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Moa, climate, and eruptions: radiocarbon ages on habitat-specific moa show that their distributions were controlled by volcanic eruptions as well as climate

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Abstract: The species composition of moa assemblages reflected the local vegetation. These assemblages have been used as indicators of the geological age – glacial or Holocene – of the fauna. Within the assemblages, some species of moa have been associated with specific vegetation types, including *Anomalopteryx didiformis* with lowland rain forest, and *Euryapteryx curtus*, with dry shrubland. The sequence of radiocarbon ages for *A. didiformis* and *E. curtus* in the Waitomo karst, in the west central North Island, New Zealand, records changes in the distributions of their habitats over the past 28,000 years. The presence of *A. didiformis* shows that, contrary to current reconstructions, there was lowland rain forest in the karst during the Last Glacial Maximum. An abrupt change to *E. curtus* and hence of its shrubland habitat coincided with the Oruanui super eruption of Taupo volcano 25,400 years ago. *Anomalopteryx didiformis* and its rain forest habitat did not return to the karst until *c.* 13,000 years ago. *E. curtus* disappeared from the karst some time before that, during the gradual post-glacial warming, but remained elsewhere on the Volcanic Plateau, probably in the seral vegetation that followed the continual eruptions. Moa distributions were not always altered just by climate change. Major eruptions such as the Oruanui could change their habitat and hence their distribution over much of both main islands.

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INTRODUCTION

Changes in the distribution of moa (Aves: Dinornithiformes) and the composition of their species assemblages as the New Zealand vegetation responded to a warming climate at the end of the most recent (Otiran-Weichselian) glaciation have been reported for both the North (Worthy 1984, 1987, 2000; Holdaway & Worthy 1993; Worthy & Holdaway 2000, 2002; Worthy & Swabey 2002) and South islands (Worthy & Mildenhall 1989; Worthy & Holdaway 1993, 1994, 1995, 1996, 2002; Worthy 1997, 1998a, 1998b). Some moa were associated with particular vegetation types (Worthy 1990, 2000; Worthy & Holdaway 1993, 1994, 1995, 1996, 2002; Worthy & Swabey 2002) and have been used

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as "broad brush" indicators of climate in terms of "glacial" and "Holocene" faunas. However, changes in moa species dated by radiocarbon can also record rapid environmental change (Holdaway 2021), although the method requires a sufficiently complete series of radiocarbon ages for the taxa in the area of interest.

To date, radiocarbon ages have been measured on only a small proportion of the well preserved moa material available in museum collections. However, there are still enough radiocarbon ages on moa, from many sites with wide geographic coverage, to demonstrate that they are a largely unexploited but potentially extremely useful resource for following changes in vegetation – and hence climate and other phenomena – through space and time. The geographic coverage is wider, and sampling sites more abundant, than for pollen and other lake and bog deposit proxies. In addition, ages on individual moa provide chronological precision for the type of vegetation beyond that of even the most intensively dated stratigraphic profile, for which age-depth models are required. The moa were witness to the vegetation where they lived, during a period defined by the radiocarbon age for their death.

Five moa taxa – *Anomalopteryx didiformis*; *Euryapteryx curtus* sensu lato; *Pachyornis australis*; *P. elephantopus*; *P. geranoides* – all members of the family Emeidae, were sufficiently closely associated with particular vegetation types, such as lowland rain forest, shrublands, or dry forests, to be useful proxies for vegetation. Comparison of their dated presence with reconstructions of the surrounding vegetation during the Holocene shows that *A. didiformis* was always associated with lowland rain forest (Worthy 1990; Worthy & Holdaway 2002). Similarly, pollen-based reconstructions of contemporary vegetation contemporary with their fossil remains show that *E. curtus* was found in dry forest such as that in the eastern South Island during the Holocene (Worthy & Holdaway 1996; Holdaway & Worthy 1997; Worthy 1997, 1998b) and, during glacial periods, shrublands and dry forests elsewhere (Worthy 1994; Worthy & Holdaway 1994; Worthy 1997, 1998b, 2000). On the same basis, it is accepted that *P. elephantopus* in the South Island and *P. geranoides* (formerly *P. mappini*) in the North Island similarly required dry forest and shrubland (Worthy 1987, 1990, 1997, 1998b; Worthy & Holdaway 1993, 1994, 1996; Rawlence *et al.* 2012). Lastly, *P. australis* was confined to low productivity, cool climate vegetation in the mountains west of the South Island's Main Divide (Rawlence *et al.* 2012; Holdaway & Rowe 2020).

Of the habitat-specific species, remains of *A. didiformis*, a small – *c.* 40–50 kg (Worthy & Holdaway 2002) – moa are nearly ubiquitous in deposits of Holocene age in the North Island south of the Auckland isthmus and in the northwest, west, and south of the South Island (Millener 1981; Worthy 1990, 1993, 1997, 1998a, 1998b; Worthy & Holdaway 1993, 1994, 2002). However, perhaps because the species has been taken to be an indicator of Holocene vegetation, fewer radiocarbon ages have been measured: the remains have instead been assumed to be of Holocene age (10,000 years ago to present).

Only two radiocarbon dates of Otiran-Weichselian Last Glacial Maximum age on *A. didiformis* are available, both from the North Island. Both are from the Waitomo karst (*c.* 38°15'S; Fig. 2), for which environmental reconstructions (McGlone *et al.* 2010; Newnham *et al.* 2013) suggest a glacial vegetation of "shrubland-grassland with some beech forest and rare patches of conifers" during the Last Glacial Maximum. These authors also map a sliver of lowland rain forest extending south along the coast to the west of the karst. Apart from this sliver, the model shows no rain forest south of the Kaipara Harbour at 36°40'S, 125 km north of Waitomo Caves. Lees *et al.* (1998) reported cold, wet conditions in bogs near the coast northwest of Waitomo between 25,000 and 20,000 years ago, with at least two species of beech in the surrounding hills. Neither analysis provides evidence for the contemporary vegetation in the Waitomo karst.

Because of a wider interest in the systematics of the genus, more radiocarbon ages have been measured on *E. curtus* than on *A. didiformis*. Of the 11 North Island ages, six are from the Waitomo karst. The species' presence there indicates a period or periods when the area vegetation was indeed as mapped by Newnham *et al.* (2013). However, throughout the Holocene, until present, the natural vegetation of the karst has been lowland rain forest. As the radiocarbon ages were measured on individuals from the same sites, it is unlikely that they record the presence of individuals from significantly different habitats.

A complicating factor in reconstructions of the vegetation of the central North Island is the prevalence there of volcanism in the Taupo Volcanic Zone. Ash falls and ignimbrite/pyroclastic flows can damage or destroy vegetation over significant areas (Clarkson *et al.* 1988; Wilmshurst & McGlone 1996; Segschneider *et al.* 2002; Manville *et al.* 2009). Prevailing westerly winds and the moderate size of most eruptions mean that most damage has been on the Volcanic Plateau itself and to its east. Extremely large eruptions have spread deep ash to the west and indeed across much of both the North and South Islands. Although many — perhaps most — people are aware of the most recent (First Millennium) eruption of Taupo Volcano, its effects were much less widely felt than those of the Oruanui super eruption of *c.* 25,000 years ago (Vandergoes *et al.* 2013).

