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REVIEW

The diets of moa (Aves: Dinornithiformes)

Jamie R Wood[1]* iD, Sarah J Richardson[1] iD, Matt S. McGlone[1] and Janet M Wilmshurst[1,2] iD

[1]Manaaki Whenua – Landcare Research, PO Box 69040, Lincoln 7640, New Zealand
[2]School of Environment, The University of Auckland, Private Bag 92019, Auckland 1142, New Zealand
*Author for correspondence (Email: woodj@landcareresearch.co.nz)

Abstract: For tens of millions of years the ratite moa (Aves: Dinornithiformes) were the largest herbivores in New Zealand's terrestrial ecosystems. In occupying this ecological niche for such a long time, moa undoubtedly had a strong influence on the evolution of New Zealand's flora and played important functional roles within ecosystems. The extinction of moa in the 15th century CE therefore marked a significant event in New Zealand's biological history, not only in terms of biodiversity loss, but in the loss of an evolutionarily and ecologically distinct order of birds. Understanding the full extent and magnitude of this loss, and its implications for New Zealand ecosystems, depends upon a detailed knowledge of moa diets. Over the past 100 years, periodic discoveries of preserved moa gizzard content and coprolites (ancient preserved dung) have gradually begun to shed light on the diets of moa and their roles within New Zealand ecosystems. Here, we review how the study of such samples has shaped our understanding of moa diets through time. We then provide a synthesis of current knowledge about moa diets, including summarising 2755 records of plant remains from 23 moa gizzard contents and 158 moa coprolites. A clear picture is now emerging of distinct differences between the feeding ecologies of moa species, which together with differences in habitat preferences facilitated niche partitioning. Such insights provide empirical data to inform the debate surrounding the role of moa herbivory in the evolution of distinctive plant traits within the New Zealand flora. These data also help identify specific ecological functions and roles that have been lost due to the extinction of moa, and resolve to what extent these could be replaced via surrogate taxa.

Keywords: birds, extinct species, herbivory, New Zealand, palaeoecology, plant communities, seed dispersal

Introduction

New Zealand's native fauna has a complex evolutionary history. Isolated for tens of millions of years, the ancient vicariant fauna of New Zealand, an emergent part of the continent Zealandia (Mortimer et al. 2017), was supplemented by the dispersal of new species from nearby landmasses (such as Australia and New Caledonia) throughout the Tertiary Period (Tennyson 2010; Gibbs 2016). Adaptation, speciation and extinction of fauna inhabiting Zealandia's dynamic landscapes was driven by natural processes such as volcanism, tectonic uplift and climate change (Fleming 1979; Tennyson 2010; Gibbs 2016). In the near-absence of terrestrial mammals, except for several bats and one small mammal of uncertain affinity (Worthy & Holdaway 2002; Worthy et al. 2006; Hand et al. 2013; 2015; 2018), groups such as birds, reptiles, amphibians, and invertebrates have dominated New Zealand's terrestrial faunal communities for much of its history (Lee et al. 2009; Jones et al. 2009; Gibbs 2010; Tennyson 2010; Worthy et al. 2011; 2013). The arrival of the first human settlers from Polynesia in the 13th century CE (Wilmshurst et al. 2008), initiated a period of unprecedented and sustained ecological transformation in New Zealand. Hunting (Anderson 1989a; Perry et al. 2014), the removal of forests by burning (McGlone 1983; McWethy et al. 2010) and the introduction of the predatory Pacific rat (*Rattus exulans*; Roff & Roff 2003), drove widespread range contractions, population declines and extinctions within New Zealand's native fauna (Worthy & Holdaway 2002; Tennyson & Martinson 2006; Wood 2013).

Of all New Zealand's recently extinct species perhaps none have evoked as much interest and attention as the moa (Dinornithiformes). This extinct order of large flightless birds had a long evolutionary history in New Zealand, and molecular dating suggests that moa were present on New Zealand at the time of (or shortly after) its separation from Gondwana (Mitchell et al. 2014). Currently, the oldest fossils of moa are from Early Miocene lacustrine deposits in Central Otago (Tennyson et al. 2010), and demonstrate that by c. 20 million years ago moa had already evolved to become large flightless birds. However, the radiation of moa into the nine species that existed at the time of first human arrival (Worthy & Scofield 2012) did not occur until after c. 8.5 million years ago (Bunce et al. 2009). This was driven initially by the uplift of the Southern Alps creating a diversity of habitats and new

ecological niches, with subsequent speciation resulting from the separation of the North and South Islands (Bunce et al. 2009). Moa were the largest herbivores in New Zealand's terrestrial ecosystems at the time of human settlement, with adult body masses ranging from c. 17 to c. 242 kg; the next largest being the extinct South Island goose (*Cnemiornis calcitrans*) at c. 18 kg (Tennyson & Martinson 2006). On insular landmasses around the world large herbivores played important roles within prehistoric ecosystems (Hansen & Galetti 2009), and this was almost certainly the case in New Zealand. For example, based on the relationship between herbivore mass and dry matter intake (Nagy 2005; Müller et al. 2013), the largest moa would have consumed several kilograms of plant matter each day, and therefore may have played a significant role in nutrient cycling (Tanentzap et al. 2013). Consumption of fruit, seeds and spore-bearing tissues meant that moa also dispersed a range of New Zealand plants (Clout & Hay 1989; Lee et al. 2010; Wood et al. 2012a), and fungi (Boast et al. 2018).

In addition to their ecological roles, moa may also have left an indelible mark upon the evolution of the New Zealand flora. Over the years a variety of New Zealand plant traits have been attributed to co-evolution with moa, as they are suggestive of reducing the impact of moa browsing. These include interlacing or filiramulate growth habit (e.g. divarication; Greenwood & Atkinson 1977; Bond et al. 2004), heteroblasty (Greenwood & Atkinson 1977; Mitchell 1980), deciduousness (Batcheler 1989), toxins (Greenwood & Atkinson 1977; Batcheler 1989), spines or spine-like structures (e.g. enlarged stinging hairs), leaf loss and photosynthetic stems, mimicry and reduced visual apparency (Burns 2010; Fadzly & Burns 2010), tough and fibrous leaves, distasteful compounds, and low nutrient status (Atkinson & Greenwood 1989). Alternative climatic or abiotic causes have also been suggested in most cases (e.g. Wardle 1963; McGlone & Webb 1981; McGlone & Clarkson 1993; Day 1998; Howell et al. 2002; McGlone et al. 2004). However, testing which selection pressures gave rise to these traits remains a difficult prospect (McGlone & Clarkson 1993), and in many cases it could have been a combination of factors including moa browsing, insect herbivory and abiotic drivers.

Although moa have now been extinct for > 500 years (Perry et al. 2014) their legacy continues to have a strong influence. Trees that were perhaps once browsed by moa still stand in forests today, and the entire range of ecological consequences associated with moa extinction may not yet be entirely realised (Wood & Wilmshurst 2016). Understanding the contribution of moa to the co-evolution of New Zealand plant traits, and the niches of moa in New Zealand's terrestrial ecosystems, relies upon a good understanding of what moa ate. Moreover, with the introduction of a suite of large mammalian herbivores to New Zealand over the past 150 years (King 2005), information on moa diets can help inform debates such as ecological replacement (Wood & Wilmshurst 2019), and rewilding (Wood et al. 2017a). Fortunately, relative to other recently extinct large herbivores around the world, there is good evidence for the diets of moa in the form of analysed preserved gizzard content and coprolites (ancient preserved dung; Fig. 1). However, reports of these analyses are widely spread throughout the scientific literature, and variability in the types of analyses performed (e.g. pollen, macrofossil, DNA) means it can be difficult to compare results between studies. Here, we attempt to resolve these issues and bring together all the existing direct evidence for moa diet, thereby providing the most up-to-date synthesis of the diets of different moa species. We also compare these diets to examine how niche

partitioning allowed different moa species to co-exist, and re-examine the roles of moa in New Zealand's pre-human ecosystems based on available diet evidence.

In search of moa diets

Early evidence and speculation about the foods of moa

For several decades after Owen (1840) concluded that New Zealand had once been home to an ostrich-like bird, scientific efforts to understand moa focussed on the collection and description of moa remains. The ecology and behaviour of moa were rarely considered during the late 19th century and mentions of moa diets in publications from this period are relatively uncommon (Worthy 1990). In perhaps the earliest published thoughts on the topic, Owen (1844) singled out several morphological features of moa (e.g. robust cervical vertebrae and strong neck muscles) and suggested that these were adaptations for "dislodging the farinaceous roots of the ferns that grow in characteristic abundance over the soil of New Zealand". Soon after this F. G. Moore, perhaps swayed by Owen's opinion, claimed in correspondence with Gideon Mantell (11 August 1849) that the diets of moa had consisted of ferns and small lizards (Anderson 1989b). The importance of ferns in sustaining moa was also mentioned by Hochstetter (1867), and again by Owen (1883), who wrote that moa ate "the peculiarly nutritious roots of the common ferns of New Zealand… with buds, foliage, or other parts of trees…"

The first direct evidence for moa diets came in 1875, when Taylor White described finding moa coprolites in a cave near Mt Nicholas (Lake Wakatipu). White reported that they "consisted of undigested fragments of what looked like the stalk of the fern" (White 1875). In another cave near Queenstown, White (1875) found more coprolites, and these too he claimed "contained undigested vegetable fragments, some of which seemed to be branches and stalks of fern broken into short pieces of three-quarters of an inch in length". It seems likely that White's description of the content of these specimens could have been biased by the earlier mentions of ferns having been an important part of moa diets. Recent examination by JRW of the specimens collected by White (now held in the collections of Te Papa Tongarewa) revealed that the "undigested fragments of what looked like the stalk of the fern" were simply the twigs of woody dicotyledonous species adhering to the surface of the droppings.

