

NEW ZEALAND JOURNAL OF ECOLOGY

RESEARCH

Growth rates and ages of some key tree species from subantarctic Auckland and Campbell Islands

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Published online: 22 November 2022

Abstract: Interspecific variation in tree growth rate and maximum age is central to understanding and predicting the dynamics of forest ecosystems. While there are abundant sources of this information for economically important New Zealand timber species and other common tree species, data for trees from subantarctic environments are almost entirely lacking. Here we present measurements of growth from Auckland and Campbell Islands for three species: *Metrosideros umbellata* (southern rātā; Myrtaceae, n = 1 site), a canopy dominant; *Dracophyllum* sp. (inaka; Ericaceae, *n* = 5 sites), a widespread small tree; and *Olearia lyallii* (tūpare, subantarctic tree daisy; Asteraceae, n = 2 sites), a species native to Snares Island that has naturalised on the Auckland Islands. Our data showed large differences in tree growth rates among and within species across islands. Growth rates varied eight-fold (i.e. from 0.34 mm yr⁻¹ to 2.78 mm yr⁻¹), being greatest in Olearia lyallii, least in Dracophyllum sp. and intermediate in Metrosideros umbellata. Comparisons of the five Dracophyllum sites suggest that these trees experience reduced growth rates and reach older ages when in competition with the bigger southern rātā (M. umbellata) trees, possibly due to the larger southern rātā providing protection from wind-throw. Measurements of resprouted southern rātā trees showed a variable juvenile-phase radial growth rate, highlighting the need for caution in extrapolating the likely ages of bigger trees. Remeasured individuals of Olearia lyallii growing among taller southern rātā trees showed slow growth rates compared to much faster rates seen in a nearby monospecific stand. Overall, the variability in growth seen by all three species illustrates that tree size cannot be used to indicate age in these subantarctic islands.

Keywords: forest conservation, radiocarbon dating, remote islands, Southern Ocean, southern tree limit, World Heritage Area

Introduction

The rate of human-driven extinction risk is increasing around the globe (Tilman et al. 2017), highlighting both the importance and vulnerability of isolated islands (Keppel et al. 2014). There is also increasing concern about terrestrial ecosystem transformations resulting from predicted global climate change (Nolan et al. 2018), with this being particularly acute in high southern latitudes (Bergstrom et al. 2020). The assessment and management of these threats require information on the rates of ecosystem processes and also tree demographic rates that underpin vegetation composition. Forest ecosystems extend to latitude c. 56°S in Chile (Buma et al. 2020) but elsewhere in the Southern Hemisphere, forest ecosystems south of latitude 50°S are confined to a handful of subantarctic islands in southern New Zealand. These peat-covered islands have hyper-oceanic climates with relatively mild temperatures but high winds, frequent cloud cover, and low insolation (de Lisle 1965; Turney et al. 2017).

The vegetation of the Auckland Islands archipelago consists of five main formations: forest and scrub, upland tussock grassland, maritime grassland/herb field, mountain tundra (fellfield), and bogs and swamps (McGlone et al. 2000). Sheltered coasts mainly support the low forests of southern rātā (*Metrosideros umbellata*) and in some localised places in the northeast, the subantarctic tree daisy *Olearia lyallii* (Lee et al. 1991; Wilmshurst et al. 2015). Above 250 m, forest intergrades into subalpine shrubland dominated by *Dracophyllum longifolium, Coprosma* spp., and *Myrsine divaricata* (with some southern rātā). By 300 m, tussock grassland predominates with tundra megaherb-fields and rushlands on higher mountain tops (Turney et al. 2016).

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Campbell Island (area c. 113 km²) has numerous steep hills, with the highest point being Mount Honey (569 m) in the south. The lowlands are dominated by low forest and scrub of two evergreen broadleaf forest canopy species, *Dracophyllum longifolium* and *Dracophyllum scoparium*, which commonly hybridise (McGlone et al. 1997). *Dracophyllum scoparium* is only found on offshore islands and can reach 3 m in height. In comparison, *Dracophyllum longifolium* can reach heights up to 5 m (but up to 12 m on the New Zealand mainland) and live up to 240 years of age on the subantarctic islands (Bestic et al. 2005; Harsch et al. 2014).