The Oruanui eruption was the largest from the Taupo Volcanic Zone since the even larger

Figure 1. The effects on the rain forest at Tikitapu, near Blue Lake, Rotorua, of 3 cm of airfall volcanic tephra from the 1886 eruption of Mt Tarawera (Pullar & Birrell 1973). Top left, before the eruption. Valentine, George Dobson, 1852–1890. In the Tiki Tapu bush – Photograph taken by George Dobson Valentine. Mair, Gilbert Henry, 1875–1966: Photographs. Ref: PA7-54-24. Top right, same place, after the eruption. Valentine, George Dobson, 1852–1890: Scenic photographs of New Zealand. Ref: PA7-54-03. Bottom, same area, post eruption, in a wider view. Images: Tiki-Tapu bush, after eruption. Coxhead, Frank Arnold, 1851–1908. Tikitapu Bush destroyed by the 1886 Tarawera eruption – Photograph taken by Frank Arnold Coxhead. Christie, Hettie Florence, 1902–1988: Photographs and album of New Zealand scenes. Ref: PA7-41-15. All images, Courtesy of Alexander Turnbull Library, Wellington, New Zealand.

Rangitawa-Whakamaru eruption *c.* 340,000 years ago. Manville & Wilson (2004) pointed out that the thick ash and ignimbrite would have been enough "…to have wholly destroyed or buried vegetation over virtually all of the central North Island". They note that even in the present climate, vegetation would have developed on the new tephra very slowly. Under the glacial climate of that time, regeneration would have probably taken millennia. This is supported by the aeolian sediments widespread in the central North Island. Dunes formed from the volcanic sands are widespread in the North Island, including along the Whanganui and Rangitikei rivers (Manville & Wilson 2004). They noted that the presence of the Oruanui ash in the lower half of the Ohakea loess, the youngest North Island loess layer, indicates that the eruption occurred before the peak of the Last Glacial Maximum. Even 2 cm of ash can defoliate a forest for a year (Fig. 1) (Oppenheimer 2011), eliminating the local avifauna so damage from the Oruanui eruption was far more widespread than presently acknowledged by, for example Manville & Wilson (2004).

To resolve the apparent contradiction of the presence of *A. didiformis* in the Waitomo karst during the depths of the Otiran-Weichselian glaciation, reconstructions of karst vegetation at that time, and the likely effects of the Oruanui eruption, I analysed patterns in the radiocarbon age sequences for that species and for *E. curtus* from the karst's cave systems in relation to the modelled vegetation pattern and dates for major, potentially landscape-changing, eruptions from the Taupo Volcanic Zone. *Anomalopteryx didiformis* and *E. curtus* were approximately the same size (Worthy & Holdaway 2002) so resident populations of both species presumably had the same probability of being trapped in cave systems.

MATERIALS AND METHODS

Radiocarbon ages

A total of 27 radiocarbon ages (Table 1) are presently available for *A. didiformis*, 14 from the North Island (10 from the Waitomo karst) – collated from Millener (1981), Worthy & Swabey (2002), and Bunce *et al.* (2009) – and 13 from the South, collated from Worthy & Holdaway (1993, 1994), Worthy (1998a), Worthy & Roscoe (2003), and Bunce *et al.* (2009). There are fewer ages for this taxon than for others in the fauna because research interest has been focused on the two giant moa (*Dinornis* spp.) and the species of *Euryapteryx* and *Pachyornis*.

For *E. curtus*, 11 ages are available for the North Island, including six from the Waitomo karst (Table 2) (Worthy & Swabey 2002), and five from other areas (Worthy 2000) and Holdaway (previously unpublished data). Of the 57 ages available for South Island birds, most (40) are from a few sites in North Canterbury. Ages for South Island birds were collated from McCulloch & Trotter (1979), Ritchie (1982), Anderson (1989), Worthy & Holdaway (1993, 1994, 1996), Worthy (1998a, 1998b), Worthy & Roscoe (2003), and Allentoft *et al.* (2014).

Statistics

The conventional radiocarbon ages were calibrated to calendar time via the OxCal4.4 (Bronk Ramsey 2009) software, invoking the SHCal20 calibration

Table 1. Radiocarbon ages (years BP) on individual *Anomalopteryx didiformis* from North and South Islands, New Zealand, from literature records. Shaded, ages used in analysis of faunal replacement around Waitomo. CRA, conventional radiocarbon age; SD, measurement 1σ; $\delta^{13}C$, measurement carbon stable isotope ratio; SHCal20, mean calibrated date in relation to SHCal20 calibration curve; SD, 1σ date range for calibrated dates; median, median calibrated date; -, data not available; AU, Geology Department, University of Auckland collection; WO, Caves Museum, Waitomo; AIM, Auckland Institute and Museum; MNZ, Museum of New Zealand Te Papa Tongarewa.

Age ref.	CRA	SD	$\delta^{13}C$	SHCal20	SD	Median	Locality	Sample and Reference	Island
NZ4838	24,100	450	-	28,323	456	28,299	Moa Cave, Stubbs Farm, Waitomo	AU4973; Millener (1981)	N
NZ4843	21,200	350	-	25,429	381	25,452	Dawson's Moa Cave, Piopio	AU5801; Millener (1981)	N
NZ4840	10,600	200	-	12,390	291	12,429	Dinornis Cave, Waitomo	AU4081; Millener (1981)	N
NZ4844	10,150	150	-	11,728	300	11,707	Zweiholen, below Entrance	AU4966; Millener (1981)	N
NZA11612	9,510	60	-22.7	10,780	154	10,737	F1c Cave, Rockfall deposit	Worthy & Swabey (2002)	N
NZ3088	7,300	150	-	8,092	150	8,091	Auckland City	Nelson & Grant-Mackie (1980)	N
NZ4841	6,150	100	-	6,994	134	6,992	Dinornis Cave, Waitomo	AU4081; Millener (1981)	N
NZA10054	5,876	60	-22.5	6,645	84	6,649	Zweiholen, ZW5, spit 1, L1	WO473; Worthy & Swabey (2002)	N
NZ4842	3,200	60	-	3,367	77	3,376	Rorison's Quarry, Piopio	AU4975; Millener (1981)	N
NZ4867	2,790	80	-	2,881	94	2,868	Waikiekie Quarry, Northland	AU5800; Millener (1981)	N
NZA7185	2,749	68	-22.3	2,836	74	2,828	Hukanui Pool rockshelter	Holdaway & Beavan (1999)	N
NZ5035	1,860	70	-	1,744	88	1,746	Peryer's Anomalopteryx Cave	AU7108; Millener (1981)	N
NZ4871	1,340	64	-	1,201	69	1,210	Clevedon	AIM 1.160; Millener (1981)	N
OxA12726	1,041	24	-21.9	890	47	910	Hangitiki, Waitomo	AM4943; Bunce *et al.* (2009)	N
OxA12728	11,575	45	-21.4	13,406	52	13,407	Takaka Fossil Cave	MNZ S38943; Worthy & Roscoe (2003)	S
NZA11614	11,354	60	-22	13,223	55	13,221	Takaka Fossil Cave	50 cm depth; Worthy & Roscoe (2003)	S
NZA3288	8,274	72	-22.66	9,217	114	9,213	Kairuru Extension Cave	Worthy & Holdaway (1994)	S
NZA3258	6,656	141	-21.01	7,500	127	7,503	Hawke's Cave	Worthy & Holdaway (1994)	S
NZA2506	5,447	87	-22.5	6,178	108	6,195	Madonna Cave site 10	Worthy & Holdaway (1993)	S
NZA8071	4,951	69	-23.5	5,667	93	5,656	Hamilton's Swamp, Winton	inner pt	S
NZA8072	4,735	72	-23.1	5,429	95	5,429	Hamilton's Swamp, Winton	outer pt	S
NZA3289	4,072	59	-21.67	4,544	117	4,524	Kairuru Extension Cave	Worthy & Holdaway (1994)	S
NZA2443	2,197	86	-23	2,153	114	2,141	Madonna Cave, site 8	Worthy & Holdaway (1993)	S
NZA13547	1,576	60	-22	1,429	65	1,425	Takaka Fossil Cave	Worthy & Roscoe (2003)	S
NZA2521	1,076	83	-22.9	936	97	936	Madonna Cave site 12	Worthy & Holdaway (1993)	S
NZA3048	670	59	-22.5	604	39	604	Irvine's Cave	MNZ S30183; Worthy & Holdaway (1994)	S
OxA12729	623	28	-21.2	588	33	603	Echo Valley Cave, Southland	Southland Museum; Bunce *et al.* (2009)	S