Ferns featured prominently in early suppositions of moa diets, although not everyone supported this view. In 1890 Vincent Pyke told the Otago Philosophical Institute "Hochstetter and others allege, without authority, that the moa lived on fern roots, which seems to me absurd when the natural capacity of the bird is considered" (Otago Witness 1890). Haast (1871) also had a different view of moa diets. He believed that moa were birds of non-forested habitats, and postulated that "seeds of the *Phormium tenax*… *Cordyline Australis* [sic]… large species of *Aciphylla*… *Coprosma*, and many other plants, had been at one time the favourite food of the *Dinornis*, whilst the roots of the *Aciphylla*, of the edible fern (*Pteris esculenta*) [bracken], and several other plants, might have provided an additional supply of food when the seeds of the former were exhausted. Moreover, I have no doubt that the different species of *Dinornis*, like those of the *Apteryx*, were omnivorous, so that they did not despise animal food, and thus lizards, grasshoppers, and other insects might also
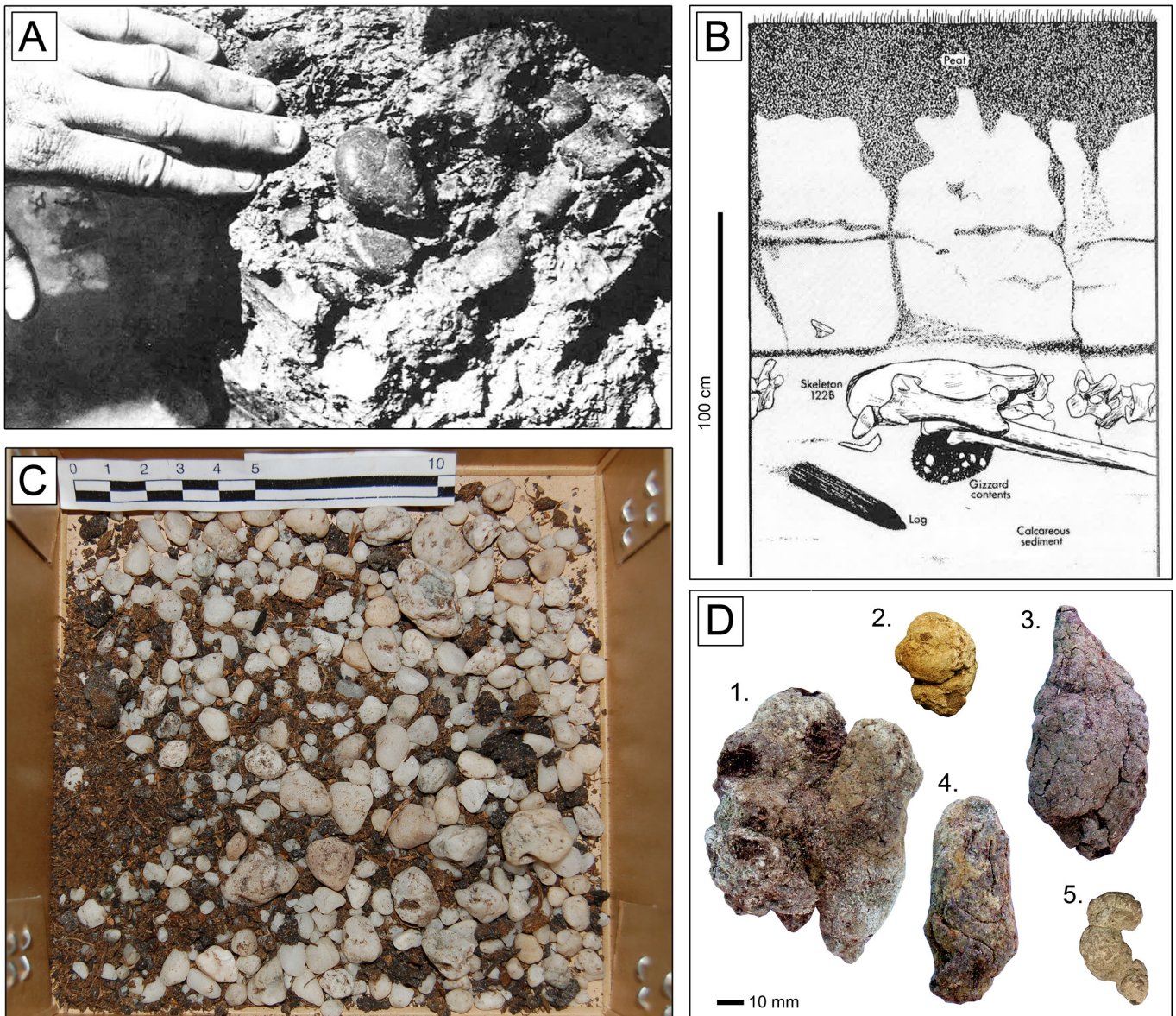
Figure 1. Sources of direct evidence for moa diets. A and B, In situ gizzard content found adjacent to the skeleton of an immature female South Island giant moa (*Dinornis robustus*), Pyramid Valley swamp, North Canterbury (images from Burrows et al. 1981); C, moa gizzard content from Scaife's Lagoon, west Otago (Otago Museum Av3647); D, Moa coprolites; 1. Heavy-footed moa (*Pachyornis elephantopus*) from Dart River Valley, West Otago; 2. Little bush moa (*Anomalopteryx didiformis*) from Mt Nicholas Station, West Otago (image from Wood et al. 2012b); 3. South Island giant moa from Dart River Valley, West Otago; 4. Upland moa (*Megalapteryx didinus*) from Dart River Valley, West Otago; 5. Upland moa from Euphrates Cave, Northwest Nelson (image from Wood et al. 2012a).

have constituted part of their diet." Evidence contradicting the fern-diet hypothesis was soon to come. In 1891, the Otago Witness newspaper reported the discovery of moa bones in a swamp at Enfield, near Oamaru, and that some of the skeletons also contained well-preserved gizzard content. The article noted that "The chewed grass from a well-preserved stomach is particularly interesting". That same year an accumulation of moa gizzard stones was found eroding out of peat deposits on Swampy Summit near Dunedin. Hamilton (1891) reported that amongst the stones was some light-coloured vegetable material that appeared to be the remains of plants consumed by the moa. This material included "vast numbers of seeds of *Leucopogon* and *Coprosmas* (?) [sic], and short twigs and branches which cannot be well identified".

Despite Owen's clear support for the idea that moa were forest herbivores adapted for consuming ferns, subsequent interpretation of morphological and dietary evidence had begun to form a different picture. Haast's (1871) view of moa ecology had come to the forefront of scientific thinking, and by the early 20th century the predominant view was that moa had been grazers of non-forested habitats. In demonstration of this, Buick (1931) wrote that moa "browsed upon the hillside grasses as the cattle do, and devoured leaves and berries when it could reach them". Subsequent discoveries of moa gizzard content appeared to support the idea of a grass-dominated diet. For example, moa gizzard contents discovered in a swamp near Whanganui in 1936 were reported to contain "triturated grass and occasional seeds of supplejack" (Northern Advocate

1936). Moa gizzard contents found at Pyramid Valley swamp in North Canterbury were described as "like a large plum-pudding in the yellow peat…often found close at hand, with seeds, grass and other vegetable matter amongst the gizzard stones" (Duff 1941). Archey (1941) reported that "the chief material in the gizzards was grass, not, however in a condition to be identified".

It is interesting to note that the repeat findings of grass in moa gizzard contents (Otago Witness 1891; Northern Advocate 1936; Duff 1941; Archey 1941) occurred after it had already been mentioned in the literature that moa were birds of non-forest habitats (Haast 1871). It is possible, therefore, that the identification of grasses within the fragmentary or digested plant material could well have been unconsciously swayed by the prevailing views of the day, in the same way that this appears to have been the case for ferns identified from moa coprolites during the late 19th century. Subsequent, more detailed analyses would reveal a distinct lack of grasses within the moa gizzard contents and create a new paradigm of moa ecology.

Detailed analysis of gizzard content establishes new paradigm for moa diet

Since 1891 several specimens of preserved moa gizzard content had been found, yet these had not been examined in any great detail. Except for the specimen from Swampy Summit near Dunedin (Hamilton 1891), all gizzard content samples had been found in association with skeletons of moa that had been mired in anoxic non-acidic bogs. In such situations the preservation conditions are ideal both for moa bones and the plant matter within their gizzards, which are often found together in situ.

The first quantitative evidence that some moa species may not have simply grazed herbaceous vegetation came with Ruth Mason's assessment of gizzard content samples from Pyramid Valley (Falla 1941). Within South Island giant moa (*Dinornis robustus*) gizzard content Mason identified many twigs and c. 200 *Coprosma rhamnoides* seeds, and in an eastern moa (*Emeus crassus*) gizzard content sample identified seeds of *Prumnopitys taxifolia*, *Myoporum laetum*, and *Nertera* (Falla 1941). Mason also reported (in Gregg 1972) that another *E. crassus* gizzard content sample, as well as a sample from a coastal moa (*Euryapteryx curtus*) gizzard, contained mainly leaves and seeds from tree and shrub species, reflecting a browsing rather than grazing feeding strategy. Supporting evidence that moa were principally browsers came with the detailed gizzard content analyses performed by Burrows (1980a; 1980b; 1989) and Burrows et al. (1981). These gizzard content samples came both from Pyramid Valley in North Canterbury and Scaife's Lagoon in West Otago and contained broadly similar assemblages of plant remains, dominated by twigs, leaves and seeds of a diverse range of tree and shrub taxa. Importantly, Burrows et al. (1981) reported that the twigs found in moa gizzards had sheared ends, indicating that the birds had cut them with their beaks rather than having pulled or snapped them. Although these findings established a new paradigm of moa having been browsers of trees and shrubs, most gizzard content samples assessed up until this time (14 out of 17) had been attributed to just one genus; *Dinornis*, which we now know included just one species in the South Island (*Dinornis robustus*; Bunce et al. 2003). The comparative rarity of gizzard content samples from *Emeus* and *Euryapteryx*, and lack of any from the other three moa genera (*Anomalopteryx*, *Megalapteryx* and *Pachyornis*), were recognised by Burrows et al. (1981) as major limitations to understanding the full dietary breadth of moa and gaining insights into niche differentiation between moa species.

New methodological approaches unlock the potential of coprolites

During the 20th century, analysis of gizzard content samples provided the greatest insights into moa diets. Consisting of relatively undigested plant material, these samples typically included numerous seeds, leaves and stem fragments that could be readily identified using comparative reference material. Wood (2007a) expanded upon the existing body of evidence for moa diet by reporting on the content of five additional moa gizzard content samples, including the first samples from heavy-footed moa (*Pachyornis elephantopus*) and two further samples of *E. crassus*, for which just two gizzard specimens from Pyramid Valley had previously been studied. A total of 23 moa gizzard content samples which can be directly associated to individual moa skeletons have now been examined, yet several additional samples in museum collections still await analysis.