To establish a baseline of growth rates on these remote islands, here we investigate three tree species: (1) the Auckland Islands canopy dominant, southern rātā (*Metrosideros umbellata*), (2) the subantarctic tree daisy (*Olearia lyallii*), a naturalised subantarctic species (Wilmshurst et al. 2015) found in some localised coastal sites in the northern Auckland Islands, and (3). *Dracophyllum* spp. (generalised because of frequent hybridisation) commonly found on both Auckland and Campbell islands but is the only canopy tree on the latter.

Methods

There are two main approaches to measuring the growth of individual trees: the repeated measurement of marked trees or the measurement of annual rings in stem cores or discs (Bowman et al. 2013). This study also includes a third approach in which trees are measured after a dated human clearance event. Different methods were adopted to obtain age and growth rate estimates for each of the three tree species.

Metrosideros umbellata

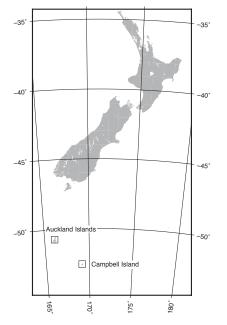
Although in young stems the growth rings are usually visible (Wardle 1971), in later growth, they become irregular in

different radii and ring boundaries become obscure. Wardle (1971) writes, "... here and there groups of well-defined rings occur, but they merge circumferentially and radially into nondescript wood." Knowing this, we did not take increment core samples but instead measured the diameters of saplings that had resprouted from stumps at the Erlangen Clearing in Carnley Harbour (EC in Fig. 1). The clearing was created during September 1939 when the German merchant vessel (the Erlangen) cut c. 250 tons of *M. umbellata* wood for fuel in their bid to sail to Chile to avoid being impounded (Bagley et al. 2009; Fig. 2). We measured the diameters of the largest resprouted saplings from 43 stumps in the clearing (Table 1; Fig. 3).

Olearia lyallii

Two different approaches were used to assess the growth rates of O. lyallii. The first consisted of a transect of 18 trees located in Enderby Settlement that had been repeatedly measured over several years to document their diameter increment. A notebook, instructions, map and tape measure were left in a container near the primary landing site for visitors to Enderby Settlement to help the study by recording remeasurements. The study began in November 2014, and the last measurements were taken in January 2019. The total diameter increment was recalculated to an annual basis (Table 1). The second method was the measurement of ring widths from three cross-sections of trees collected in 1982 and held at Manaaki Whenua -Landcare Research, Lincoln, as part of the original research reported in Lee et al. (1991) (Table 1). Ring boundaries in Olearia lyallii are not always clear, so as an independent check on the ring sequences, a sample of a single selected year around the time of the 1963/64 "Bomb Peak" from each cross-section was sent for radiocarbon dating (Turney et al. 2018; Hua et al. 2022) (Table 4).

a. New Zealand



b. Auckland Islands

66 00'

65°50'

-50°30

-50°40'

-50°50

65°50'

66°00

10

,99

,99

166°30'

km

66°30'

5

c. Campbell Island

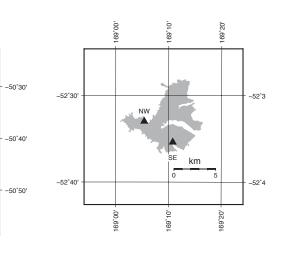


Figure 1. Maps showing locations of study sites. (a) General map showing the relative position of Auckland and Campbell Islands to the North Island and South Island of New Zealand. (b) Map of the Auckland Islands with locations of research sites. (c) Map of Campbell Island and positions of study sites.

66°10'





Figure 2. Photos of the Erlangen Clearing (Carnley Harbour, Auckland Island). (a) Metrosideros umbellata (southern rātā) being harvested during September 1939 by the crew from the German merchantvessel(S.S.Erlangen). (b) Loading firewood on the grounded S.S. Erlangen. (c) Example of resprouted southern rātā with Palmer for scale, November 2014. (d) Research group in November 2014 standing on the same pier as shown in image (b). Both (a) and (b) images reproduced with permission from papers relating to the Voyage of the S.S. Erlangen from Dunedin via the Auckland Islands to Puerto Montt, Chile, Misc-MS-1198, Hocken Collections, Uare Taoka o Hākena, University of Otago.

d.





Dracophyllum spp.