Table 2. Radiocarbon ages (years BP) for the taxon known presently as *Euryapteryx curtus*. Shaded rows, individuals from the Waitomo karst. Abbreviations as in Table 1.

Age no.	CRA	SD	$\delta^{13}C$	SHCal20	SD	Median	Locality, Sample, and Reference	Island
NZA9985	20,920	180	-24.1	25,191	255	25,188	Zweiholen, ZW5, BL3; WO612; Worthy & Swabey (2002)	N
NZA9277	20,150	130	-22.6	24,143	180	24,126	Zweiholen, ZW2; WO442; Worthy & Swabey (2002)	N
NZA9950	20,120	180	-24.2	24,149	227	24,120	Zweiholen, ZW5, BL2A; small moa; WO590; Worthy & Swabey (2002)	N
NZA9342	19,170	150	-24.3	23,123	230	23,084	Zweiholen, ZW1; WO440; Worthy & Swabey (2002)	N
NZA10055	18,040	140	-23.2	21,870	218	21,900	Zweiholen, ZW5, spit 3, L2; WO542; Worthy & Swabey (2002)	N
NZA11613	13,144	70	-25.1	15,719	118	15,718	F1c Cave, Rockfall; ; Worthy & Swabey (2002)	N
NZA9513	11,551	85	-21.8	13,389	83	13,389	Te Aute Swamp; MNZ S121; Worthy (2000)	N
NZA 34021	2,026	35	-20	1,940	44	1,943	Taupo Bypass Highway pitfall; Holdaway, this paper	N
NZA 34019	1,617	35	-21.5	1,464	45	1,465	Taupo Bypass Highway pitfall; Holdaway, this paper	N
NZA 34022	1,354	35	-24.3	1,227	41	1,228	Taupo Bypass Highway pitfall; Holdaway, this paper	N
NZA 34020	1,343	35	-23	1,222	43	1,225	Taupo Bypass Highway pitfall; Holdaway, this paper	N
NZA7553	37,080	950	-22.6	41,683	597	41,715	Kauana Swamp; MNZ S34502; Worthy (1988a)	S
NZA7749	32,000	370	-22.5	36,348	411	36,334	Kauana Swamp; MNZ S34501; Worthy (1988a)	S
NZA2445	23,780	210	-21.8	27,964	249	27,924	Madonna Cave, site 16; Worthy & Holdaway (1993)	S
NZA3050	14,080	100	-22.6	17,096	154	17,093	Irvine's Cave; Worthy & Holdaway (1994)	S
NZA3051	13,889	95	-21.7	16,805	153	16,813	Irvine's Cave; Worthy & Holdaway (1994)	S
NZA1567	13,400	130	-23.4	16,083	196	16,082	Kairuru Cave; MNZ S27794; Worthy & Holdaway (1994)	S
NZA13267	12,450	65	-23.24	14,563	206	14,547	Takaka Fossil Cave; Rock fall slope; Worthy & Roscoe (2003)	S
NZA13266	12,361	65	-22.16	14,407	223	14,349	Takaka Fossil Cave; Base of excavation; Worthy & Roscoe (2003)	S
NZA2779	11,090	100	-22.6	12,971	101	12,977	Madonna Cave, site 13; Worthy & Holdaway (1993)	S
NZ1728	9,490	200	-	10,756	279	10,747	Pukemata; Anderson (1989)	S
NZ7924	6,359	100	-23.4	7,225	123	7,235	Madonna Cave, site 13; redone NZA2779; Worthy & Holdaway (1993)	S
NZA 29908	4,736	25	-23	5,417	70	5,399	Rosslea Swamp; Allentoft *et al.* (2014)	S
NZA 31038	3,649	25	-23.8	3,927	57	3,922	Pyramid Valley; Allentoft *et al.* (2014)	S
NZ623	3,450	71	-	3,667	103	3,662	Pyramid Valley; gizzard, Anderson (1989);	S
NZA 30225	3,077	25	-22.8	3,249	60	3,246	Pyramid Valley; Allentoft *et al.* (2014)	S
NZA 29240	2,828	35	-23.8	2,892	59	2,893	Pyramid Valley; Allentoft *et al.* (2014)	S
NZA 30691	2,680	55	-23.8	2,762	78	2,766	Pyramid Valley; Allentoft *et al.* (2014)	S
NZA 34181	2,572	25	-24	2,616	81	2,614	Bell Hill Vineyard; Allentoft *et al.* (2014)	S
NZA 30099	2,570	25	-23.8	2,614	80	2,610	Bell Hill Vineyard; Allentoft *et al.* (2014)	S
NZA 30274	2,544	20	?	2,595	77	2,585	Bell Hill Vineyard; Allentoft *et al.* (2014)	S
NZA 34195	2,503	25	-24.6	2,555	98	2,561	Bell Hill Vineyard; Allentoft *et al.* (2014)	S
NZA6747	2,438	64	-23.3	2,486	128	2,467	Hamilton Swamp, Otago; OM Av4754; Worthy (1988b)	S

