

Response to Reviewer 1

I thank the reviewer for their rich and extended summary of the palynological and moraine literature on the New Zealand Late Quaternary. I will respond to those matters later but first, I will deal with the reviewer's brief references to the data and arguments presented in the paper itself.

The few sentences in the review devoted to the data reveal a fundamental misunderstanding of both moa biology and depositional regimes in New Zealand caves. Firstly, the reviewer contends that a few moa in a few caves does not constitute a climatic record because moa were large animals that freely wandered through the landscape. There is no evidence at all to support this statement: it is pure *ex cathedra* conjecture which could be seen as a throwaway line on which to reject the data. There is, of course, ample evidence that *populations* expanded and contracted their distributions over decades, centuries, and millennia, as would be expected in species responding to changing environments¹⁻⁹. But there is no evidence at all that individual moa wandered across the landscape.

What little evidence that is available, from ancient genetics and trace elements from a species not referred to in the paper, suggests the contrary, i.e. that moa were sedentary. For example, closely related adult females of the South Island giant moa (*Dinornis robustus*) were deposited in the same site (Pyramid Valley) in the late Holocene¹⁰. An exploratory analysis of trace elements in the bones of giant moa from adjacent (< 6 km apart) sites in North Canterbury showed that all but one of the 11 had died in its natal area; the other one had moved only to the other site (Fig. 1). The issue of cave system "sampling" of moa faunas is covered below.

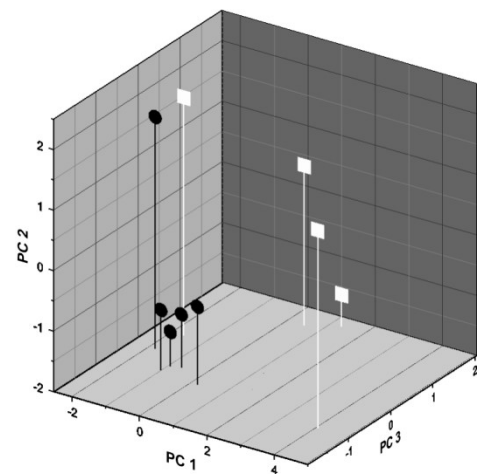


Fig. 1 Principal component analysis of heavy metal composition of giant moa from Pyramid Valley (black) and Bell Hill Vineyard (white).

The reviewer also asserts that some moa were not confined to particular habitats. That is true, so far as it goes, but it does not include the taxa in the paper. Remains of giant moa have been found in situations where they would have occupied lowland rain forest, dry eastern forest, and high altitude shrubland and fellfield^{5,6,11}. The upland moa, *Megalapteryx didinus* has also been found in areas of rain forest and high altitude shrubland and fellfield^{1,11}. However, neither of these species is referred to in the paper. Of the moa actually referred to, the "crested" moa, *Pachyornis australis*, is well attested to have occupied glacial shrubland¹²⁻¹⁴, and it "retreated" to high altitudes during the late Holocene^{15,16}.

For example¹⁵, Abstract

"We show that *Pachyornis* changed altitudinal, longitudinal and latitudinal ranges through the Late Quaternary in response to alterations in the distribution of suitable habitat... The results suggest that crested moa [i.e. *Pachyornis australis*] tracked habitat through time with little consequence to population size."

Also¹, page 224

“At the higher altitude of Honeycomb Hill Cave, the Otiran fauna is dominated by *M. didinus* and *P. australis*, both of which were upland species (Worthy, 1990)”

And⁶, page 217

“The upland moa (*Megalapteryx didinus*) and the crested moa (*Pachyornis australis*) were found to be the predominant moas in a montane forest -subalpine scrubland habitat whereas the little bush moa *Anomalopteryx didiformis* and large bush moa *D. novaezealandiae* [now the wet forest morph of both the North Island *D. novaezealandiae* and the South Island *D. robustus*] probably preferred wet dense lowland forests. We suggested that *Pachyornis elephantopus* primarily preferred open dry habitats. These conclusions were further endorsed by (Worthy 1989a) and (Worthy 1989c). Also, I have (Worthy 1987) presented biological observations relating to the proposed ecology of *Pachyornis elephantopus* and *Euryapteryx geranoides* [now *E. curtus*] and concluded that their preferred habitat was dry lowland mosaics of shrubland, grasslands and forests.”

In the Abstract¹

“The Holocene fauna [of the South Island West Coast, including *Anomalopteryx didiformis*] is assumed to have lived in vegetation similar to that found by the first Europeans, i.e. wet, dense, podocarp-hardwood forest, with swamp vegetation on riverbed flats.”

As above, the little bush moa, *Anomalopteryx didiformis* has always and only been seen as a rain forest species^{1-3,5,6}, as cited above (highlighted). Lowland rain forest is still present in the central North Island “King Country”, as it was throughout the Holocene, where Worthy¹⁷ noted that:

“*Anomalopteryx didiformis* dominated the moa assemblages in all sites, as it does in the King Country fauna as a whole (Millener 1981).”