By the 1980s more moa coprolites had been discovered than moa gizzard content samples, yet this alternative source of moa diet data had largely been unutilised. Being more digested than gizzard content, the content of coprolites was not as easily identified. Many gizzard content samples had been found in situ with moa skeletons, allowing them to be associated with a moa species (Falla 1941; Gregg 1972; Burrows et al. 1981). Coprolites, on the other hand, were never found in association with skeletons and so it was impossible to confirm whether they were even from moa, let alone identify which moa species might have deposited them. Neville Moar (in Trotter 1970) performed the first quantitative assessment of the content of a putative moa coprolite when he undertook pollen analysis on a specimen collected from a rock overhang at Shepherd's Creek in the Waitaki Valley. Although the results were entirely consistent with what is now known about the diets of moa from dryland localities (Wood and Wilmshurst 2013), Moar was aware of the potential for the coprolite to have been contaminated by soil from the floor of the rock overhang, and of the multiple pathways through which the pollen may have been incidentally ingested. Accordingly, he concluded in a letter to Trotter that "It is not possible to offer any reliable interpretation of these results" (Moar 1966, unpubl. correspondence).

Horrocks et al. (2004) presented the first multiproxy analysis of putative moa coprolites, assessing the macrofossil (seed, leaf, twig) and microfossil (pollen, phytoliths, starch) content of five coprolites from a rock overhang in Takahe Valley, Fiordland. The results supported the idea that moa browsed trees and shrubs, but also provided evidence for grazing of grasses and herbs around the margin of a nearby lake. With at least three moa species having formerly inhabited the area – *D. robustus*, little bush moa (*Anomalopteryx didiformis*), and upland moa (*Megalapteryx didinus*) – it was not possible to attribute a specific identity to the coprolites (Horrocks et al. 2004).

A breakthrough for coprolite analyses came with the development of techniques for extracting, amplifying and sequencing DNA molecules from ancient specimens in the 1980s. The first ancient DNA (aDNA) study of coprolites (of the extinct ground sloth) was performed in the late 1990s (Poinar et al. 1998), and less than a decade later the potential for aDNA to allow species-level identification of moa coprolites was demonstrated (Wood 2007b; Wood et al. 2008). Within

the following decade, aDNA was used to identify c. 100 moa coprolites to species, and in combination with conventional diet proxies (e.g. pollen, macrofossils) provided further insights into moa diets, niche partitioning and even parasite faunas (Wood and Wilmshurst 2013; Wood et al. 2012a; 2012b; 2013a; 2013b; Boast et al. 2018). Evidence from coprolite analyses supported the idea that some moa species browsed trees and shrubs, as had previously been demonstrated by gizzard content analyses (e.g. Burrows et al. 1981). However, the coprolite analyses also revealed that a broader range of feeding ecologies existed between (and even within some) moa species, which included the grazing of small herbs in non-forest communities. Moreover, coprolite analyses provided answers to the age-old question of whether introduced ungulates were performing the same ecological roles as moa had within New Zealand ecosystems (Caughley 1983; 1988); in short, they weren't (Wood et al. 2008; 2013b; Wood & Wilmshurst 2019). Over 2000 moa coprolites are now known from more than 30 different localities across the South Island (Wood and Wilmshurst 2014).

Inferring diet from indirect evidence

In addition to the direct evidence of consumed plant species and plant tissue types provided by coprolites and gizzard content, other sources of information can also provide complementary insights into moa diets. The first of these are dietary stable isotopes. The stable isotope ratios of animal body tissues, including bone collagen, are heavily influenced by diet and have been widely used (particularly carbon and nitrogen isotopes) in palaeodietary analyses of extinct species (e.g. Hildebrand et al. 1996; Bocherens et al. 2011). Specifically, carbon and nitrogen isotope ratios ($\delta^{13}C$ and $\delta^{15}N$) can provide general insights into the trophic level of an extinct species and details about habitats and sources of food (e.g. marine v. terrestrial). Although stable isotopes cannot provide dietary insights at the resolution of individual prey species, in situations where the range of potential prey is constrained, mixed-models can be used to infer the relative proportions of different food types that contributed the diet (e.g. Bocherens et al. 2005).

Bone isotopes have been used in a relatively limited capacity to study moa diets. While useful for discriminating diets at a broad level, using $\delta^{13}C$ and $\delta^{15}N$ to resolve fine-scale diet details can be complicated by the fact that $\delta^{13}C$ and $\delta^{15}N$ values are also influenced by environmental or climatic factors, such as shading (e.g. forest vs non-forest conditions) or precipitation. Such influences may obscure isotopic signals of diet if they are not controlled for by using samples with restricted geographic and temporal ranges (e.g. Wood et al. 2017b). A good example of this is $\delta^{13}C$ values of moa bones, which became more depleted through time over the past 40000 years, reflecting increasing forest extent after the end of the last ice age (Worthy & Holdaway 2002). The $\delta^{15}N$ values of *P. elephantopus* bones also show marked differences between eastern and western South Island sites which, rather than reflecting dietary differences, are likely influenced by higher aridity in the east (Rawlence et al. 2012). Huynen et al. (2014) found larger isotopic differences between deposit types (e.g. caves, dunes) than between moa species, though these differences were likely due to the environmental/climatic regions that the bones were from, rather than taphonomy. Even within discrete environmental or climatic regions there can be discrepancy between the diet interpretation based on isotopes and the evidence provided by coprolites or gizzards, revealing a complexity in interpreting isotope signals that

remains to be resolved (Rawlence et al. 2016). An interesting application of bone isotopes to understanding moa diet was the assessment of chick bones by Huynen et al. (2014), who found isotopic values consistent with feeding on insects, as is known for chicks of other ratites (e.g. Milton et al. 1993).

The second source of indirect evidence comes from anatomy. Richard Owen's descriptions of moa as specialist fern consumers (Owen 1844) provides an early example of how anatomical, and in particular osteological, features have been used to infer aspects of moa feeding ecology. While anatomical features cannot provide direct evidence of what moa ate, they can provide insights into adaptations related to feeding that can then be used to make inferences about diets. Worthy & Holdaway (2002) provided an assessment and comparison of the structure of moa skulls and beaks, revealing differences between genera that seemed to reflect different feeding strategies. For example, the distinct mandibular groove in *Dinornis* spp. appears to have been an adaptation for gripping food (Worthy & Holdaway 2002), whereas the robust bill and large temporal fossa of *Anomalopteryx*, combined with a sharp edge on the mandible at the base of the gape suggest the species was capable of a powerful secateur-like bite (Worthy & Holdaway 2002).

Techniques for making such inferences have advanced greatly in recent years (Wood & De Pietri 2015). Attard et al. (2016) used three-dimensional FEA, a technique for modelling and visualising stresses and strains within complex three-dimensional structures (Young et al. 2012), to examine the performance of moa skulls under different feeding modes. Their analyses supported niche partitioning between moa genera, revealing better structural performance by skulls of different taxa under different feeding modes. The results indicated that *A. didiformis* was adapted for tugging (pulling backwards) and support the contention that it performed unilateral clipping (clipping twigs with one side of beak in a secateur-like fashion), coastal moa (*Euryapteryx curtus*) had a relatively weak skull adapted for plucking soft leaves and fruits, crested moa (*Pachyornis australis*) was adapted for both lateral shaking and pulling downwards (in a dorsoventral direction), *M. didinus* for tugging and *D. robustus* for lateral shaking (Attard et al. 2016). However, while these differences were noted, the authors did not discuss the types of plants that might specifically require these different feeding modes.

A synthesis of direct evidence for moa diets: Methods

Assembly of moa herbivory database

We assembled data on moa herbivory within a spreadsheet (see Supplementary Materials Appendix S1). Each row contained a single observation, with columns for: moa species, unique sample identification number, sample type (coprolite or gizzard), locality, proxy (e.g. pollen, seed, leaf, DNA), high taxonomic level identity (where it was not possible to resolve the identity to family, genus or species, e.g. monocotyledon), family-level identification, genus-level identification, species-level identification, count, data source and notes. Plant nomenclature follows the Ngā Tipu Aotearoa – New Zealand Plants database (Allan Herbarium 2000).