Table 2. *continued*

Age no.	CRA	SD	$\delta^{13}C$	SHCal20	SD	Median	Locality, Sample, and Reference	Island
NZA 31011	2,378	35	-23	2,339	105	2,348	Pyramid Valley; Allentoft *et al*. (2014)	S
D-AMS 1219-099	2,336	29	-13.2	2,250	70	2,225	Bell Hill Vineyard; Allentoft *et al*. (2014)	S
NZA 34193	2,319	25	-24.7	2,240	64	2,220	Bell Hill Vineyard; Allentoft *et al*. (2014)	S
D-AMS 1219-091	2,302	30	-15.6	2,236	61	2,223	Bell Hill Vineyard; Allentoft *et al*. (2014)	S
NZA 30113	2,267	30	-24	2,232	59	2,234	Bell Hill Vineyard; Allentoft *et al*. (2014)	S
NZA 31040	2,238	25	-24.4	2,227	64	2,246	Pyramid Valley; Allentoft *et al*. (2014)	S
NZA 34250	2,205	25	-23.9	2,187	80	2,142	Pyramid Valley; Allentoft *et al*. (2014)	S
NZA4615	2,176	76	-24.4	2,131	109	2,114	Earnscleugh Cave; Ritchie (1982)	S
D-AMS 1219-083	2,075	27	-17.8	1,984	43	1,986	Bell Hill Vineyard; Allentoft *et al*. (2014)	S
NZ1727	2,020	70	-	1,931	87	1,931	Enfield; Anderson (1989); McCulloch & Trotter (1979)	S
D-AMS 1219-085	1,951	27	-19.8	1,850	44	1,854	Bell Hill Vineyard; Allentoft *et al*. (2014)	S
D-AMS 1219-088	1,797	30	-9.4	1,657	41	1,653	Bell Hill Vineyard; Allentoft *et al*. (2014)	S
D-AMS 1219-090	1,771	32	-8.9	1,641	42	1,644	Bell Hill Vineyard; Allentoft *et al*. (2014)	S
NZA 31044	1,734	25	-23.5	1,605	47	1,594	Pyramid Valley; Allentoft *et al*. (2014)	S
D-AMS 1219-089	1,718	30	-23.9	1,586	47	1,577	Bell Hill Vineyard; Allentoft *et al*. (2014)	S
NZA 34253	1,679	25	-24.2	1,532	40	1,539	Bell Hill Vineyard; Allentoft *et al*. (2014)	S
NZ4874	1,670	75	-	1,524	91	1,521	Awamoa; Anderson (1989)	S
NZA 30519	1,540	270	-23	1,440	292	1,429	Rosslea Swamp; Allentoft *et al*. (2014)	S
NZ918	1,525	60	-	1,384	62	1,374	Timpendean rockshelter; Worthy & Holdaway (1996)	S
NZA 29127	1,492	35	-23.5	1,341	29	1,338	Pyramid Valley; Allentoft *et al*. (2014)	S
NZ4900	1,445	50	-	1,305	51	1,308	North Dean, North Canterbury; Anderson (1989)	S
NZA 34194	1,410	25	-22.5	1,274	37	1,288	Bell Hill Vineyard; Allentoft *et al*. (2014)	S
NZA30223	1,293	30	-24.4	1,174	61	1,167	Pyramid Valley; Allentoft *et al*. (2014)	S
D-AMS 1219-084	1,249	30	-25.2	1,122	50	1,119	Bell Hill Vineyard; Allentoft *et al*. (2014)	S
NZA 31042	1,172	25	-23.5	1,016	38	1,014	Pyramid Valley; Allentoft *et al*. (2014)	S
NZA 31054	1,168	25	-23.9	1,014	36	1,014	Bell Hill Vineyard; Allentoft *et al*. (2014)	S
NZA 31041	1,116	25	-23.9	981	40	969	Pyramid Valley; Allentoft *et al*. (2014)	S
NZA 31037	1,102	25	-23.9	963	36	951	Pyramid Valley; Allentoft *et al*. (2014)	S
NZ5321	1,070	60	-	923	75	930	Firewood Creek, Cromwell; Anderson (1989); Ritchie (1982)	S
NZA 28039	1,027	30	-23.9	872	45	862	Bell Hill Vineyard; Allentoft *et al*. (2014)	S
NZ1724	1,025	60	-	874	63	869	Castle Hill; Anderson (1989);	S
D-AMS 1219-086	930	27	-25.2	799	51	784	Bell Hill Vineyard; Allentoft *et al*. (2014)	S
D-AMS 1219-081	655	25	-20.2	601	28	606	Bell Hill Vineyard; Allentoft *et al*. (2014)	S
D-AMS 1219-098	655	26	-15.9	601	28	606	Bell Hill Vineyard; Allentoft *et al*. (2014)	S
D-AMS 1219-094	619	28	-	585	34	600	Bell Hill Vineyard; Allentoft *et al*. (2014)	S

curve (Hogg *et al.* 2020). Mean, with 1σ error, and median calibrated dates are given in Tables 1&2. Calibrated dates are given as "before present", BP, conventionally 1950 CE.

The temporal patterns in the numbers of dated North and South Island individuals of both *A. didiformis* and *E. curtus* were summarised by box-whisker plots, with outliers, using the PAST® statistical software (Hammer *et al.* 2001).

Calibrated date probability distributions were generated using the OxCal4.4 software and the SHCal20 curve. For the two moa taxa from sites in the Waitomo karst, Bayesian probability distributions for the end of the initial presence of *A. didiformis* and first presence of *E. curtus* were generated using the Sequence option in OxCal4.4. Similarly, the probabilities for the last occurrence of *E. curtus* and renewed presence of *A. didiformis* were generated and plotted. It was assumed *a priori*, because their habitat requirements were mutually exclusive, and the date series were also mutually exclusive between the change events, that the first and last occurrences of each taxon marked faunal turnover events.

Eruption dates and volumes

A revised date of 25,360 ± 160 calendar years before present for the Oruanui eruption and its resulting Kawakawa/Oruanui tephra was presented by Vandergoes *et al.* (2013). In their title, the authors maintain that the tephra "is a key stratigraphic marker for the Last Glacial Maximum in New Zealand". Dates for other major eruptions are from the list in Lowe *et al.* (2013). Eruptive volumes are from Froggatt & Lowe (1990) and Vandergoes *et al.* (2013).

RESULTS

General

Of the 27 *A. didiformis* which have been radiocarbon dated so far, only two have ages greater than 13,500 calendar years before present (Table 1). Both of these are from caves in the Waitomo karst (Fig. 2). These two ages are extreme outliers in the available series (Fig. 3). The two coeval outliers in the South Island series (Fig. 3) are from Takaka Hill, where the species made a brief pre-Holocene appearance before being replaced by *P. australis* during the period of the Younger Dryas (Holdaway 2021). No older *A. didiformis* is known from the South Island, or indeed from the North Island south of Waitomo. Indeed, apart from the Waitomo birds, nothing is known of the distribution of *A. didiformis* before the Holocene (Fig. 2).

The oldest radiocarbon ages for *E. curtus* in the North Island are all from the Waitomo karst (Table 2). The cluster in the glacial and late glacial of the Waitomo karst has no parallel in the South Island (Fig. 3). The next oldest North Island individual was from the glacial-interglacial transition site of Te Aute in southern Hawke's Bay (Table 2). All others are from the Holocene. In contrast, radiocarbon ages for *E. curtus* (taken in the broad sense of the taxon) in the South Island include ten older than 10,000 years BP (Table 2), from sites at both ends of the island. The many North Canterbury records are all of mid- to late-Holocene age (Table 2).

