site at Mason Bay	NEI–Rakiura	NS	20.3 ± 1.2	0.50 ± 0.09	-25 ± 6
	BSH–DC	-1.7 ± 0.7	-1.6 ± 0.7	NS	NS
	BSH–Dune	-3.8 ± 1.0	-1.7 ± 1.0	NS	NS
	DC–Dune	-2.0 ± 1.0	NS	NS	NS
Species at Mason Bay	DI–GI	NS	1.8 ± 0.9	-0.39 ± 0.07	32 ± 5
	Br–DI	1.7 ± 0.8	-1.2 ± 0.8	0.21 ± 0.06	-25 ± 4
	Br–GI	1.1 ± 0.8	NS	-0.18 ± 0.06	7 ± 4

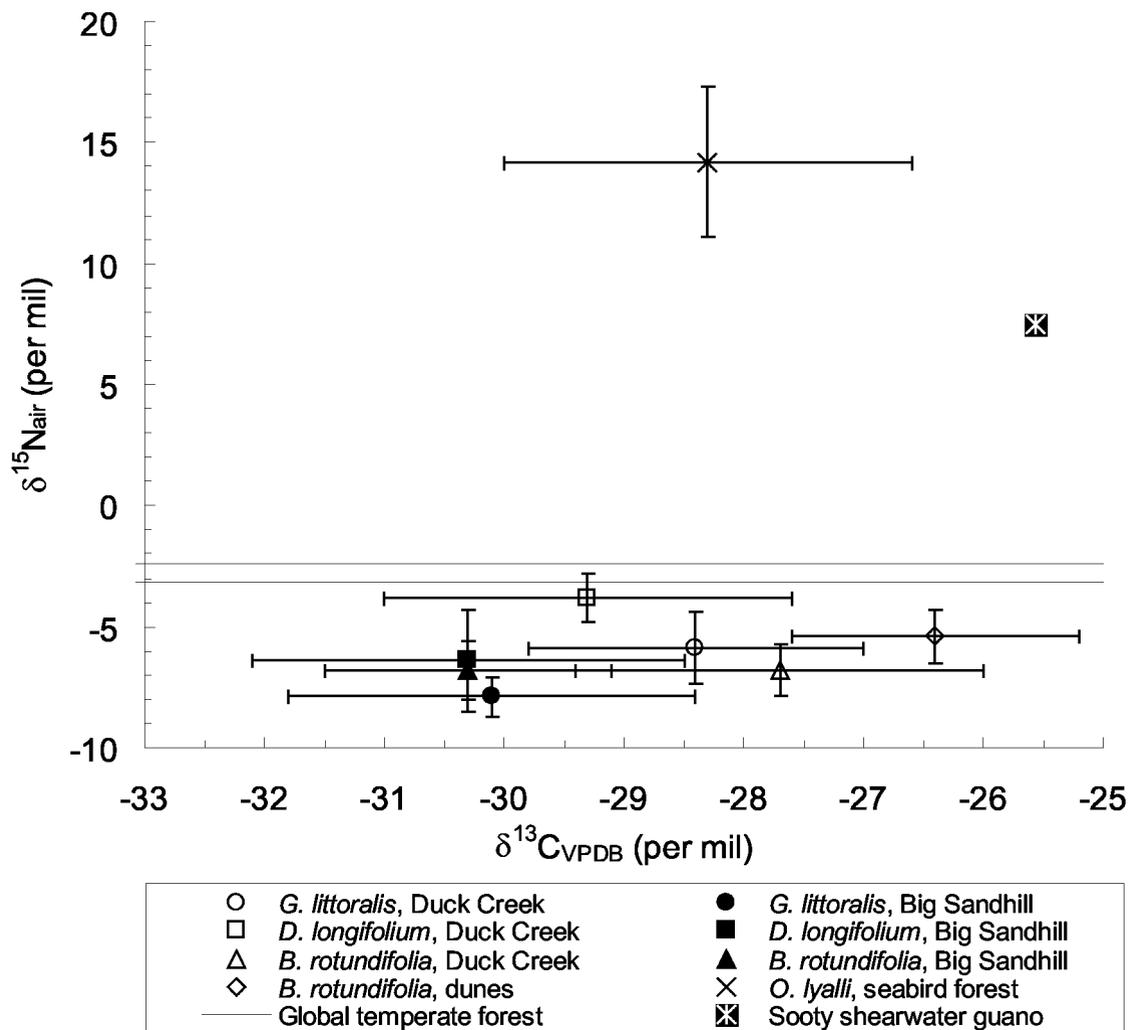


Fig. 1 Plot of $\delta^{13}\text{C}$ against $\delta^{15}\text{N}$ showing means for each species at each location. The error bars show ± 1 standard deviation; sample sizes are given in the Methods. The global temperate forest foliage data for $\delta^{15}\text{N}$ collated by Martinelli et al. (1999) are shown as the upper and lower bounds of the 95% confidence interval of the sample mean. The isotopic signature of sooty shearwater guano is shown for comparison; the $\delta^{13}\text{C}$ data are from Thompson et al. (2000) and the $\delta^{15}\text{N}$ data from Hobson et al. (1994), corrected for guano-tissue fractionation of -5.0‰ ($\delta^{13}\text{C}$) and -4.2‰ ($\delta^{15}\text{N}$) calculated from data for Westland petrels *Procellaria westlandica* (DH unpubl. data).

Table 2 Elemental composition data for each species, as mean ± 1 standard deviation.

Species; n	N (%)	C:N (m:m)
<i>D. longifolium</i> ; 21	0.60 ± 0.08	77 ± 10
<i>G. littoralis</i> ; 21	0.99 ± 0.15	45 ± 6
<i>B. rotundifolia</i> ; 36	0.81 ± 0.14	53 ± 9
<i>O. lyalli</i> ; 7	1.30 ± 0.12	33 ± 3

DISCUSSION

The comparison between nutrient poor (Mason Bay) and seabird-enriched (North East Island) locations yielded remarkable differences in $\delta^{15}\text{N}$ but insignificant effects on $\delta^{13}\text{C}$. Foliage $\delta^{15}\text{N}$ at Mason Bay was among the lowest reported anywhere in the world, with nearly all results falling below the mean for