Samples from these species were collected initially to explore their potential for developing tree-ring chronologies for past climate reconstructions. The sites included Ross Harbour (site code = RH), Deas Head (DH), Mount Eden (ME) on Auckland Island and North-West Harbour (NW) and South-East Harbour (SE) on Campbell Island (Fig. 1). Some limited cross-dating success was achieved (Turney et al. 2017) from the southernmost site at South-East Harbour (SE), and two other sites have some prospects for chronology development (DH and NW), but further sampling is needed. The Ross Harbour and Mount Eden sites had no cross-dateable ring patterns between trees. We obtained cores of 4.5 mm diameter from selected trees by using increment borers. In addition to these core samples, cross-sections were sawn from recently dead or dying trees. These cross-sections helped considerably with chronology development by tracing rings around the entire tree trunk and selecting the clearest or best radius for measurement. All the tree-ring measurements were summarised (e.g. mean, median, standard deviation) and assessed for symmetry (e.g. skewness and kurtosis; Table 1). The tree rings were also evaluated for their year-to-year variability using the Gini coefficient of inequality (Biondi & Qeadan 2008), where lower values indicate lower variability between years of measurements.

Results

Metrosideros umbellata

Diameters near the base of 43 surviving, resprouted southern rata stems ranged from 10.0 to 20.5 cm. Thus, with 74 years since disturbance, and assuming all trees initiated growth in

Table 1. Summary of tree radial growth rates (mm yr⁻¹) for the different sites on Auckland and Campbell Islands. EC = Erlangen Clearing, ES = Enderby Settlement, EW = Ewing Island, RH = Ross Harbour, ME = Mount Eden, DH = Deas Head, NW = North-West Harbour, SE = South-East Harbour. MEUM = *Metrosideros umbellata* (southern rātā), DRSP = *Dracophyllum* sp. (inaka), OLLY = *Olearia lyallii* (tūpare, subantarctic tree daisy). *Diameter measurements only (no tree-ring width measurements).

			Auckland Islands				Campbell Island	
Site	EC*	ES*	EW	RH	ME	DH	NW	SE
Species	MEUM	OLLY	OLLY	DRSP	DRSP	DRSP	DRSP	DRSP
Sample size	43	18	3	25	15	25	15	15
Minimum	0.68	0.48	0.93	0.09	0.12	0.19	0.21	0.20
Mean	0.98	1.16	2.78	0.34	0.47	0.75	0.75	0.61
Std Dev	0.21	0.55	0.86	0.16	0.21	0.32	0.33	0.23
Median	0.96	0.98	2.85	0.31	0.44	0.69	0.73	0.59
Maximum	1.39	2.50	4.62	0.86	1.12	1.61	1.65	1.29
Kurtosis	2.080	0.956	2.911	4.073	3.273	2.692	2.685	3.015
Skewness	0.330	1.105	-0.226	0.897	0.656	0.471	0.482	0.480
No. Tree-rings			153	4846	2746	5577	1937	2017
Gini coef.			0.252	0.366	0.282	0.286	0.287	0.250

the year following disturbance, we estimate radial growth rates as 0.98 ± 0.21 mm yr⁻¹ (Table 1).

Olearia lyallii

The two measurement methods and sites produced markedly different growth rates (Table 4; Fig. 3). The trees on Ewing Island appear to be growing at a rate more than double that of those at the Enderby Settlement. The radiocarbon measurements confirmed the fast growth rates observed at Ewing Island (Table 4). We know the samples came from trees cut down in 1981, so the options of probable radiocarbon calibrated dates that were more recent than 1982 were not possible (e.g. D8AK1, Table 4).

Dracophyllum spp.

There was a wide range of radial growth rates and ages between the three different sites on Auckland Island (Table 1). In each case, the same general pattern emerged. The Ross Harbour (RH) site had less than half the growth rate obtained from Deas Head (DH), with the Mount Eden (ME) collection falling in between (Table 2). Similarly, the Ross Harbour site trees were the oldest and those at Deas Head the youngest, with Mount Eden in between (Table 3). The trees from Ross Harbour were the oldest, the slowest growing and the smallest sized. The two sites from Campbell Island had similar growth rates and ages (Table 1) and were similar to that of Deas Head (DH) on Auckland Island. All the sites had similar Gini coefficients except for RH which had the highest value, so the greatest ring-to-ring variability. Usually, this would indicate a site thought to capture a climate signal and have the better prospect of matching tree-ring patterns. However, this was not the case as the ring patterns did not match between trees and were often variable between radii within the same tree (analyses not shown).