The Waitomo karst

Neither *A. didiformis* nor *E. curtus* was present continuously in the fossil record from the Waitomo karst (Fig. 4). *A. didiformis* was present before 25,400 calendar years BP, *E. curtus* between 25,400 calendar years BP and *c.* 15,000 years BP. *Anomalopteryx didiformis* reappeared in the caves *c.* 12,500 years BP and was present then until moa extinction

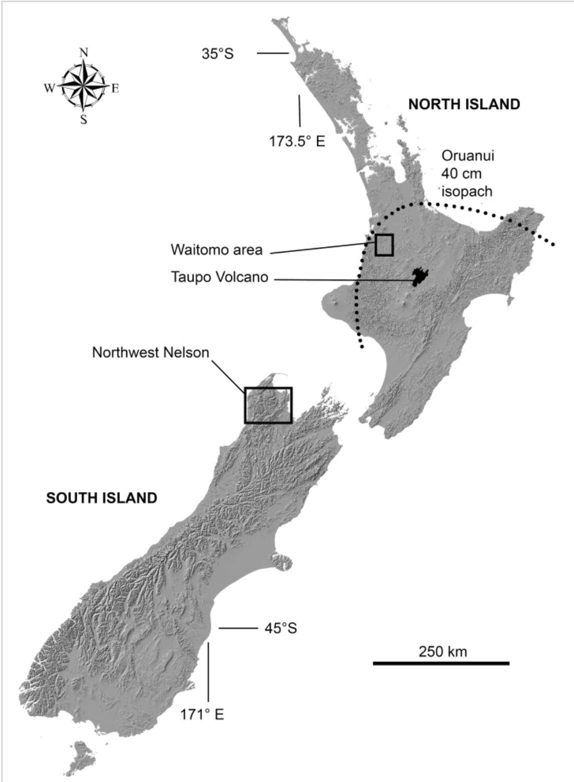

Figure 2. Location of Waitomo study site in relation to Taupo Volcano (site of the Oruanui super eruption) and Northwest Nelson (site of evidence for Younger Dryas cold period in New Zealand, Holdaway [2021]). Oruanui 40 cm isopach from Vandergoes *et al*. (2013).

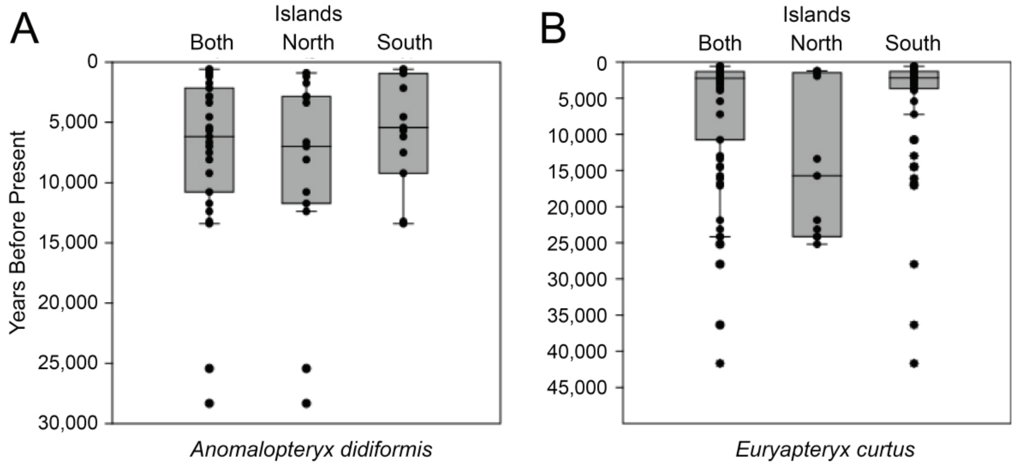

Figure 3. Box-whisker plots (quartile rounding, with outliers) of mean calibrated radiocarbon ages for (**A**) *Anomalopteryx didiformis* (the two outliers at >25,000 BP are both from the Waitomo karst), and (**B**) *Euryapteryx curtus*.

after 1000 CE (Fig. 4). *Anomalopteryx didiformis* reappeared in the Waitomo karst contemporary with the moa-signalled cooling event in Northwest Nelson (Holdaway 2021).

The change from *A. didiformis* to *E. curtus* coincided with the date of the Oruanui super eruption from Taupo Volcano (Figs 4&5). There is a gap in the available date sequence for *E. curtus* between *c.* 22,000 and *c.* 15,500 years BP and another between the final record of *E. curtus* at *c.* 15,500 BP and the first *A. didiformis* at *c.* 12,500 years BP. Several major eruptions affected the central North Island between the Oruanui and Taupo First Millennium eruptions but they each involved *c.* 2 orders of magnitude less ash than the Oruanui (Fig. 4A).

Glacial-Interglacial Transition

There was a gap in the date series for the two taxa from 22,000 to 15,500 years ago, before the final record of the (continued?) presence of *E. curtus* in the karst (Fig. 4). At 12,500 BP, *A. didiformis* replaced *E. curtus*, with its radiocarbon-dated presence attested until moa extinction (Fig. 4).

DISCUSSION

Climate is taken conventionally to be the major control on the distribution of vegetation types including grassland, shrubland, dry forest, and lowland rain forest (McGlone 1985; Newnham *et al.* 2013) and therefore of bird habitat, including that of moa (Worthy 1990, 2000; Worthy & Holdaway 1993, 1994, 1996; Worthy & Swabey 2002), in New Zealand. Volcanism has been seen as affecting vegetation only in the central North Island, around the volcanoes of the Taupo Volcanic Zone (McGlone 1985; Wilmshurst & McGlone 1996). As long ago as the 1950s, however, volcanism was seen as having a wider role in controlling the distribution of fauna, at least of soil fauna (Lee 1953, 1959).

A few of the largest eruptions, such as the Rangitawa/Whakamaru (*c.* 340 ka) and Oruanui/Taupo (25.4 ka), have deposited ash over significant areas of both main islands (Pillans *et al.* 1996; Vandergoes *et al.* 2013). The area covered by the Kawakawa-Oruanui tephra ejected during the Oruanui super eruption included the Cook Strait land bridge and the other land areas exposed by glacial low sea levels (Vandergoes *et al.* 2013). The mapped isopachs (ash depths) for the Oruanui eruption (Vandergoes *et al.* 2013) are consistent with widespread destruction of vegetation (Oppenheimer 2011), and hence of its associated avifauna, including moa.

Super eruptions, at least, must be seen as major factors determining the distribution and composition of vegetation between the Auckland isthmus and the Waitaki River, the limits of the 2 cm isopach mapped by Vandergoes *et al.* (2013). Many, if not most, New Zealand pollen records post-date the Oruanui eruption. The question therefore arises as to whether the vegetation (and faunal) patterns ascribed to glacial climate were not actually the result of the damage caused by the Oruanui eruption, exacerbated by the cold climate in which it took place, and not driven just by the climate itself. Indeed, contrary to the current model, the presence of *A. didiformis* indicates the presence of lowland rain forest in the Waitomo karst more