The completed database (Appendix S1) includes 2755 records from 23 gizzard content samples and 158 coprolites (Figs. 2, 3). Data included are as follows:
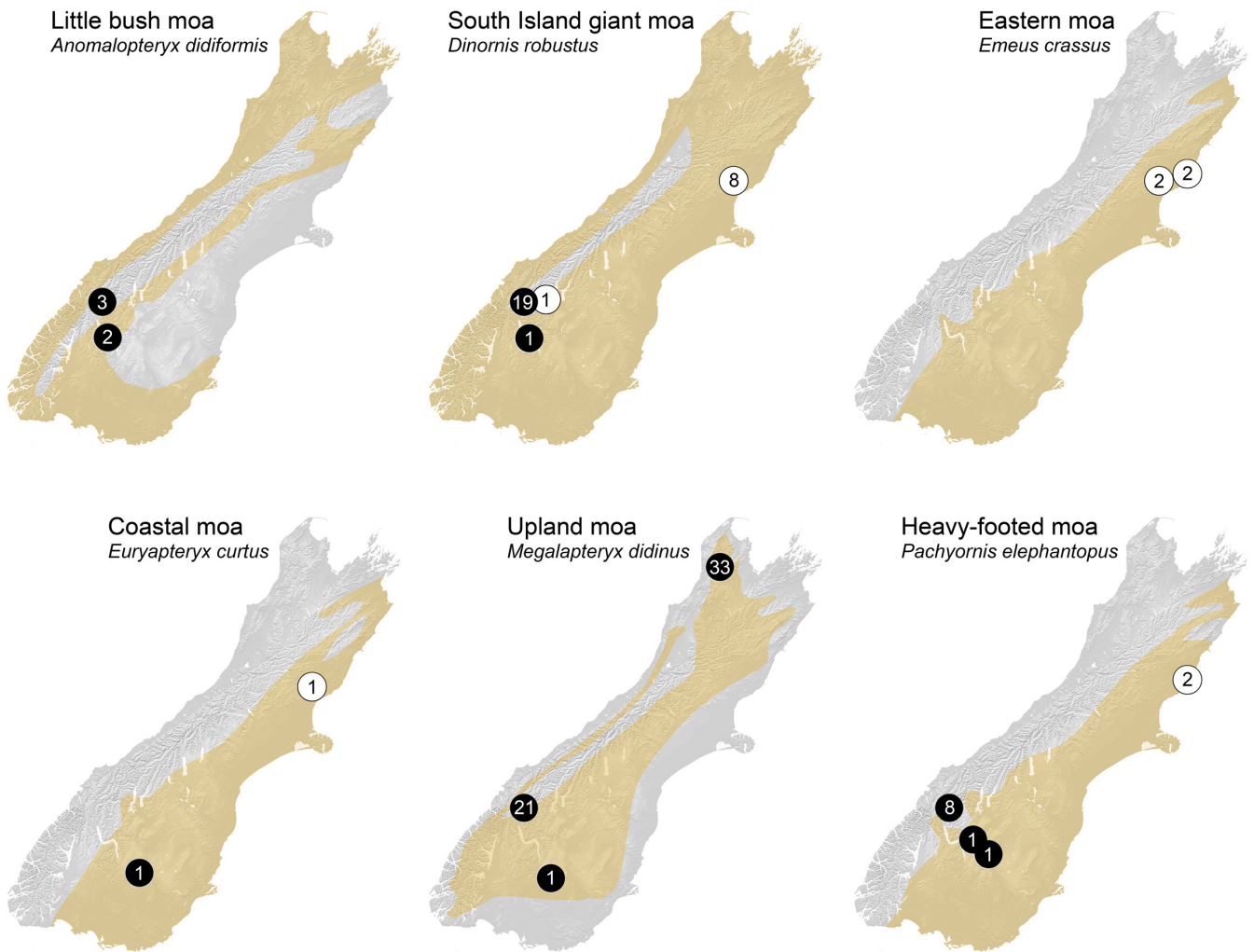
Figure 2. Locations and numbers of gizzard content samples (white circles) and coprolites (black circles) for each moa species that have been analysed for dietary remains. Orange shaded areas reflect distributions of moa species based on Worthy & Holdaway (2002).
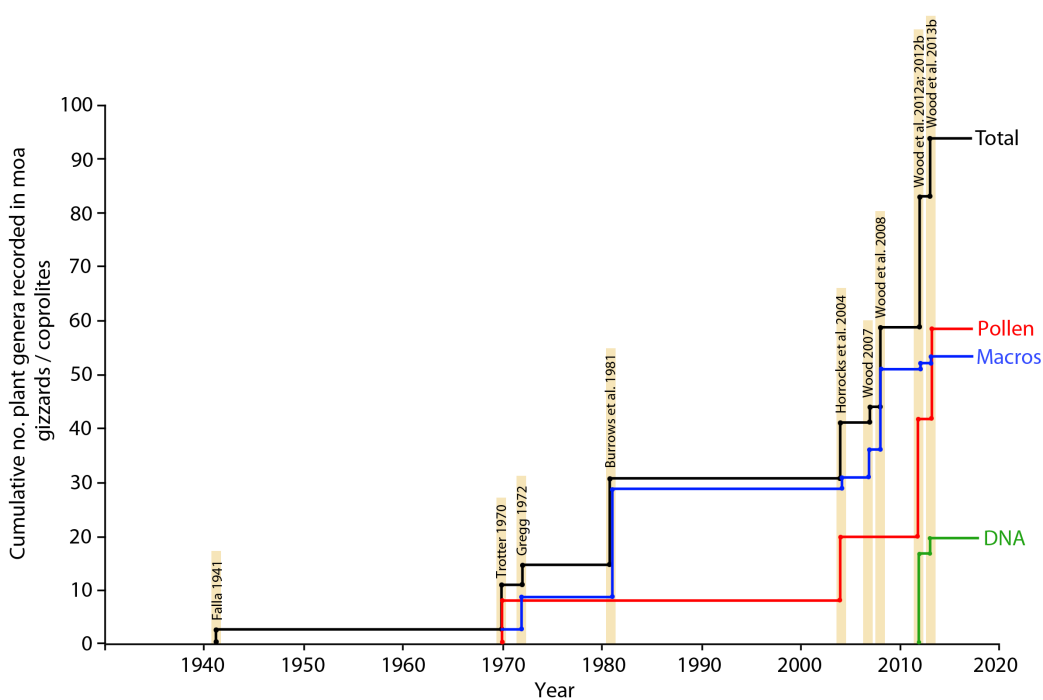

Figure 3. Cumulative number of plant genera recorded from moa gizzard content and coprolite samples since 1941, in total, and by each proxy type (macros includes seeds, leaves, stems and bark).

Gizzards. Pyramid Valley, North Canterbury (macrofossils from Falla 1941; Gregg 1972 and Burrows et al. 1981); Scaife's Lagoon, West Otago (macrofossils from Burrows et al. 1981; Wood 2007a); Styx mire, East Otago (macrofossils from Wood 2007a); Treasure Downs, North Canterbury (macrofossils from Wood 2007a).

Coprolites. Dart River Valley, West Otago (macrofossils from Wood et al. 2008; pollen, macrofossils and rbcl DNA sequence data from Wood et al. 2013b); Euphrates Cave, Northwest Nelson (pollen, macrofossils and rbcl DNA sequence data from Wood et al. 2012a); Takahe Valley, Fiordland (pollen and macrofossils from Horrocks et al. 2004); Shepherd's Creek, Waitaki (pollen from Trotter 1970); Central Otago rock overhangs (macrofossils from Wood et al. 2008; pollen from Wood & Wilmshurst 2013); Mount Nicholas, West Otago (pollen from Wood et al. 2012b; JRW unpubl. pollen data); Old Man Range, Central Otago (JRW unpubl. pollen data); Borland Burn, Western Southland (JRW unpubl. pollen data).

Data excluded from the database, and reasoning for these exclusions, are as follows: phytoliths from the Takahe Valley coprolites (Kondo et al. 1994; Horrocks et al. 2004), due to their relatively poor taxonomic resolution and discrimination of plant taxa; pre-1920s accounts of gizzard or coprolite content, as the observers were unlikely to have had access to comprehensive comparative material for identifying the plant remains in the samples; gizzard content samples from Glencrieff (Rawlence et al. 2011) due to the indistinct boundary between the putative gizzard content and surrounding peat matrix; 18S rDNA sequence data from Dart River and Euphrates Cave coprolites (Boast et al. 2018), as the universal primers used provided relatively poor discrimination of plant taxa and, as they were not specifically designed for use on plants, may have held inherent biases in the taxa they detected. The database was solely for herbivory on plants. Therefore, the limited information on fungi consumption by moa (Boast et al. 2018) was also excluded from the database but is discussed in later sections of this paper.

Data in the database are raw counts unless otherwise stated (in the notes column). A count value of 0.01 denotes that an item was noted as being present in a sample, but its abundance was not quantified. Where an indication of minimum abundance was provided (e.g. values of > 100 or > 600 in Burrows et al. 1981), the minimum value (i.e. 100 or 600) was used.

We took a conservative approach with attributing gizzard samples to moa species. Accordingly, specimens identified as "?*Dinornis*" or "probably *Dinornis*" (Burrows 1980b) were listed as unidentified in the database. Moreover, we used original field notes and sketches (from box labelled 'Field Notes and Records, Pyramid Valley', held by the Canterbury Museum) to re-assess the identity of moa gizzard content samples from Pyramid Valley, and to determine the sex of the *D. robustus* individuals that had gizzard content associated with them. Our research revealed that one gizzard (121D) identified as *Dinornis* by Burrows et al. (1981) had an unclear association in the original field notes. The gizzard content sample was positioned halfway between two adjacent skeletons of *D. robustus* and *E. curtus*. A sketch plan of the excavation square by Roger Duff noted "Which bird? Prov.[isionally] assigned to F", F being the *E. curtus* skeleton. Another note on the same specimen read "Large gizzard, many stones, green, ?No. 121D, depth 53", D being the *D. robustus* skeleton. Due to this uncertain association, we have listed this specimen as 'unidentified' in the database.

Apart from these instances, all other Pyramid Valley *Dinornis* gizzard content samples examined by Burrows et al. (1981) were confirmed as being from *D. robustus*. The following are details of their associated skeletons (excavation square/specimen and Canterbury Museum registration number) with details of the age and sex (* denotes sex confirmed by DNA analysis of Allentoft et al. 2010) of individuals: 122B (Av28434) immature female*; 76D (XXIID, Av8468) adult female*; 76K (XXIIK, Av8471) adult female*; 76M (XXIIM, Av8473) adult female; 108D (Av15025) adult female*; 108E (Av15024) immature; 89B (XVIIB, Av8462) adult female (skeleton on display in Canterbury Museum); XA (Av13899) immature female*.

We also found reference to gizzard content samples in field notes that appear to relate to samples that have not previously been examined. For example, on page 50 of Duff's second notebook of the 1949 excavation of Pyramid Valley held by Canterbury Museum, the *D. robustus* skeleton excavated from square 70G is noted to have had an associated sample of "Crop content very well preserved and no sign of semi digestion… Twigs, seeds & leaves of a small shrub". However, due to a lack of detailed assessment of the content, these samples are not included in the database.

Statistical analyses

The database was restructured into a dataframe with one row for each specimen and columns for: (1) moa species, (2) sample id, (3) sample type, (4) locality; followed by one column for each unique combination of plant taxonomic hierarchy that enabled us to capture the data regardless of the taxonomic resolution for the row (columns 'high', 'family', 'genus' and 'species' in database where 'high' was any taxonomic level higher than family when that was the only taxonomic data available for the row) and proxy type (e.g. NA-Araliaceae-*Pseudopanax-ferox*-seed, NA-Araliaceae-*Pseudopanax-ferox*-pollen, Monolete fern-NA-NA-NA-spore etc.) using the spread function of the tidyr package (Wickham & Henry 2018) in R v.3.3.2 (R Core Development Team 2017). This dataframe was manipulated depending on the analysis being performed (e.g. subset for particular proxies or localities, or quantitative data converted to presence/absence). Non-metric multidimensional scaling (MDS) analyses were performed using the vegan package (Okansen et al. 2010) in R using default settings.

Plant avoidance assessment

To assess plant avoidance by moa, we first selected three sites with rich data on moa diets: (1) Dart Valley, (2) Euphrates Cave/Garibaldi Plateau, (3) north Canterbury limestone forests (a compilation of Cheviot and Pyramid Valley). For each site, we extracted a unique list of plant taxa eaten by moa ('eaten list').

We then compiled a list of native plant species present at each of these three sites ('present list'). Our goal was to be as comprehensive as possible to account for species turnover between the time that the moa coprolites were formed and the present day. For the Dart Valley we pooled Mark (1977) and unpublished species lists downloaded from the New Zealand Plant Conservation Network (NZPCN) website (NZPCN 2019; Dart Valley track by BD Rance; Dart-Rees Track by BD Rance; Mt Aspiring National Park by JW Barkla and M Thorsen). For Euphrates Cave/Garibaldi Plateau we used species lists (Druce lists 189, 198, 306) accompanying Druce et al. (1987) downloaded from NZPCN (2019). For north Canterbury limestone forests, we merged species lists from ecologically comparable sites to our two gizzard content

localities: (1) the Tiromoana Scenic Reserve at Mt Cass (citizen science records sourced from https://www.inaturalist.org/), (2) the Waipara Gorge Scenic Reserve (citizen science records sourced from https://www.inaturalist.org/), (3) Coringa Station near Motunau (Molloy 1981, 1983, 1986). These three sites include both limestone outcrop vegetation and alluvial valley bottoms where tall forest occurs, as these habitats would both have been available to moa at Cheviot and Pyramid Valley.