Discussion

Forest inventory data and tree growth rate data are relatively widely available for high latitude forest ecosystems in the

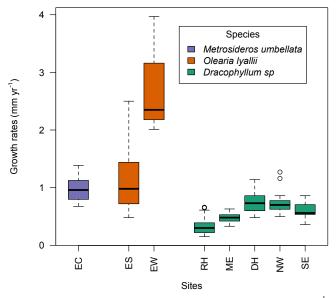


Figure 3. Boxplots of annual radial growth rates (mm yr⁻¹) from the different sites and species. The line in the middle of the box is the median. The box itself represents the middle 50% of the data. The box edges are the 25th and 75th percentiles. The default setting for the whiskers was used, which is 1.5 times the interquartile range (IQR), and outliers are shown as circles. Note EC = Erlangen Clearing (*Metrosideros umbellata*), ES = Enderby Settlement (*Olearia lyallii*), EW = Ewing Island (*Olearia lyallii*), RH = Ross Harbour (*Dracophyllum* sp.), ME = Mount Eden (*Dracophyllum* sp.), DH = Deas Head (*Dracophyllum* sp.), NW = North West Harbour (*Dracophyllum* sp.), SE = South East Harbour (*Dracophyllum* sp.).

Northern Hemisphere (Devi et al. 2020). In contrast, fewer data are available in the Southern Hemisphere, a situation particularly acute in remote subantarctic islands (Jones et al. 2016; Smith et al. 2002). Here, our results clearly show a wide range of growth rates between the different studied species and within species across the subantarctic islands, critical for establishing a baseline for understanding the impacts of

		Auckland Islands							
Site	EC*	ES*	EW	RH	ME	DH	NW	SE	
Species	MEUM	OLLY	OLLY	DRSP	DRSP	DRSP	DRSP	DRSP	
Sample size	43	18	3	25	15	25	15	15	
Minimum	74	49	32	75	134	60	90	86	
Mean	74	109	51	194	183	143	127	134	
Std Dev	0	44	17	81	36	39	15	33	
Median	74	109	56	199	174	145	129	130	
Maximum	74	209	65	392	244	233	144	226	
Kurtosis		0.000		0.293	-1.005	0.237	2.380	3.853	
Skewness		0.418		0.550	0.512	-0.024	-1.395	1.517	

Table 2. Summary of tree ages (years) for the different sites on Auckland and Campbell Islands. EC = Erlangen Clearing, ES = Enderby Settlement, EW = Ewing Island, RH = Ross Harbour, ME = Mount Eden, DH = Deas Head, NW = North-West Harbour, SE = South-East Harbour. MEUM = *Metrosideros umbellata* (southern rātā), DRSP = *Dracophyllum* sp. (inaka), OLLY = *Olearia lyallii* (tūpare, subantarctic tree daisy). *Diameter measurements only (no tree-ring width measurements).

Table 3. Summary of tree diameters (cm) for the different sites on Auckland and Campbell Islands. EC = Erlangen Clearing, ES = Enderby Settlement, EW = Ewing Island, RH = Ross Harbour, ME = Mount Eden, DH = Deas Head, NW = North-West Harbour, SE = South-East Harbour. MEUM = *Metrosideros umbellata* (southern rātā), DRSP = *Dracophyllum* sp. (inaka), OLLY = *Olearia lyallii* (tūpare, subantarctic tree daisy). *Diameter measurements only (no tree-ring width measurements).

			Auckland Islands				Campbell Island	
Site	EC*	ES*	EW	RH	ME	DH	NW	SE
Species	MEUM	OLLY	OLLY	DRSP	DRSP	DRSP	DRSP	DRSP
Sample size	43	18	3	25	15	25	15	15
Minimum	10.0	11.3	15.0	6.3	12.5	18.5	15.0	12.5
Mean	14.6	25.1	29.7	11.0	15.6	24.7	18.6	16.4
Std Dev	3.1	10.1	19.3	2.8	2.4	3.1	3.2	1.9
Median	14.4	25.2	22.5	10.3	15.3	24.0	17.5	17.0
Maximum	20.5	48.5	51.6	18.2	21.3	32.0	26.5	19.5
Kurtosis	-0.964	0.033		-0.255	1.117	0.184	1.408	0.117
Skewness	0.323	0.419		-0.728	1.105	0.370	1.315	-0.260

Table 4. Radiocarbon dates from *Olearia lyallii* tree rings sampled on Ewing Island, Auckland Islands. Calibrations are based on the Southern Hemisphere calibration curve (SHCal13) from Hogg et al. (2013). Note that the D8AK1 calibrated radiocarbon result with the greatest probability was impossible (shown in *italics*) since the tree was collected in 1982.