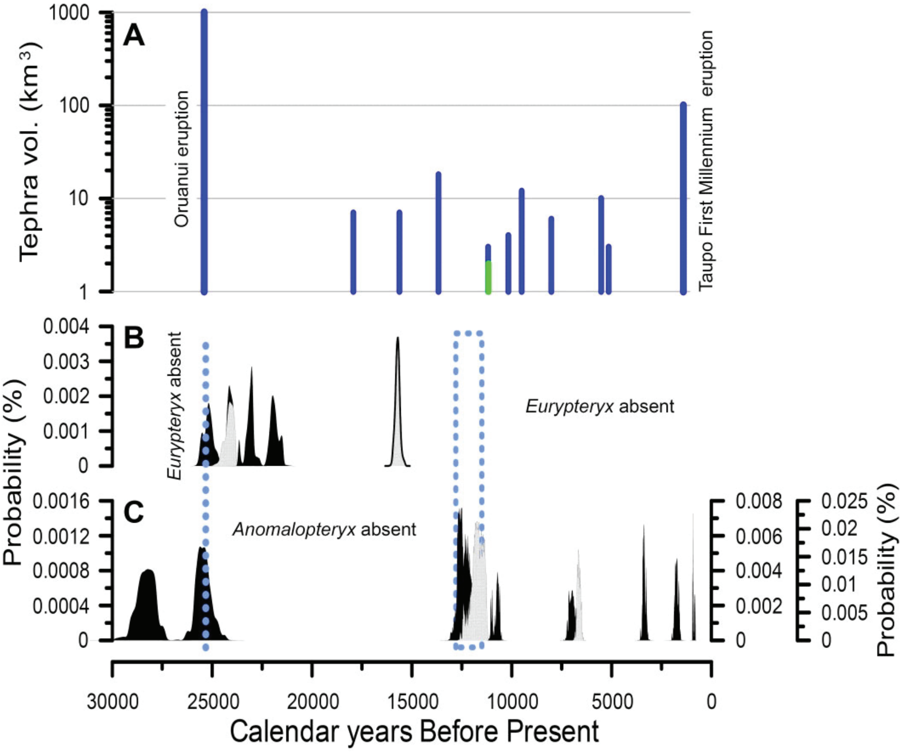

Figure 4. Calibrated calendar date probability distributions for radiocarbon ages showing alternation of the presence of two moa taxa, *Anomalopteryx didiformis* (rain forest) and *Euryapteryx curtus* (shrubland and dry forest), in the Waitomo area, western central North Island, New Zealand in relation to major volcanic eruptions. **A**, Tephra volumes for eruptions ($\log_{10}$ scale). **B**, *E. curtus* ages. **C**, *A. didiformis* ages. Dotted line, date for the Oruanui super eruption of Taupo Volcano (*c.* 1,000 km^3 tephra); dotted rectangle, timing and duration of Younger Dryas post-glacial cold period. Two distributions have grey fill to differentiate them from nearly synchronous individuals. Two almost coeval eruptions (Poronui; Karapiti) are shown with different colours for clarity. Multiple y-axes for probabilities allow better comparison of date distributions. See Table 1 for details of radiocarbon ages.

than 25,400 years ago, during the extended Last Glacial Maximum (eLGM) (Newnham *et al.* 2007). Although Newnham *et al.* (2007) suggested that pollen records from Auckland, 145 km north of Waitomo, show that the Oruanui eruption fell "within a period of climate amelioration" that lasted for *c.* 2,000 years (26,000 to 24,000 BP) within their 29,000 to 19,000 year-long BP eLGM. To what extent that "amelioration" would have allowed lowland rain forest to spread south again is unknown, but the *A. didiformis* that died in Moa Cave nearly 29,000 years ago (Table 1) shows that rain forest was in the karst at the start of their period of warmer climate.

Previous environmental reconstructions for the Waitomo karst

There are no significant pollen records from the Waitomo karst so reconstructions of the vegetation have depended on records from surrounding areas, especially from the Waikato Basin to the north (Worthy 1984; Worthy & Swabey 2002). Worthy & Swabey (2002) noted that Newnham *et al.* (1989) suggested that that landscape was "largely unforested" from 18,000 to 14,000 ^{14}C years ago, a period corresponding to a calendar date range from 21,900 to 17,000 years BP. The presence of the shrubland moa *E. curtus* in the karst during this period is consistent with the pollen-based interpretation of the vegetation.

The most intensively dated fossil deposits within the karst are those near the Zweiholen entrances in Gardners Gut Cave, just west of Waitomo Caves, *c.* 30 km east of the present coastline, and F1c cave, 9.5 km to the south (Worthy & Swabey 2002). All of the dated *E. curtus* and three of the *A. didiformis* individuals were from these two cave systems. Both species were living, for protracted but nonoverlapping – at least in terms of the present sample – periods around the entrances to these caves. The change in their recorded presence is therefore unlikely to have resulted from a local spatial difference in their distributions, for example if one or other lived in riparian vegetation while the other was on the intervening hills.

The two ages were measured early in the application of radiocarbon in moa research when any age measurement was important. That these are still the only two pre-Holocene radiocarbon ages for *A. didiformis* is, as noted above, partly because most programmes have focused on other taxa and dating is expensive. It may also be in part because there are fewer or even, as in the Marlborough Sounds no, fossil deposits in possible ice age rain forest refugia. Indeed, where South Island *A. didiformis* survived until the Holocene is still a mystery. The two pre-Holocene *A. didiformis* may indicate that one of the elusive refugia was near Waitomo, until Oruanui.

The nine radiocarbon ages from the Zweiholen system include one on *A. didiformis* (Table 1) and five on *E. curtus* (Table 2). The oldest dated *E. curtus* was in the ZW5 deposit. It died 25,191 ± 255 years ago (NZA9985), just after the Oruanui eruption. Its remains were within Layer 4, "a fluvial layer of sand and gravel (< 10 mm)… bones in these sediments were water-worn, indicating that they had been transported some distance" (Worthy & Swabey 2002). The thin Layer 4 lay on "the original clay infill of the passage transported to the site from a considerable distance away by the last presence of the stream that formed this high level of the Zweiholen passages … The surface of Layer 5 in the excavation reveals the extent to which these clays were excavated before sedimentation recommenced." (Worthy & Swabey 2002). Based on the NZA9985 date on the moa, the interface of Layers 4 and 5 is contemporary with the Oruanui eruption.

The ZW5 deposit represented mostly the fauna in the 3,500 years following the Oruanui eruption. Throughout this period, the presence of *E. curtus* records a local shrubland environment. One *E. curtus*, about 20 cm above the oldest, and in Layer 3, lived 24,149 ± 227 years ago (NZA9950), about 1,000 years after the Layer 4 bird and the eruption. Deposition in that site continued for at least another 2,500 years, with a third *E. curtus* 20 cm above the Layer 3 bird dated at 21,870 ± 218 BP (NZA10055). Sometime after that, a long hiatus in the dated fauna began that lasted until the early Holocene. The only dated moa from their Layer 1 was an *A. didiformis*: it lived in the Holocene lowland rain forest there 6,645 ± 84 years ago (NZA10054). The next oldest dated *E. curtus* from the cave system was from ZW2; this individual was, at 24,143 ± 180 years ago (NZA9277), contemporary with the oldest bird in ZW5, just after the Oruanui eruption.

Other than the two *A. didiformis*, the only dated evidence from the avifauna for the vegetation preceding the Oruanui eruption is the presence of a North Island goose (*Cnemiornis gracilis*). The goose's radiocarbon date of 26,879 ± 226 years BP (NZA9071) places it over 1,000 years before both the eruption and the final presence of *A. didiformis* at 25,452 ± 381 BP (NZ4843), but c. 1,500 years after the earlier *A. didiformis* (28,323 ± 456 BP, NZ4838). The two *A. didiformis* show that rain forest was present in the karst up to the Oruanui eruption. The presence there of the goose at that time might be seen therefore as anomalous. Based on its distant relationship to the Cape Barren goose (*Cereopsis novaehollandiae*) of Australia (Rogers 1990; Worthy *et al.* 1997), its habitat has traditionally been thought to have been grassland. Worthy & Swabey (2002) suggested that the goose and the waterfowl preserved in the Holocene deposits when the local vegetation was certainly rain forest reflected the presence of water bodies within the forest: "the presence of both *E. finschi* [= *Chenonetta finschi*] and *A[ptornis] otidiformis* in F1c may be related to the surroundings of the cave, which was probably a small glade with a tarn in an otherwise forested habitat (Worthy 1984b)". However, Finsch's duck (*Chenonetta finschi*) was a forest species whose presence is not an indicator of standing or running water (Worthy & Holdaway 1994). Neither the North Island goose nor the South Island goose (*C. calcitrans*) may have been confined to grassland (Johnston *et al.* 2022).