As noted above in the extract from reference 6, *Euryapteryx curtus* was a dry forest and shrubland species that has never been found in association with either wet forest or at high altitudes^{1,2,4-6,18}.

Hence, there is no reason to suppose that the sequence of moa in the Takaka area represented anything other than a succession of replacement of populations.

Together, the extensive literature on moa distribution through space and time support my use of, primarily, *P. australis* and *A. didiformis*, as indicators of the presence of their characteristic habitats of alpine/glacial vegetation and lowland rain forest, respectively. Hence the reviewer’s rejection of their use as environmental indicators has no basis.

Samples from caves

The second component of the reviewer’s rejection of moa as environmental indicators is that of a perception of its being based on “a few moa in a few caves”. This statement ignores the pattern and process of deposition in caves, and their role as natural “pit traps” collecting individuals from resident moa populations through time. The likelihood of the presence of “wanderers” amongst the residents therefore becomes amenable to basic statistical analysis.

More than 125 moa have been identified in large and small caves in the Takaka area. They were deposited in the caves, based on the oldest 14C-dated individual, over the past 30,000 years. That represents an average rate of c 4 per 1000 years, or one every 250 years. The probability that any of those birds being a wanderer from another area rather than being from a resident population whose members daily traversed the area around the caves is remote. For those extremely rarely

trapped wanderers to be incorporated in exactly the pattern observed on Takaka Hill and in Takaka Valley is beyond remote.

The observed pattern, if generated by wandering birds, would require only wandering *A. didiformis* to be present and ¹⁴C-dated before the Younger Dryas, only wandering *P. australis* to be trapped and ¹⁴C-dated during the period of the Younger Dryas (among the local populations of whatever other resident taxa whose individuals were not trapped), and then only wandering *A. didiformis* to be trapped and dated thereafter. No *P. australis* wandered to Takaka Hill after the Younger Dryas from the populations which were definitely present in the mountains to the south throughout the Holocene^{15,16}.

These factors show that the sequence of habitat-specific moa in the Takaka area does indeed map a sequence of climate-driven vegetation types. The data therefore must be taken at face value. The discussion in the paper is an attempt to interpret the reality of the vegetation changes and their chronology in terms of data from other sources, which have their own issues, as below.

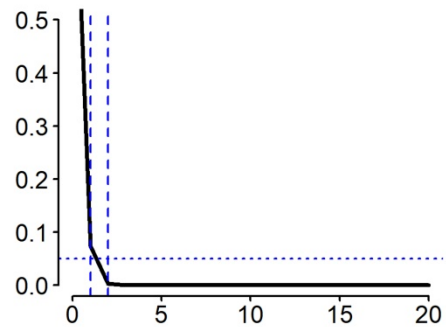


Fig. 2 Probabilities of 1 or 2 wandering moa being incorporated in a Takaka Cave rather than a local population of 20 of another taxon

The New Zealand pollen record

The pollen record, comprehensively summarised by the reviewer, concentrates on taxa with high, often masting, pollen output, including podocarp trees, southern beeches, and *Chionochloa* grasses. No mention is made, in most instances, of the considerable number of insect- or bird-pollinated trees and shrubs. No attempt is made in New Zealand to weight the pollen record by pollen output, as is now standard practice in Europe and the United Kingdom. Examples of the changes in interpretation that can follow from weighting and factoring in habitat-related flowering and pollen production include^{19,20} the replacement of the concept of a Holocene oak forest in England by that of a lime-dominated forest, and the recognition that hazel pollen in a deposits indicates the presence of hazel forest and not a hazel understorey as hazel does not flower under a canopy of other trees.

A very recent example from New Zealand of the potential mismatch between pollen and the distribution of vegetation, is the domination of the late Holocene vegetation of Central Otago by bird-pollinated *Sophora* trees, and not by anemophilous podocarp conifers²¹.

Almost never mentioned are the results of studies of modern pollen distribution^{22,23}. These suggest that pollen, particularly of some important taxa can accumulate far from their source(s). As can be seen from the cited references below, the reviewer is fully aware of these issues.

From²², pages 263 and 271.

“Sites above the treeline on the Main Divide showed anomalous high counts of exogenous Podocarpaceae pollen. This seems to be washed out of strong NW winds by orographic precipitation. Peat cores taken from 3 sites confirm that exogenous podocarp pollen influx has continued over at least the last 500 years.