For each site, we removed all plant species from the compiled lists if that species, or a higher taxon containing that species, was recorded in the moa diets from that site. For example, because 'Apiaceae' DNA was recorded from moa diets in the Dart Valley, we removed all members of the Apiaceae from the list of native species from the Dart Valley. The resulting lists for each site are an estimate of the taxa not eaten by moa – or not detected in the diets of moa. To minimise the chance that non-detection of a plant taxon in a moa gizzard or coprolite was due to insufficient diet sampling rather than avoidance we generated a list of plant species that would have been locally available but not present in moa diets at ≥ 2 localities. From these we removed plant genera that were known to have been eaten by moa, based on gizzard content or coprolites from other localities. Twenty-five plant species remained (See Supplementary Materials Appendix S2).

Results and discussion

Moa diets

Evidence from gizzard content samples and coprolites demonstrate that adult moa were strictly herbivorous. No animal remains have been found in any sample, except for rare invertebrate fragments in coprolites that were likely co-ingested with plant material (Wood et al. 2008). It has previously been suggested that moa chicks could have fed on insects, and this has been supported by limited bone isotope data for moa chicks (Huynen et al. 2014). Moreover, several small coprolites exist from a former moa nesting site at Sawers' rock shelter, some of which do include visible insect remains (Wood & Wilmshurst 2014). Unfortunately, poor DNA preservation at this site has prevented confirmation that these were deposited by moa (Boast 2016), and coprolite morphotypes attributed to other bird species (e.g. laughing owl, *Ninox albifacies*) and reptiles are also present in this site (Wood & Wilmshurst 2014). Below we provide a species-by-species summary of moa diets.

Little bush moa (*Anomalopteryx didiformis*)

Gizzards: (0) None.

Coprolites: (5) Dart River Valley, Otago (3) (Wood et al. 2013b); Mt Nicholas Station, Otago (2) (Wood et al. 2012b) (Fig. 2).

Plant taxa occurring in more than one sample: Ground ferns (monolete spore types) (5), *Fuscospora* (5), *Dacrydium cupressinum* (5), *Hymenophyllum* (4), *Lophozonia menziesii* (4), *Coprosma* (4), Asteraceae (3), *Myrsine* (3), Nothofagaceae (3), *Ophioglossum* (3), Poaceae (3), *Phyllocladus alpinus* (3), *Podocarpus* (3), *Prumnopitys taxifolia* (3), *Muehlenbeckia* (3), Cyperaceae (2), *Prumnopitys ferruginea* (2), *Acaena* (2), Rubiaceae (2).

Most frequently recorded items excluding pollen/spores: Nothofagaceae leaves (3), Rubiaceae DNA (3).

Diet and habitat notes: *Anomalopteryx didiformis* had powerful jaw muscles and a robust beak that appears to have been adapted for cutting twigs (Attard et al. 2016). Their sharp-edged mandible that overlapped the premaxilla at the base of the gape would have had a secateur-like action (Worthy & Holdaway 2002). Although limited coprolite samples exist for this species, the dominance of leaf cuticle and DNA of trees and shrubs in these samples and the distribution of this moa species being restricted to forest indicates that it was most likely a browser of plants within the forest understorey. Based on the relatively enriched ^{13}C isotope values for *A. didiformis* bones (Rawlence et al. 2016) it has been suggested that this species may have fed around forest margins (Worthy & Holdaway 2002; p.215), as the canopy effect results in depleted ^{13}C isotope values within forest understoreys (van der Merwe & Medina 1991). However, this is at odds with the lack of non-forest plant species in coprolites of this moa species. An alternative explanation is that fallen fruit and leaves from the canopy, where ^{13}C isotope values are enriched, may have contributed a large component of the diet of *A. didiformis* (Rawlence et al. 2016).

South Island giant moa (*Dinornis robustus*)

Gizzards: (9) Pyramid Valley, North Canterbury (8) (Burrows et al. 1981); Scaife's Lagoon, Otago (1) (Burrows et al. 1981) (Fig. 2).

Coprolites: (20) Dart River Valley, Otago (19) (Wood et al. 2008; 2013b); Mt Nicholas Station, Otago (1) (Wood et al. 2012b) (Fig. 2).

Plant taxa occurring in more than one sample: *Coprosma* (29), *Fuscospora* (20), ground ferns (monolete spore types) (18), Asteraceae (15), Cyperaceae (15), Poaceae (14), *Muehlenbeckia* (14), *Lophozonia menziesii* (13), *Ophioglossum* (11), *Acaena* (11), *Gonocarpus* (10), *Dacrydium cupressinum* (10), *Prumnopitys ferruginea* (10), *Rubus* (9), *Olearia virgata* (9), *Prumnopitys taxifolia* (8), *Coprosma rotundifolia* (7), *Carex secta* (7), *Leucopogon fraseri* (7), Nothofagaceae (7), *Epilobium* (7), *Pimelea* (7), *Plagianthus betulinus* (6), *Myrsine divaricata* (6), *Aristotelia fruticosa* (6), *Geranium* (6), *Gunnera* (6), *Mentha* (6), *Myrsine* (6), *Ranunculus* (6), Rubiacae (6), *Melicope simplex* (6), *Hydrocotyle* (5), Brassicaceae (5), *Phyllocladus alpinus* (5), Caryophyllaceae (5), *Coriaria* (5), indeterminate monocotyledon (4), Apiaceae (4), *Phormium tenax* (4), *Corokia cotoneaster* (4), *Gaultheria/Pernettya* (4), *Podocarpus* (4), Polygonaceae (4), *Cordyline australis* (3), *Einadia* cf. *allanii* (3), *Muehlenbeckia australis* (3), *M. axillaris* (3), *M. complexa* (3), *Rubus* cf. *squarrosus* (3), *Urtica* (3), *Pseudopanax* cf. *ferox* (2), *P. ferox* (2), Danthonioideae (2), *Hymenophyllum* (2), *Teucridium parviflorum* (2), *Leptospermum scoparium* (2), *Lophomyrtus obcordata* (2), *Halocarpus* (2), *Coprosma* cf. *rhamnoides* (2), *Stackhousia minima* (2), Violaceae (2)

Most frequently recorded items excluding pollen/spores: *Coprosma* seeds (13), *Olearia virgata* stems (9), *Coprosma rotundifolia* seeds (8), *Rubus* stems (8), *Carex secta* seeds (7), Cyperaceae seeds (7), *Myrsine divaricata* leaves (6), *Plagianthus betulinus* stems (6), Rubiaceae DNA (6), *Melicope simplex* seeds (6), *Prumnopitys taxifolia* leaves (6), *Rubus* seeds (5), *Prumnopitys taxifolia* seeds (5), *Coriaria* seeds (5), Nothofagaceae DNA (5), *Phormium tenax* seeds (4), monocotyledon leaves (4), *Corokia cotoneaster* seeds (4), *Gaultheria/Pernettya* seeds (4), *Leucopogon fraseri* leaves (4), *Myrsine divaricata* seeds (4), Nothofagaceae leaves (4), Polygonaceae DNA (4), *Ranunculus* cf. *gracilipes* seeds (4), *Rubus* leaves (3), *Cordyline australis* seeds (3), *Einadia*

cf. *allanii* seeds (3), *Gonocarpus* seeds (3), *Muehlenbeckia australis* seeds (3), *M. axillaris* seeds (3), *M. complexa* seeds (3), *Ranunculus* seeds (3), *Rubus* cf. *squarrosus* leaves (3), *Urtica* seeds (3), *Pseudopanax ferox* seeds (3), Danthonioideae DNA (2), *Leucopogon fraseri* seeds (2), *Teucridium parviflorum* seeds (2), *Plagianthus betulinus* bark (2), *Plagianthus betulinus* seeds (2), *Leptospermum scoparium* capsules (2), *Lophomyrtus obcordata* seeds (2), *Coprosma* cf. *rhamnoides* seeds (2), Violaceae DNA (2)

Diet and habitat notes: *Dinornis robustus* had powerful jaw muscles and a robust beak (Attard et al. 2016), which may have supported a sharp cutting edge (Atkinson & Greenwood 1989). Gizzard content samples from *D. robustus* contain twigs with sheared ends, demonstrating that the beak could act like secateurs. However, two distinct diets are reflected in *D. robustus* coprolites from the Daley's Flat: (1) a diet consisting mainly of browsed forest trees and shrubs, dominated by beech (Nothofagaceae) and *Coprosma*, (2) a diet dominated by grazed herbs in non-forested habitats. Wood et al. (2013b) suggested that these two distinct diets may reflect sex-related niche-partitioning, with the females (being significantly larger than males) having fed on lower nutrient status trees and shrubs while the males extended into non-forest habitats. This interpretation is supported by the *D. robustus* gizzard content samples from Pyramid Valley, which are exclusively from females and reflect browsing of trees and shrubs. In future, the detection of sex-linked genetic markers (e.g. Bunce et al. 2003) from *D. robustus* coprolites may help test this hypothesis.

Eastern moa (*Emeus crassus*)

Gizzards: (4) Treasure Downs, North Canterbury (2) (Wood 2007a); Pyramid Valley, North Canterbury (2) (Falla 1941; Gregg 1972) (Fig. 2).

Coprolites: (0) None.