Comparison of moa-derived and pollen evidence for eLGM forest near Waitomo

Lees *et al.* (1998) described the composition of the coastal forest from pollen in a bog ("Airstrip bog") presently at 135 m a.s.l., 90 km NNW of Waitomo (Fig. 5). That pollen record began somewhat earlier than the 24,000 years BP proposed by the authors, based on the lower of the two radiocarbon ages measured on dried, untreated peat samples. The calibrated mean date for radiocarbon age Wk-1139A (23,400 ± 340 ^{14}C years BP) from 7.0–7.20 m depth using the SHCal20 curve (Hogg *et al.* 2020) gave a revised calendar date of 27,619 ± 321 years BP. Between the sample and 7.0 m depth, the pollen record ceased: the next counts were not until 6.60 m (fig. 4 in Lees *et al.* [1998]). No sample was collected from 6.80–7.0 m because of "a possible water pocket". The gap, which is near the base of Lees *et al.*'s (1998) Zone 1A, is not discussed by those authors, but the stratigraphic record (their Table 1) describes the sediment at 7.10 m as being "Black coarse sand, pollen very scarce, large amount of organic matter", and that the pollen grains were severely clumped, as might be expected in a forest soil developed in tephra. That tephra could have been the Oruanui.

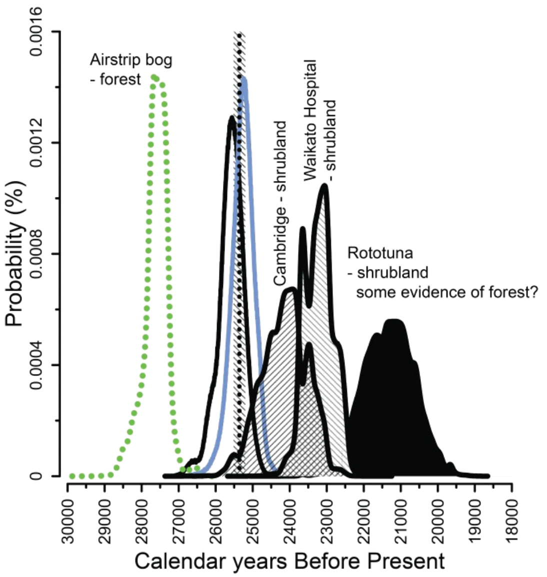

Figure 5. Date distributions for coastal rain forest (green dotted line) (Lees *et al.* 1998), and shrubland (dashed and solid fill) in the lower Waikato (McGlone *et al.* 1978) around the eLGM, in relation to the date of the Oruanui eruption and of the change from *Anomalopteryx didiformis* to *Euryapteryx curtus* in the Waitomo karst, as shown Figure 4&6.

The authors calculated dates for changes in the pollen spectrum assuming a constant accumulation rate of 0.75 mm year^{-1} (an interval of 7,350 years for the 5.5 m between 1.6 m and the bottom of the core). However, the radiocarbon age for the 1.58–1.62 m sample (Wk-1137A 16,050 ± 180 ^{14}C years) yielded a calibrated date of 19,330 ± 216 years BP. The new calibration means that a period of 8,290 years was encompassed by the 5.5 m between the samples, giving a lower accumulation rate of 0.664 mm year^{-1}. The 4.10 m level would then have an approximate calendar date of 23,100 years BP rather than the 20,400 years BP suggested by Lees *et al.* (1998).

The new calibrated dates suggest that Lees *et al.*'s (1998) Zone 1A (7.55 to 4.10 m) lasted from c. 27,600 years BP to 23,100 years BP. This range encompasses the revised date of 25,400 BP for the Oruanui eruption (Vandergoes *et al.* 2013), which, if the accumulation rate was indeed constant, corresponds to a depth of 5.70 m in the core. *Leptospermum* and *Coprosma* peaked just above this level in their figure 3, *Dacrydium* started a decline, and *Metrosideros* dropped out. However, if the rate was not constant, the eruption may have occurred in the interval corresponding to the "water pocket" and the rise in *Leptospermum* and other shrubs after 7.0 m may reflect ash damage to the rain forest in the area.

Assuming, as the authors did, a constant accumulation rate within the revised chronology, Lees *et al.*'s (1998) Zone 1B dated from 23,100 to 22,200 BP, Zone 2 from 22,200 to 19,500 BP, Zone 3 from 19,500 to 18,600 BP, and Zone 4 from 18,600 BP to present. Consequences for these changed dates for the patterns of vegetation change at the site are not explored here, but should be taken into account in future modelling of vegetation in the area.

Inland, in the Waikato River basin, McGlone *et al.* (1978) described the pollen records in three peat lenses exposed in the alluvium of the Hinuera Formation near Hamilton (Waikato Hospital, 0.5 m thick; Rototuna, 0.1 m thick) and Cambridge (0.3 m thick), respectively 55 km NNE and 50 km NE of Waitomo. Only one radiocarbon age was obtained for each peat layer. For the Waikato Hospital site, the Wk-23 ^{14}C age of 19,804 ± 340 years BP (new $T_{1/2}$) gives a conventional Libby $T_{1/2}$ age of 19,243 ± 340 years BP; calibration using the SHCal20 curve gives a calendar date of 23,214 ± 387 years BP. For the Rototuna site, the reported age (Wk-59, 18,100 ± 550 ^{14}C years BP [new $T_{1/2}$] [17,587 ± 550 ^{14}C, Libby $T_{1/2}$]), the calibrated date is 21,312 ± 676 years BP. Similarly, the Cambridge peat (NZ330, 20,600 ± 500 ^{14}C years BP [new $T_{1/2}$] [20,016 ± 500 ^{14}C, Libby $T_{1/2}$]), yields a calendar date of 24,130 ± 615 years BP (95.4% confidence interval of 25,321 to 22,961 years BP) (Fig. 5).

These dates show that all the pollen records post-date the Oruanui eruption: none provides evidence of the vegetation before the eruption. The Cambridge peat immediately follows the eruption, the Waikato Hospital peat was laid down 2,000 years, and the Rototuna peat 4,000 years, after the eruption. All three pollen profiles suggest that the post-eruption vegetation was "dominated by scrub, grassland and swamp", with perhaps more forest several thousand years after the eruption.