Label	Tree-ring span (CE)	Radiocarbon Lab Code	Modern Carbon (%)	CE calibrated years, 2 sigma calibration (with the relative area) and closest age in bold	Actual Tree-ring sampled
D8EW1	1949–1980	Wk 41154	104.9 ± 0.3	1956.40–1956.49 (0.012) 1957.14–1958.13 (0.618) 2007.09–2007.20 (0.007) 2007-93–2007.95 (0.001) 2008.27–2008.46 (0.001) 2008.71–2008.85 (0.044) 2010.13–2011.11 (0.301)	1958
D8EW2	1916–1980	Wk 41155	160.6 ± 0.5	1964.64–1965.65 (0.136) 1966.36–1968.30 (0.864)	1966
D8AK1	1925–1980	Wk 41156	107.9 ± 0.3	1957.94–1958.66 (0.152) 2000.43–2000.45 (0.001) 2001.75–2001.80 (0.003) 2002.00–2002.14 (0.012) 2002.42–2006.15 (0.832)	1958

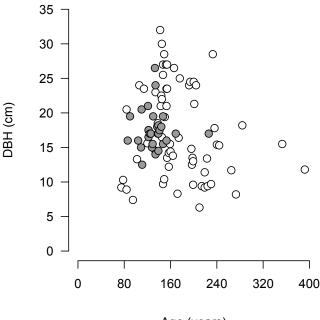
future climate change (Nel et al. 2021). The information on M. umbellata from the Erlangen Clearing indicates growth rates during a sprouting phase for the species but needs to be cautiously used for estimating the age of larger or mature trees as their radial growth would be expected to decline with age (Harper 1977). For example, some large trees occur towards the southeast of Auckland Island in Waterfall Inlet, with the largest diameter measured at 1.27 m. Using our results from the Erlangen Clearing would give an age of c. 650 years, and similar ages were encountered by Smith et al. (1985) on mainland southern New Zealand. In this specific case, we believe the sheltered location of the trees at Waterfall Inlet may have enabled them to have a faster growth rate and that our age calculation is a maximum estimate. Wardle's (1971) Westland results suggested a more normal range of 400–500 years. However, in the absence of any other information, the Erlangen Clearing provides a baseline for local growth rates on Auckland Island, although more monitoring of growth over a range of sizes and locations would be desirable.

The Olearia lyallii growth rates showed that one site is more than double the other. The presence of M. umbellata may have played a role in this difference, but there are also some different soil nutrient attributes (Wilmshurst et al. 2015). The monitored trees at Enderby Settlement compete with M. umbellata, but the tree sections sourced from Ewing Island came from a pure O. lyallii stand. As pointed out by Lee et al. (1991), the canopy trees of O. lyallii at Enderby Settlement appear suppressed and show signs of dying as the species cannot match the longevity and height of M. umbellata. Consistent with this interpretation, Fig. 3 shows Enderby Settlement having a growth rate of virtually half of that seen on Ewing Island. Olearia lyallii is indigenous to the Snares Islands group 300 km to the north, where it grows on peaty soils exposed to ocean spray and a heavy marine nutrient subsidy from seals, penguins and burrow nesting seabirds. Ewing Island matches this typical habitat, whereas the sheltered, rata-dominated Enderby Settlement site has soil with much lower concentrations of soluble salts and seabird guano (Lee et al. 1991; Wilmshurst et al. 2015).