Plant taxa occurring in more than one sample: *Prumnopitys taxifolia* (4), *Rubus* (3), Bryophyte (2), *Corokia cotoneaster* (2), *Olearia* (2), *Carex* (2), *Eleocharis* cf. *acuta* (2), *Elaeocarpus hookerianus* (2), *Leptospermum scoparium* (2), *Dacrycarpus dacrydioides* (2), *Ranunculus gracilipes* (2), *Coprosma* (2), *Veronica* cf. *pimeleoides* (2)

Most frequently recorded items excluding pollen/spores: *Prumnopitys taxifolia* seeds (3), *Rubus* seeds (3), Bryophyte leaves (2), *Corokia cotoneaster* seeds (2), *Olearia* stems (2), *Carex* seeds (2), *Eleocharis* cf. *acuta* seeds (2), *Elaeocarpus hookerianus* seeds (2), *Leptospermum scoparium* capsules (2), *Dacrycarpus dacrydioides* leaves (2), *Prumnopitys taxifolia* leaves (2), *Ranunculus gracilipes* seeds (2), *Coprosma* seeds (2), *Veronica* cf. *pimeleoides* leaves (2)

Diet and habitat notes: With the limited number of samples known from *E. crassus*, it is difficult to infer much more than this moa species appears to have been adapted for a diet of soft plant tissues, mainly leaves and fruit of trees and shrubs. The diet appears to have been broadly like that of *E. curtus*, but the two species may have had slightly different habitat preferences and distributions (Worthy & Holdaway 2002). Although the two species are found together at many sites, *E. crassus* appears to have preferred coastal lowlands while *E. curtus* is more dominant at inland sites in the eastern South Island (Worthy & Holdaway 2002).

Coastal moa (*Euryapteryx curtus*)

Gizzards: (1) Pyramid Valley, North Canterbury (1) (Gregg 1972) (Fig. 2).

Coprolites: (1). Earnscleugh Cave, Otago (1) (Wood et al. 2008; Wood & Wilmshurst 2013) (Fig. 2).

Plant taxa occurring in more than one sample: *Prumnopitys taxifolia* (2)

Diet and habitat notes: As with *Emeus crassus*, the limited number of coprolite and gizzard content samples from *Euryapteryx curtus* makes it difficult to infer too much about the diet of this species. As with *E. crassus* there appears to have been a bias towards leaves and fruits of trees and shrubs. This is supported by the high stresses experienced by *E. curtus*' relatively weak skull when tested under different feeding strategies (Attard et al. 2016). With weakly constructed mandibles and a relatively blunt bill tip (Worthy & Holdaway 2002), *E. curtus* appears to have been better adapted for plucking fruit and leaves (Attard et al. 2016) rather than cutting like secateurs.

It is worth noting that one of the unidentified gizzard content samples from Pyramid Valley (121D) may also be from *E. curtus*. Positioned midway between sterna of *E. curtus* and *D. robustus*, this sample was originally attributed to *E. curtus* (excavation notes, Canterbury Museum) but later this changed to *D. robustus* (excavation notes, Canterbury Museum and Burrows et al. 1981). However, Burrows et al. (1981) noted that this sample differed "from all other *Dinornis* samples so far examined by having a relatively large number of *Podocarpus spicatus* [*Prumnopitys taxifolia*] seed and a very large number of leaves of the same species. There is also a relatively large amount of *Rubus* sp. leaves and petioles". This corroborates what is known from other *E. curtus* gizzard content in a bias towards softer plant material such as leaves and fruits.

Upland moa (*Megalapteryx didinus*)

Gizzards: (0) None.

Coprolites: (55) Euphrates Cave, Northwest Nelson (33) (Wood et al. 2012a); Dart River Valley, Otago (21) (Wood et al. 2013b); Old Man Range, Otago (1) (Wood et al. 2008) (Fig. 2).

Plant taxa occurring in more than one sample.: *Fuscospora* (54), ground ferns (monolete spore types) (50), Poaceae (49), Asteraceae (45), *Lophozonia menziesii* (43), *Ranunculus* (41), *Dacrydium cupressinum* (37), Cyperaceae (36), *Coprosma* (35), *Myosotis* (34), Brassicaceae (30), *Acaena* (29), *Ophioglossum* (27), *Prumnopitys taxifolia* (27), Apiaceae (25), *Cyathea colensoi* (25), *Gentiana* (25), Caryophyllaceae (23), *Hymenophyllum* (21), *Astelia* (19), *Myrsine* (19), *Plantago* (19), *Phyllocladus alpinus* (19), *Muehlenbeckia* (19), *Epilobium* (18), *Podocarpus* (18), Lactuaceae (17), Bryophytes (16), *Prumnopitys ferruginea* (16), *Phormium* (12), Cyperaceae cf. *Scirpus* (12), Ericaceae (12), Rubiaceae (12), *Gonocarpus* (11), *Fuchsia excorticata* (11), *Leucopogon fraseri* (10), *Mentha* (10), *Bulbinella* (9), *Gaultheria* (9), Nothofagaceae (9), *Pseudopanax colensoi* (8), Polygonaceae (8), *Ranunculus* cf. *gracilipes* (8), *Urtica* (8), *Hydrocotyle* (7), Campanulaceae cf. *Pratia* (7), *Coriaria* (7), Elaeocarpaceae (7), *Geranium* (7), *Pseudopanax* (6), *Neomyrtus pedunculatus* (6), Oxalidales (6), *Griselinia* (5), *Veronica* (5), Urticaceae cf. *Urtica* (5), *Drosera* (4), *Aristotelia fruticosa* (4), *Metrosideros* (4), *Anisotome* (3), *Oreomyrrhus* (3), Cyperaceae cf. *Carex* (3), Haloragaceae (30), Loranthaceae (3), *Halocarpus* (3), Scrophulariaceae (3), *Pimelea* (3), Pteridiophyta (3), *Anthoceros* (2), *Colobanthus* (2), *Ascarina lucida* (2), *Gaultheria/Pernettya* (2), *Peraxilla* (2), *Lycopodium australinum* (2), *L. scariosum* (2), *Euphrasia* (2), Oxalidaceae (2), *Phymatosorus* (2), *Rubus* (2), *Acaena* (2), *Donatia novae-zelandiae* (2)

Most frequently recorded items excluding pollen/spores:. *Ranunculus* seeds (17), Bryophyte leaves (16), Cyperaceae cf. *Scirpus* seeds (12), Rubiaceae DNA (12), *Gaultheria* seeds (9), Polygonaceae DNA (8), *Ranunculus* cf. *gracilipes* seeds (8), Campanulaceae cf. *Pratia* seeds (7), Cyperaceae seeds (7), Elaeocarpaceae DNA (7), *Lophozonia menziesii* leaves (6), Nothofagaceae DNA (6), Oxalidales DNA (6), *Leucopogon fraseri* seeds (5), *Myrsine* DNA (5), Urticaceae cf. *Urtica* seeds (5), Asteraceae seeds (4), *Griselinia* DNA (4), *Coprosma* seeds (4), Asteraceae DNA (3), *Coriaria* seeds (3), Cyperaceae cf. *Carex* seeds (3), *Leucopogon fraseri* leaves (3), Haloragaceae DNA (3), Loranthaceae DNA (3), Nothofagaceae leaves (3), Poaceae florets (3), Scrophulariaceae DNA (3), Pteridiophyta leaves (3), *Myosotis* DNA (2), *Colobanthus* seeds (2), *Coriaria* DNA (2), Cyperaceae DNA (2), *Gaultheria/Pernettya* seeds (2), *Fuchsia excorticata* seeds (2), *Euphrasia* DNA (2), Oxalidaceae DNA (2), Poaceae seeds (2), *Acaena* DNA (2), *Veronica* DNA (2), *Urtica* seeds (2)

Diet and habitat notes: *Megalapteryx didinus* had a widely-varied diet, which included browsing of trees, shrubs and herbs. *Megalapteryx didinus* is the only moa species for which a preserved ramphotheca (the sheath over the beak) is known (Worthy & Holdaway 2002), but this has not yet been described in detail. Finite element analyses suggest that *M. didinus* was better adapted for more precise twisting than other moa species and shared broad functional similarities with emu (*Dromaius novaehollandiae*) skulls (Attard et al. 2016).

   Megalapteryx didinus may have exhibited some seasonal diet variation, feeding in non-forested habitats most of year but within forest during winter. Bones have been found in mountainous regions that would have been snow-covered during winter, suggesting the species may have had seasonal altitudinal migration, from subalpine herbfields in spring/summer to valley forests in autumn/winter, as the South Island takahē (*Porphyrio hochstetteri*) does. *Megalapteryx didinus* was not restricted to high-altitude sites as its common name (the upland moa) suggests, but instead was a specialist of steep and rocky habitats. With sharp claws and slender legs this agile moa may have specialised in feeding on plants growing in sites that were inaccessible to other moa species.

Heavy-footed moa (*Pachyornis elephantopus*)

Gizzards: (2) Treasure Downs, North Canterbury (2) (Wood 2007a) (Fig. 2).

Coprolites: (10) Dart River Valley, Otago (8) (Wood et al. 2013b); Kawarau Gorge, Otago (1) (Wood et al. 2008; Wood & Wilmshurst 2013); Roxburgh Gorge, Otago (1) (Wood et al. 2008; Wood & Wilmshurst 2013) (Fig. 2).

Plant taxa occurring in more than one sample: *Coprosma* (12), Asteraceae (10), Cyperaceae (10), Poaceae (10), *Muehlenbeckia* (10), *Fuscospora* (9), ground ferns (monolete spore types) (8), *Ophioglossum* (7), *Gonocarpus* (6), *Lophozonia menziesii* (6), *Ranunculus* (6), *Hydrocotyle* (5), Brassicaceae (5), *Leucopogon fraseri* (5), Polygonaceae (5), Apiaceae (4), Caryophyllaceae (4), *Mentha* (4), *Myrsine* (4), *Dacrydium cupressinum* (4), *Prumnopitys ferruginea* (4), *P. taxifolia* (4), *Acaena* (4), *Myosotis* (3), *Gentiana* (3), *Geranium* (3), *Epilobium* (3), *Plantago* (3), *Phyllocladus alpinus* (3), *Podocarpus* (3), *Ranunculus* cf. *gracilipes* (3), *Rubus* (3), *Urtica* (3), Apiales (2), Bryophyte (2), *Einadia triandra* (2), Chenopodiaceae (2), *Eleocharis* cf. *acuta* (2), *Polystichum vestitum* (2), Ericaceae cf. *Cyathodes empetrifolia* (2), *Gaultheria/Pernettya* (2), Ericaceae (2), Rubiaceae (2), *Veronica* cf. *pimelioides* (2), *Pimelea* (2)

Most frequently recorded items excluding pollen/spores: *Coprosma* seeds (6), Polygonaceae DNA (5), *Leucopogon fraseri* seeds (4), *Leucopogon fraseri* leaves (4), *Ranunculus* seeds (4), *Ranunculus* cf. *gracilipes* seeds (3), *Urtica* seeds (3), Apiales DNA (2), Bryophyte leaves (2), Asteraceae seeds (2), *Einadia triandra* seeds (2), *Carex* seeds (2), *Eleocharis* cf. *acuta* seeds (2), Cyperaceae seeds (2), *Polystichum vestitum* leaves (2), *Gaultheria/Pernettya* seeds (2), *Gonocarpus* seeds (2), Rubiaceae DNA (2), *Veronica* cf. *pimeleoides* leaves (2)