Glacial-Interglacial Transition

The discussion of F1c in Worthy (1984) was revisited by Worthy & Swabey (2002), who also added more radiocarbon ages. An *E. curtus* preserved in the F1c rockfall deposit was, at 15,719 ± 118 BP (NZA11613, Table 2), the geologically youngest of that species known from the karst, shows that shrubland was present near Piopio, 25 km south of Waitomo, at that time. The date of 10,780 ± 154 BP for the *A. didiformis* in F1c (NZA11612) shows that the species, and its rain forest habitat, had reached the karst 5,000 years later. It is unfortunate that the sample dated for NZ4844 was "Mixed *D.*[*inornis*] *struthoides* and *A. didiformis*" (Worthy & Swabey 2002). As

"*Dinornis struthoides* is now recognised as being the smaller male of, in the North Island, the giant moa *D. novaezealandiae*, whose habitats included rain forest as well as shrubland, the species presence does not contradict that of *A. didiformis* and lowland rain forest at, perhaps, 11,728 ± 300 years BP. The date is uncertain because radiocarbon dating of a mixed sample that includes not only more than one individual but more than one taxon must yield a geometric mean age. There was no evidence that the sampled birds were contemporary. Fortunately, accelerator mass spectrometric radiocarbon dating requires such small samples that mixed samples are no longer necessary.

None of the eruptions between the Oruanui and Taupo First Millennium was as large as the Oruanui (Fig. 4). The few ages on Waitomo karst moa from the period between 21,000 and 15,000 BP limit the temporal resolution of the moa record of environmental change. A denser coverage begins with two ages (NZ4840, NZ4844) on *A. didiformis* and these are the more interesting because they confirm a change to lowland rain forest around Waitomo at the same time as a change from *A. didiformis* to *Pachyornis australis* on Takaka Hill (at 41°S) signalled a return to glacial climate contemporary with the Northern Hemisphere Younger Dryas event (Holdaway 2021). As reported there (Holdaway), there is less evidence for a cold period in tree rings in the northern North Island. The disjunction in moa-derived records in the two areas, three degrees of latitude apart, suggests that a possible northward movement of the Subtropical Convergence Zone, or the appearance of a jet of subantarctic water from south of the zone (Nelson *et al.* 2000), may have affected the climate of the northern South Island but not farther north, where the landmass would still have been surrounded by the subtropical water mass.

Conclusions

Half to one degree of latitude south of the pollen sites, the Waitomo karst was, until the 19th century, clothed in lowland rain forest. The presence of *A. didiformis* in the fauna >25,400 years ago shows that the vegetation then was also lowland rain forest (Worthy 1990; Worthy & Holdaway 1993, 1994, 2002), despite its being within the period of the eLGM. Then, precisely at the time of the Oruanui eruption (Fig. 4A), the rain forest moa was replaced rapidly by the shrubland species *E. curtus* (Worthy 1990, 2000; Worthy & Holdaway 2002).

Changes in the distribution of habitat-specific taxa such as these imply changes in the distribution of their habitats. The 40 cm isopach for the

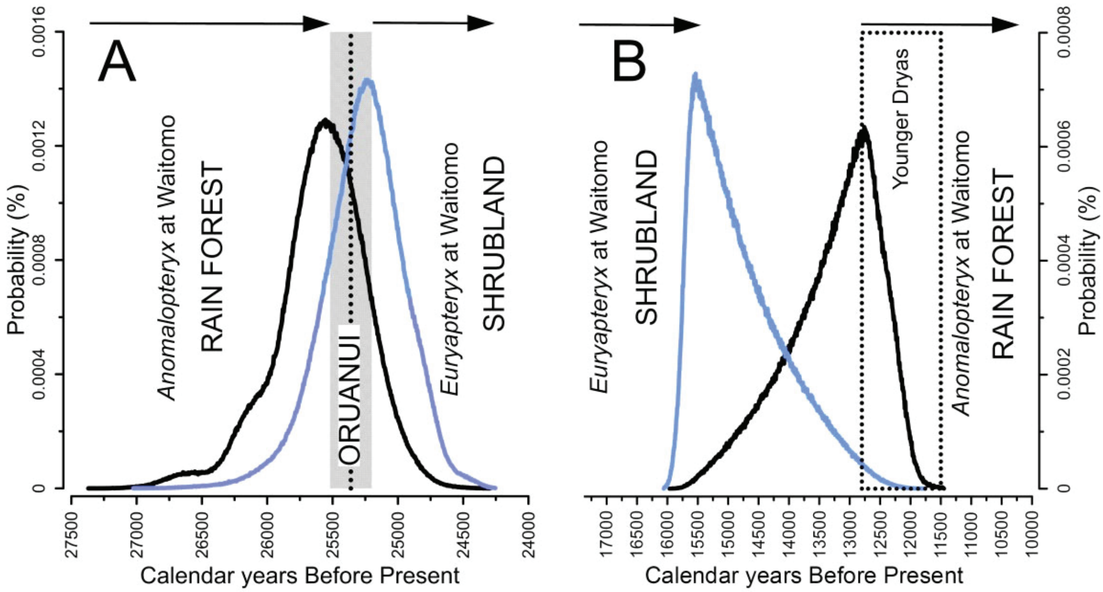

Figure 6. Bayesian estimated date distributions for (**A**) end of presence of *Anomalopteryx didiformis* (black) and arrival of *Euryapteryx curtus* (blue) in the Waitomo area, indicating a change of vegetation at time of the Oruanui eruption. **B**, end of presence of *E. curtus* (blue) and return of *A. didiformis* (black) during the transition between the Weichselian-Otiran glaciation and the Holocene interglacial, and the indicated change in vegetation. Oruanui eruption date: dotted line, mean; shaded rectangle, 95.4% confidence interval, from Vandergoes *et al.* (2013). Younger Dryas, dotted rectangle indicates duration of Younger Dryas post-glacial cold period.

Kawakawa-Oruanui tephra (Vandergoes *et al.* 2013) extends across the Waitomo karst (Fig. 2). Volcanic ash that deep will not only kill the vegetation but sterilise the soil (Oppenheimer 2011). The extent of the ashfall suggests that it would have taken some time (some centuries perhaps) for propagules from surviving vegetation to arrive from refugia that may have been hundreds of kilometres away. From an unknown refugium of its own, *E. curtus* colonised the developing shrubland.

The presence of rain forest in the karst until the eruption suggests that the present reconstruction of the LGM vegetation for that area is not correct. In addition, the abrupt change from forest to shrubland at, so far as it is possible to tell, the time of the Oruanui eruption suggests that the shrubland in the Waitomo karst and indeed farther north in the Waikato Basin during the eLGM was volcanogenic. It was probably not the normal vegetation in the area under a glacial climate.

Abruptness of faunal change at 25,400 years BP, contemporary with the Oruanui eruption in a period of glacial climate, is consistent with the eruption having been the driver of the vegetation (and faunal) change. In contrast, the apparently protracted change to lowland rain forest from shrubland is consistent with a (slower) climatic driver. As the global climate has been "glacial" for most of the past million years (Ehlers & Gibbard 2007), the recent post-glacial southward spread of rain forest through the main islands can be seen as a brief anomaly rather than – as usually done – a "recovery". The normal southern boundary of rain forest and its avifauna during glacial periods was probably south of its presently accepted position, which is itself probably an artefact of the effects of the super eruption. In that respect, the southward spread of *A. didiformis* into the Waitomo karst was, for that species at least, a recovery of its pre-eruption distribution. *Euryapteryx curtus* remained in the central North Island avifauna at the behest of the ongoing lesser eruptions, as its presence after the Taupo First Millennium eruption attests. The species may there have been a "volcanic nomad", its distribution ebbing and flowing with the changing patterns of post-eruption shrublands.

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