“The present study establishes some general principles about aerial pollen deposition across the Southern Alps. There is little evidence of podocarp pollen being deposited locally; instead it is carried by strong westerlies to the Main Divide where the high rainfall causes deposition of large amounts of

it. Is this feature peculiar to upper valleys such as Otira? The phenomenon of transport of podocarp pollen upslope has been noted by previous workers (Moar, 1970; McGlone, 1982; Pocknall, 1982). Pocknall (1982) presumed it to be due to low pollen production of the local sub-alpine vegetation but the present results suggest that a different interpretation is warranted. Low podocarp pollen count values are apparent for all four Westland valley sites. Other observations in Westland (Pocknall, 1980) show podocarp pollen being deposited locally, although low frequencies of *Dacrydium cupressinum* have also been observed at some sites. These apparently anomalous results were considered by Pocknall (1978) to be due to the effects of vegetation structure and dispersal of large amounts of pollen of other taxa in the vegetation, but it appears that wind carriage of pollen to distant sites is a normal feature for this species. The dispersal pattern of *Nothofagus fusca* type pollen is such that it is not possible to distinguish between a few trees near the sample site and many trees at a great distance. *Nothofagus* pollen appears to be dispersed from east to west but only in trace frequencies. This is probably due to the predominant north-west wind flow. Poaceae pollen dominates in the grassland sites, with only low frequencies in forested areas. This has been considered to be due to only small amounts of Poaceae pollen being transported into and through forested sites (Pocknall, 1978). This study suggests that Poaceae pollen may not be well dispersed.”

From²³, page 215

“The accumulation of *Nothofagus fusca* type pollen increased with increasing distance from the forest, as in other wind-pollinated taxa (Davis et al., 1973). It was likely that within the forest, only the trees immediately around the site contributed pollen, whereas in open sites (e.g. at Lake Hawdon and Cave Stream) a larger number of trees contributed pollen. The accumulation data showed that there was a high accumulation of *Nothofagus* pollen in the grassland sites, representing only 12 to 15% of the total pollen. These results suggest that *Nothofagus* pollen was being dispersed into the grassland, but was masked by the local herbaceous pollen. This could explain Pocknall's (1982) observations of low percentage of *Nothofagus* pollen in the grassland sites, although beech forest was nearby.”

Moraines

Early moraine studies in New Zealand also hypothesised a Younger Dryas²⁴, but these have been rejected more recently. However, moraine-based chronologies of glacial advances and retreats in the Southern Alps of New Zealand are perhaps not as straightforward to interpret as the reviewer implies. In particular, there is an ongoing discussion as to whether moraines can be distinguished from large rockfalls in the tectonically very active Southern Alps region²⁵⁻²⁹.

In addition, the moraine chronologies can be based on assumptions that are somewhat circular. For example, from³⁰, page 17

“We made no corrections for snow cover or for erosion of boulder surfaces. In the central part of the Southern Alps, winter (June-July-August) snow cover is generally persistent only at altitudes above ~1500 m. Below that altitude a winter snowfall of 1 m is an exceptional event and generally melts away within a few weeks. Moreover, the sampled boulders protrude from the crests of moraine ridges and are likely to be swept clear of snow by the wind. Thus, at the elevation of our sample sites (1150 - 1450 m above sea level), significant shielding due to snow is unlikely, especially given the northerly (sunny) aspect of Reischek knob and Meins Knob.”

The highlighted text assumes that present observations are directly relevant to the late glacial, which is by no means assured. The ¹⁰Be chronology itself, which is at variance with previous estimates of ¹⁰Be production³¹ was based on a radiocarbon sequence from macrofossils³¹ that may have been from (based on their figure 4) the same tree. None of the radiocarbon ages from those samples, and none cited as from sediments was assessed with respect to possible old carbon contamination from the soil³².

With the timing of the environmental changes, it was natural to compare the sequence with those from other cave proxies from the same area (which lacks pollen records apart from a scanty one from Honeycomb Hill Cave over 50 km to the west of Takaka and on the other side of the northwest Nelson mountain ranges¹⁴. The most comprehensive of those records³³ related speleothem $\delta^{18}\text{O}$ values to temperature, at least in general terms, and a “significant negative excursion ... spanned the Younger Dryas”, as in the quote from the Abstract below:

“Late-glacial warming commenced between 18.2 and 17.8 ka and accelerated after 16.7 ka, culminating in a positive excursion between 14.70 and 13.53 ka. This was followed by a significant negative excursion between 13.53 and 11.14 ka of up to 0.55x depth that overlapped the Antarctic Cold Reversal (ACR) and spanned the Younger Dryas (YD). Positive $\delta^{18}\text{O}$ excursions at 11.14 ka and 6.91–6.47 ka represent the warmest parts of the Holocene.”

It was appropriate, therefore, to compare these results with the moa records from Takaka.

As the moa record and part at least of the speleothem record (above) both suggested a cool climate episode synchronous with the Younger Dryas, it was only appropriate then to compare the results with those showing an undoubted Younger Dryas. Hence the comparisons with the GISP 2 ice core records. Greenland was chosen because of the solid chronology for the cold period and because the land mass is, as is New Zealand, subject to westerly winds. Antarctica, by contrast, is isolated from the belt of strong westerly winds and has its own climate. There have been suggestions of a Younger Dryas event in South and Central America^{34,35} on the other side of the Pacific, in South Africa³⁶, and in a Southern Ocean core³⁷.

Summary

The reviewer’s bald rejection of the moa chronology for a Younger Dryas period in the northern South Island of New Zealand is based on a lack of understanding of the habitat requirements of the moa taxa involved, and of the processes of deposition in cave systems. Hence the data can be validly set against the pollen- and moraine-based chronologies and should not be just set aside because they run counter to current views.

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