Diet and habitat notes: *Pachyornis elephantopus* appears to have been mainly a grazer. Coprolites of this species are dominated by short-statured plants of non-forested habitats and lianes. Matted grass leaves cf. Poaceae found between a *P. elephantopus* sternum and gizzard stones at Glencrieff swamp (Rawlence et al. 2016) could also represent grazing, although could not be definitively demonstrated to have been eaten by the moa. Large twigs were found in a gizzard content sample from Styx swamp attributed to *P. elephantopus* on the basis that this moa species was the most abundant at the site (Wood 2007a). However, the gizzard content was actually not associated with a particular skeleton and so this association is tentative. Finite element analysis of the congeneric crested moa (*P. australis*) revealed adaptation of skulls in this genus for pulling down in a dorsoventral direction (Attard et al. 2016). Such a motion is often exhibited by birds such as geese while grazing small herbs, with a small downwards tug being used to break the plant before consuming. Such a motion also appears ideal for breaking filiramulate plants such as lianes, as the fibrous stems would resist against tugging backwards or lateral shaking. The *P. elephantopus* diet, being dominated by non-forest plant taxa, would have been particularly well-suited to glacial periods, when forest extent became restricted and non-forest habitats expanded (Wood et al. 2016). In support of this, genetic evidence indicates that the population size of *P. elephantopus* may have increased around the height of the last ice age (Rawlence et al. 2012), and this species tends to dominate glacial loess bone deposits from the eastern South Island (Worthy 1993).

Moa spp. (unidentified specimens)

Specimens for which dietary remains have been quantified but the associated moa species has not been reliably identified.

Gizzards: (7) Pyramid Valley, North Canterbury (3) (Burrows et al. 1981) (specimen 121D is unidentified, but is either *D. robustus* or *E. curtus*); Scaife's Lagoon, Otago (3) (Burrows et al. 1981; Wood 2007); Styx, Otago (1) (Wood 2007).

Coprolites: (67) Borland Burn, Southland (2) (Wood unpublished); Dart River Valley, Otago (39) (Wood et al. 2008); Euphrates Cave, Northwest Nelson (2) (Wood et al. 2012b); Kawarau Gorge, Otago (2) (Wood et al. 2008); Old Man Range (1) (Wood unpublished); Roxburgh Gorge, Otago (10) (Wood et al. 2008); Sawers' rock shelter, Otago (5) (Wood et al. 2008); Shepherd's Creek, Otago (1) (Trotter 1970); Takahe Valley, Fiordland (5) (Horrocks et al. 2004).

Caveats with interpreting moa diet from gizzard and coprolite analyses

When interpreting moa diets from gizzard and coprolite content, it is prudent to consider the inherent biases of these two sample types. Gizzard content samples are less digested than coprolites, offering a comparatively good chance of identifying soft plant tissues (e.g. leaves) that may be rendered an unidentifiable

'mush' in coprolites. It has also been demonstrated that large seeds, which are preserved in gizzards, were destroyed by moa digestive tracts and hence not preserved in moa coprolites (Carpenter et al. 2018a). Having undergone more digestion, plant remains within coprolites are more difficult to identify than those in gizzards and may be biased towards resistant objects (such as small hard seeds). However, the content of gizzards could be biased towards the plants that were growing around the margins of the mire, and may therefore provide a biased representation of the diets of free-ranging birds. Moreover, gizzard samples are biased towards those moa species of regions where miring sites are more frequent (lowlands east of the main axial range). There is also significant potential for the contamination of gizzard content samples with plant remains from the surrounding sediments (Wood 2007a). In contrast, coprolites are discrete samples that can easily be separated from the surrounding sediment (Wood & Wilmshurst 2016). However, coprolites are not found in association with moa skeletons, as gizzards commonly are, and so attributing them to a moa species requires aDNA analysis (Wood 2007a). Moreover, many coprolite deposits may represent former moa nesting sites (Wood 2008), and this could introduce seasonal biases into dietary interpretations.

The different diet proxy types also have biases. Plant macrofossils, such as twigs, leaf fragments and seeds, provide relatively reliable information on plant species consumed by moa. However, while abundant items – such as the hundreds of *Coprosma* seeds present in some gizzards (Burrows et al. 1981) – allow robust inference about diet, rare macrofossils could represent accidental ingestion or sample contamination.

DNA metabarcoding of coprolites has allowed further insights into moa diets. The unique benefits of this approach come from the potential for identifying consumed plant taxa where no visually identifiable remains are preserved. This may be particularly important where moa consumed easily-digested soft tissues (e.g. leaves, fruit or flowers). The exact source of plant DNA in moa coprolites is usually unclear, but based on relative proportions of material comprising the coprolites is likely to be dominated by consumed plant tissues rather than environmental by-catch or pollen/spores. However, with high-throughput sequencing there is the potential for some of the latter to be detected.

Pollen and spores in coprolites can represent either the consumption of flowers or cones, or 'environmental by-catch' – i.e. wind-dispersed pollen and spores that had settled on the plants consumed by moa or the water they drank. Trees that produce large amounts of wind-dispersed pollen (e.g. Nothofagaceae, Podocarpaceae) are frequently present in the pollen/spore assemblages of moa coprolites, and at low proportions are likely to reflect environmental by-catch. In contrast, pollen from plant taxa that have limited pollen production, and which have insect, or bird-pollinated flowers, are more likely to represent plants that were eaten by moa. So, while pollen can provide important insights into moa diet (e.g. consumption of *Phormium*, *Astelia*, and *Fuchsia*; Wood et al. 2012b) a certain degree of judgement is required in assessing whether a particular pollen-type is likely to reflect consumption by moa. Wood et al. (2012b) proposed a method for separating diet-related pollen/spore types from environmental by-catch in moa coprolites using a combination of rank abundance and trait scores. The method assumed that if all pollen-types were environmental by-catch then their relative abundance should reflect production and dispersal traits (following Moar et al. 2011). Any pollen types that were more abundant than

expected on this basis were more likely to reflect plant taxa intentionally consumed by moa.

Overall, each of these different proxies also introduced some taxonomic bias. For example, plant macrofossils can often be resolved to species, while pollen is typically resolved to genus or family. The amount of taxonomic resolution provided by DNA sequences depends partly upon the length of the sequence, which in ancient specimens such as coprolites is usually restricted to < 200 bp. Most plant taxa resolved from moa coprolites have been to family or higher taxonomic ranks.

Niche partitioning

In addition to looking at the diets of moa species individually, we compared specimens from different species and localities to examine niche partitioning. However, when interpreting the results of such analyses it is important to consider that different combinations of proxies have been used on different samples (for example, there are no pollen data for gizzards, and not all coprolites have DNA or pollen data), and that vegetation communities vary between localities. Therefore, it is necessary to subset the entire dataset into specimens with comparable data from distinct ecological regions before analysis. With these restrictions in mind, two subsets offer the potential for examining niche partitioning in moa: gizzard content samples from North Canterbury and coprolites from the Wakatipu Basin in western Otago.

North Canterbury

Plant macrofossils in gizzard content samples from the two swamp sites in North Canterbury (Pyramid Valley and Treasure Downs) show relatively good separation between moa species (Fig. 4). Gizzard 121D from Pyramid Valley, which was excavated halfway between the skeletons of *D. robustus* and *E. curtus*, clusters with *D. robustus* gizzards, as do the other two samples of uncertain affinity (Fig. 4). This is despite Burrows et al. (1981) noting that the content of gizzard 121D differed "from all other *Dinornis* samples", and reinforces the uncertainty about the identity of this sample. Gizzard content samples from Treasure Downs formed a cluster distinct from those of Pyramid Valley, despite the two sites being in relatively close geographic proximity. Gizzard content samples from *E. crassus*, which was the only species to occur at both localities, were also quite distinct between localities (Fig. 4). This highlights the fact that variability between plant communities at different localities has a relatively large effect, and can prevent attempts to assess niche partitioning between moa species when pooling samples from many different localities.