temperate forests of $-2.8 \pm 2.0\%$ (Martinelli et al. 1999). By comparison, the minimum reported values for forest tree foliage are c. -11% , from Alaska (Hobbie et al. 2000, 2005). Conversely, the results for *O. lyalli* from North East Island were higher than for all other sites, tropical or temperate, reported by Martinelli et al. (1999). The only comparable enrichments we know of were not in forest but in tussock near a penguin colony on Macquarie Island (Erskine et al. 1998).

^{13}C enrichment

All $\delta^{13}\text{C}$ results fell within the range of terrestrial C_3 plants (typically -34 to -22% ; O'Leary 1995); the difference between Mason Bay and North East Island was insignificant. The absence of a location effect was contrary to expectations, because N stress usually decreases $\delta^{13}\text{C}$ by maximising the physiological discrimination against $^{13}\text{CO}_2$ (Clay et al. 2001). The absence of a significant difference may be the result of differences in foliage $\delta^{13}\text{C}$ between species (Edwards et al. 2000).

We observed significant site effects at Mason Bay. Foliage from Big Sandhill forest had more negative $\delta^{13}\text{C}$ values than Duck Creek forest, with foliage from the dunes being the most depleted. The depletion at Big Sandhill was very likely a canopy effect, due to the low light levels experienced by subcanopy plants (Heaton 1999). Water stress leads to less negative values of $\delta^{13}\text{C}$ (Edwards et al. 2000). Nitrogen stress implies a shortage of N for protein formation hence less depletion of CO_2 within the leaf, and more negative $\delta^{13}\text{C}$ values. With respect to water stress, we sampled canopy plants from Duck Creek forest but dune *B. rotundifolia* were totally exposed to salt-laden winds. It is hard to imagine that dune *B. rotundifolia* were less water stressed than plants from Duck Creek, so the difference is probably due to N availability.