The *Dracophyllum* spp. sites showed a range of growth rates that appears unrelated to either latitude or elevation (as they were located at similar low elevations). The two sites from Campbell Island (i.e. farthest south; 52.5°S) had similar growth rates and ages to the Deas Head (DH) site, some 300 km away, on Auckland Island (50.6°S). Unexpectedly, they were all faster growing than the other two sites on Auckland Island (i.e. Ross Harbour (RH) and Mount Eden (ME); Table 1). Our explanation for this growth rate pattern is the effects of competition with the longer-lived and larger M. umbellata. Both the Ross Harbour and Mount Eden sites were mixed stands with both species, whereas the Deas Head site was virtually a monospecific stand of only the *Dracophyllum* sp. Metrosideros umbellata is absent from Campbell Island, so those sites are also monospecific. The larger and longer-lived *M. umbellata* is strongly competitive with *Dracophyllum* spp. especially for canopy light, similar to that seen with Olearia lyallii. However, the suppressed Dracophyllum trees appear to live longer than those found in monospecific stands. We found several tilted and dead or dving Dracophyllum in the monospecific stands that we suspect were uprooted by strong gales. For example, on Campbell Island, the maximum windgust speed recorded during 24 hours was 71 m s⁻¹ (c. 240 km hr^{-1}), with many other days with gusts of around 40 m s⁻¹ (ca. 144 km hr⁻¹, source: NIWA-CliFlo, https://cliflo.niwa.co.nz). In

contrast, we believe *M. umbellata* affords greater wind-throw protection in the mixed-species sites. *Dracophyllum* trees in the exposed monospecific stands (DH, NW, SE) tend to grow faster but are shorter-lived than those sheltered from extreme winds by *M. umbellata* (i.e. RH, ME).

A key finding from this study was the lack of any relationship between the age and size of Dracophyllum trees. The data has been plotted in Fig. 4 separately for Auckland and Campbell Islands Dracophyllum trees and show no statistically significant relationship between the two variables, either within or between islands. There is clearly great variation in the ages of similar-sized trees and vice-versa. The fact that the results between the islands were not significantly different is perhaps unsurprising given the similarity of the subantarctic climate conditions. However, the difference in climate is sufficient to preclude tall tree growth on Campbell Island, whereas tall forest is widespread up to 180 m elevation on Auckland Islands (de Lisle, 1965). Several studies have reported a comparable magnitude of variation in age-size relations (cf. Ogden & West 1981; Worbes et al. 2003; Bowman et al. 2013), which reaffirms that diameter is a poor indicator of tree age (Harper 1977; Speer 2010). In our examples, this applies to both mixed-species stands and monocultures. These results have implications for future tree-ring chronology sampling efforts and studies of forest dynamics. For dendroclimatic studies in particular, larger sample sizes are needed – both in terms of the number of trees sampled per site as well as the number of sites. This ensures an adequate sample depth progressively back in time for obtaining a reliable climate signal from the tree-ring measurements (Wigley et al. 1984). The conventional practice of targeting larger trees at a site may



Age (years)

Figure 4. Relationship between tree age (years) and tree diameter at breast height (DBH, cm) in *Dracophyllum* sp. on Auckland (open symbol) and Campbell (filled symbol) Islands, in subantarctic New Zealand. There was no statistically significant relationship between the two variables, either within or across islands. Note; the particularly wide range in tree diameters (8.3–30 cm) for individuals ages between 145 and 185 years.

not capture the oldest trees. Similarly, for forest management, the increasingly widespread use of light and detection ranging (LiDAR) to provide landscape-scale forest inventory (e.g. Zörner et al. 2018) could be more helpful with information on associated forest tree ages. This data provides important baseline information for understanding future biological and ecological effects that will help inform on the management of these unique archipelagoes in the remote Southern Ocean.

Acknowledgements

We wish to express our thanks to the captain and crew of the *MV Akademik Shokalskiy* and Henk Haazen and Kali Kahn on the *Tiama* for help in the field. This work was supported by the Australasian Antarctic Expedition 2013–2014, the Australian Research Council (CE170100015; FL100100195, FT120100004, and DP130104156) and the University of New South Wales. SJR, JMW and MSM were supported by SSIF funding for Crown Research Institutes from the New Zealand Ministry of Business, Innovation and Employment's Science and Innovation Group. Research on the New Zealand subantarctic Auckland and Campbell Islands was undertaken under Department of Conservation National Authorisation Numbers 37687-FAU and 39761-RES.

Data and code availability

All associated data is available upon request from the lead author. The *Dracophyllum* sp. tree-ring measurements from South-East Harbour on Campbell Island are also available from the International Tree-Ring Data Bank (ITRDB) as Site Code NEWZ117 at https://www.ncdc.noaa.gov/paleo-search/ study/ 21591.

Author contributions

JGP and CSMT developed the concept for the paper; All authors helped collect the field samples. JGP, PF and SJR led analyses. JGP wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

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Received: 3 November 2020; accepted: 12 May 2022 Editorial board member: Sarah Wyse