At Mason Bay, only the species contrasts involving *B. rotundifolia* were significant. The differences (c. 2%) were small in relation to the spread of values expected across the range of C_3 plants.

^{15}N enrichment

Three explanations have been proposed for the low $\delta^{15}\text{N}$ values found in some environments. Handley et al. (1999) proposed that foliage $\delta^{15}\text{N}$ depends on water availability, with greatest depletion in cold, wet environments. Martinelli et al. (1999) proposed that low $\delta^{15}\text{N}$ reflects a "closed" N cycle within the forest ecosystem, with proportionally smaller losses (Martinelli et al. 1999). Tozer et al. (2005) proposed

that depleted $\delta^{15}\text{N}$ values in N-poor environments reflected increasing reliance on atmospheric ammonia for meeting N requirements. Although sea surface temperature around The Snares is up to 2°C cooler than off the western coast of Rakiura (Chiswell 1994), both sites are surrounded by water with a large subtropical component (Butler et al. 1992) so that neither site is unduly cold nor wet. Our results are therefore better explained by a nutrient limitation model, especially given the high C:N values found in all species at Mason Bay. Superimposed on this, small but significant variations were found between pairs of species from the same sampling sites. Such differences between species may be found in most forest communities (Stewart 2001).

The most likely non-soil sources of N available to plants at Mason Bay are atmospheric ammonia (Tozer et al. 2005) and sea spray. Virginia & Delwiche (1982) found increased foliar $\delta^{15}\text{N}$ close to the Californian coast but Vitousek et al. (1989) found no such effect in Hawaii even though sea spray directly affected some samples. We conclude that sea spray would not deplete $\delta^{15}\text{N}$ in vegetation at Mason Bay.

Conversely, strongly depleted $\delta^{15}\text{N}$ values can be caused by isotopic fractionation during diffusion of gaseous ammonia as the principal N source (Tozer et al. 2005). Ectomycorrhizal infections cause depletions of c. 5 – 6% over uninfected plants, and probably underlie the extreme depletions observed in some temperate and boreal locations (Hobbie et al. 2005). Indeed, the amount of mycorrhiza-induced depletion reported by Hobbie et al. (2005) would shift the Mason Bay data to values more typical of temperate forests. However, the relative contributions of mycorrhiza and atmospheric ammonia to the extreme depletions at Mason Bay are unknown.

The differences between species at Mason Bay are typical of those found in plant communities world-wide. Although engagingly simple, the idea that variations in plant $\delta^{15}\text{N}$ are a simple reflection of N source $\delta^{15}\text{N}$ is no longer accepted (Stewart 2001). Rather, foliage $\delta^{15}\text{N}$ results from the interaction of N source $\delta^{15}\text{N}$ with fractionation due to plant metabolism (Robinson et al. 1998). Although species effects were observed at Mason Bay, they were small in comparison with the difference between the islands. Similarly, the location effects at Mason Bay were small; the highly enriched *O. lyalli* at North East Island parallels the large enrichment found in seabird breeding colony soils (Mizutani et al. 1986; Harrow et al. 2006). High values of $\delta^{15}\text{N}$ reflect an "open" N cycle, with losses via emission

to the atmosphere of ammonia and nitrous oxide, and leaching of nitrate and soluble organic N beyond the rhizosphere (Martinelli et al. 1999). Measurements at another, nearby seabird breeding island with peat soil and *O. lyallii* forest showed that >98% of N contributed by seabirds is lost (Hawke & Newman 2004). Therefore, our $\delta^{15}\text{N}$ results from the *O. lyallii* forest on North East Island indicate an extreme example of an ecosystem with large N losses and correspondingly large ^{15}N enrichment.

ACKNOWLEDGMENTS

This research is part of the Kia Mau Te Titi Mo Ake Tonu Atu (Keep the Titi Forever) research project. D. Fletcher carried out the statistical analysis. J. Clark provided helpful comments on various drafts of the manuscript. Referee comments improved the presentation of the paper. The Department of Conservation kindly gave permission to collect samples. JN acknowledges financial support from the New Zealand Foundation for Research, Science & Technology.

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