Wakatipu Basin

Two localities in the Wakatipu Basin have yielded moa coprolites from multiple species: Daley's Flat in the Dart River Valley and Mt Nicholas Station. Pollen and plant macrofossils have been analysed from all identified coprolite samples, but plant DNA has only been sequenced for some. With the addition of the Mt Nicholas coprolites the patterns of moa species separation evident in the Dart River coprolites (as shown by Wood et al. 2013b) remain unchanged. The ordihulls (representing breadth of diet composition) of *A. didiformis* and *P. elephantopus* do not overlap, while *D. robustus* and *M. didinus* have broad niche ranges (Fig. 5). Based on the plant taxa present in the coprolites, *A. didiformis* is interpreted as having fed within the forest, *P. elephantopus* in non-forest
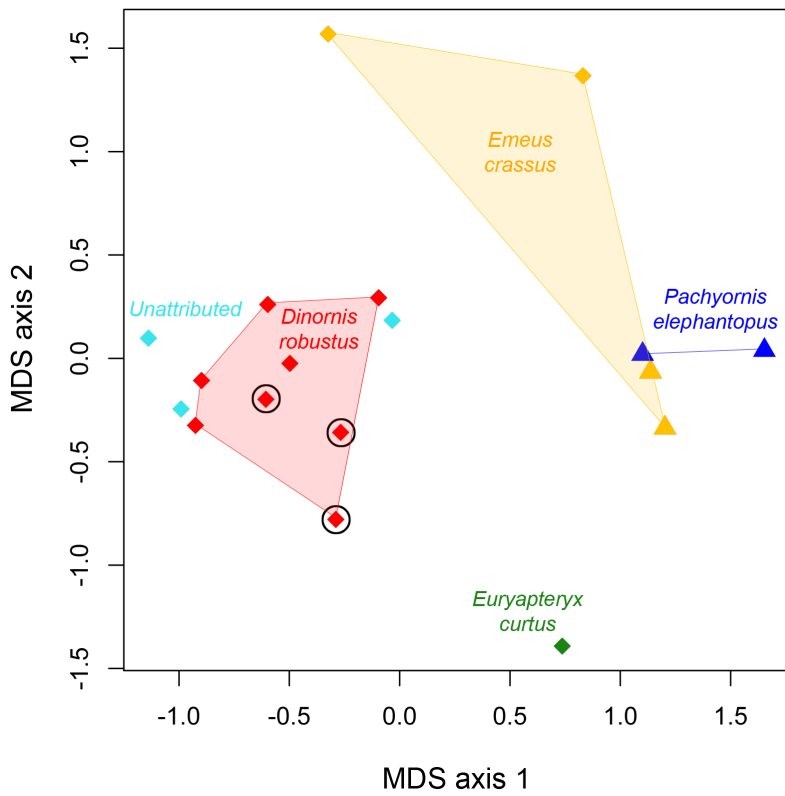
Figure 4. MDS plot of moa gizzard content samples from North Canterbury sites: diamonds, Pyramid Valley Swamp; triangles, Treasure Downs Swamp, Cheviot. Colours denote moa species: red, *Dinornis robustus*; blue, *Pachyornis elephantopus*; dark green, *Euryapteryx curtus*; orange, *Emeus crassus*; light blue, unattributed to an individual moa skeleton (unidentified). Circled *Dinornis robustus* gizzard content samples represent those from immature birds.
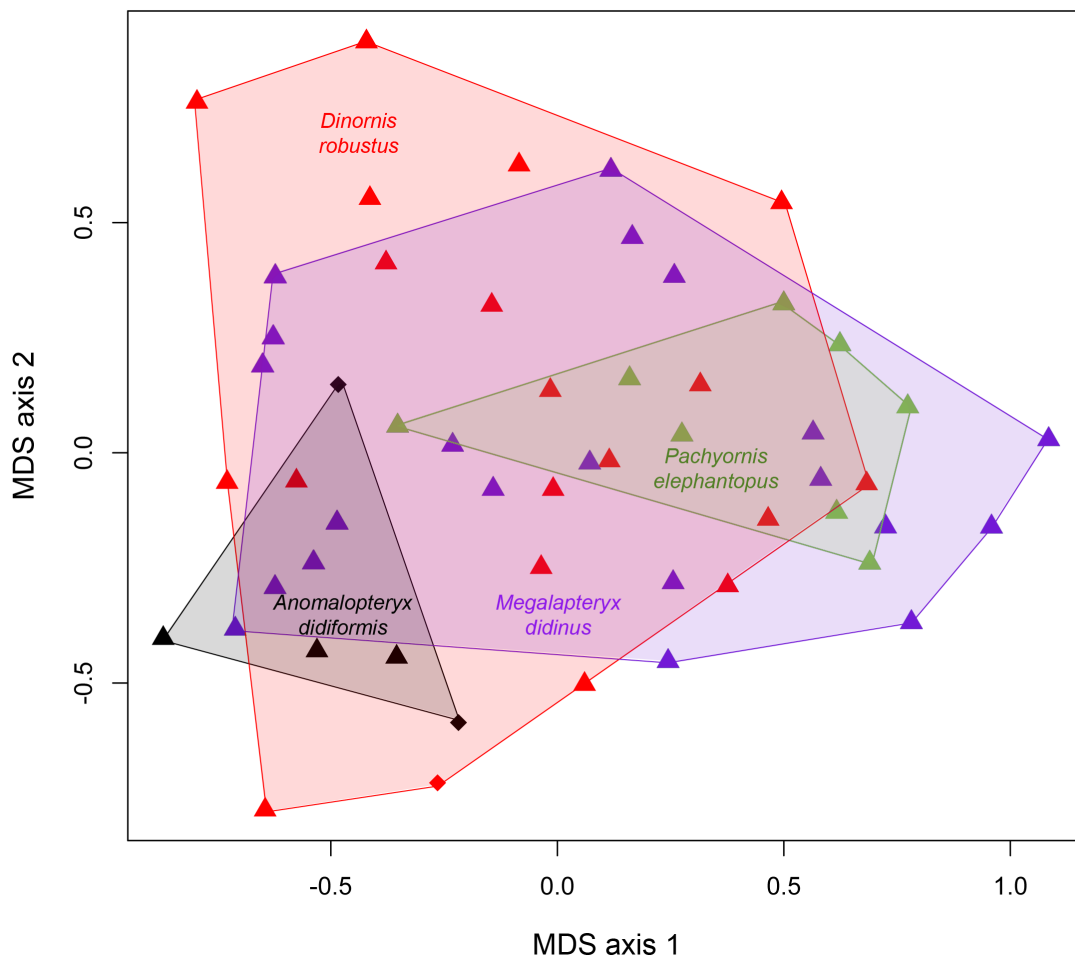

Figure 5. MDS plot of identified moa coprolites (pollen, seed and leaf content) from Wakatipu Basin sites: diamonds, Mt Nicholas Station; triangles, Dart River Valley. Colours denote moa species: red, *Dinornis robustus*; green, *Pachyornis elephantopus*; purple, *Megalapteryx didinus*; black, *Anomalopteryx didiformis*.

herbfields, and *D. robustus* and *M. didinus* across both these locally available habitat types. Within the forest, *D. robustus* appears to have favoured beech and *Coprosma*, while the diets of *M. didinus* and *A. didiformis* included a more diverse range of plants.

General patterns of moa diets

Although the nine different moa species had distinct habitat and food requirements, historically moa have been treated as a single entity when discussing differences between the diets of moa vs other New Zealand avian herbivores (e.g. Clout & Hay 1989; Lee et al. 2010; Forsyth et al. 2010) or in terms of the effects of moa herbivory in driving anti-browse adaptations in the New Zealand flora (e.g. Atkinson & Greenwood 1989; Batcheler 1989). Clearly there are aspects of their biology that set moa apart from New Zealand's other native herbivores, and in some circumstances treating moa as a single entity is warranted. Even unidentified moa gizzard content samples and coprolites (i.e. those that have not been attributed to a particular moa species) can provide insights into general 'moa diet'. In the database assembled for this paper, 7 gizzards and 67 coprolites (40.8% of all specimens) were unidentified, yet

can still contribute important insights into the overall diets of moa. With all available moa diet data now assembled, we discuss some key observations about the general diets of moa.

Preferred plants

A selection of plant taxa occurred frequently in moa diets, irrespective of moa species (Fig. 6). Those plants that were favoured by moa are more likely to have experienced selection pressure promoting the evolution of anti-browse defence structures. A detailed review of the potential role of moa in the evolution of such characteristics in the New Zealand flora is overdue but out of scope for this paper. However, some of the more frequently occurring 'moa plant' taxa are mentioned briefly here.

The most frequently occurring plant genus, both in terms of number of specimens (122, or 67.4%) and localities (12, or 75%) was *Coprosma*. *Coprosma* was also detected in specimens from all moa species (Fig. 6), and across a range of proxies (pollen, seeds, leaves). Rubiaceae DNA sequences also likely represented *Coprosma*. Interestingly, and perhaps reflecting *Coprosma* being a favoured food genus for moa, Wood & Wilmshurst (2017) observed increases in the abundance of
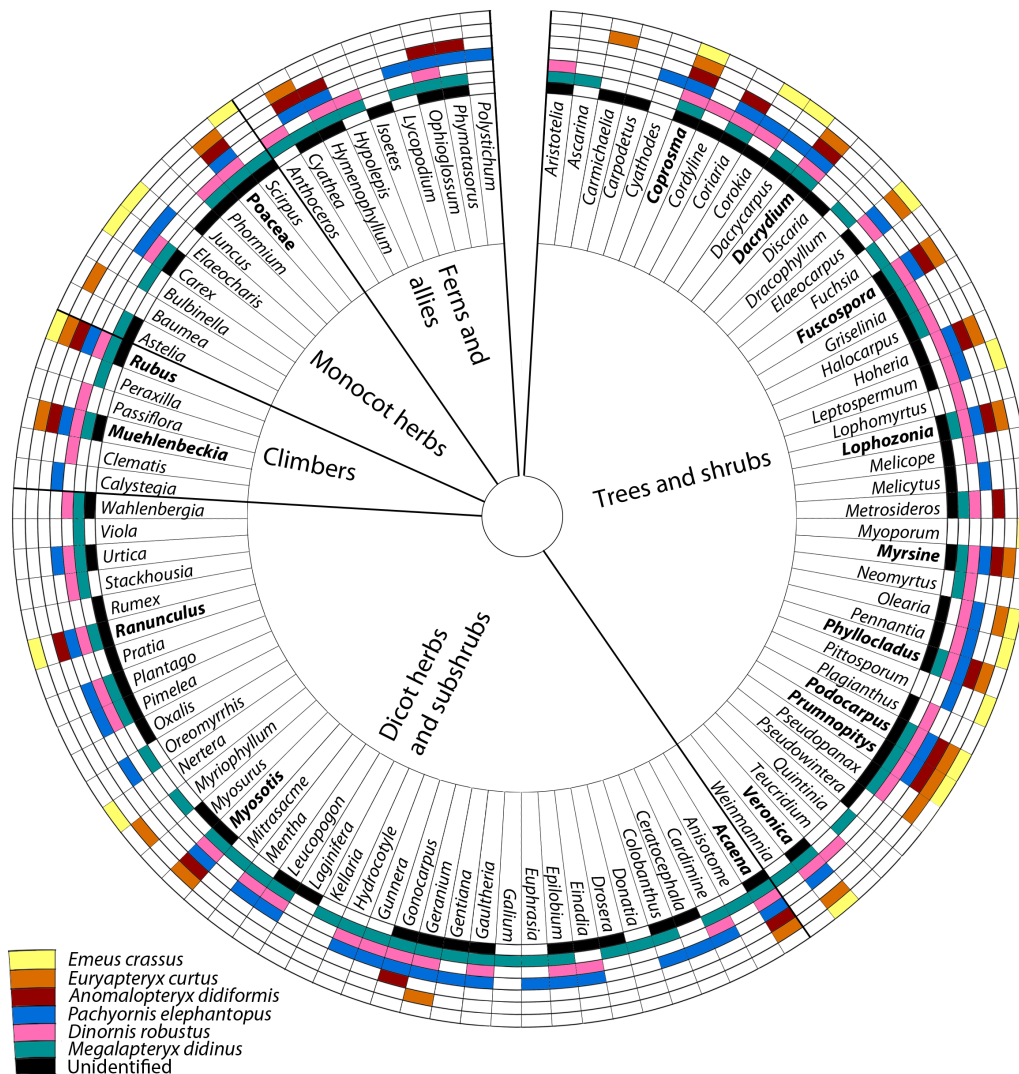

Figure 6. Summary of the occurrence of plant genera (and the grass family Poaceae) in moa gizzard content and coprolites based on all proxies (pollen, macrofossils and aDNA). Bold font indicates plant taxa recorded from gizzard content or coprolites of five or more moa species.
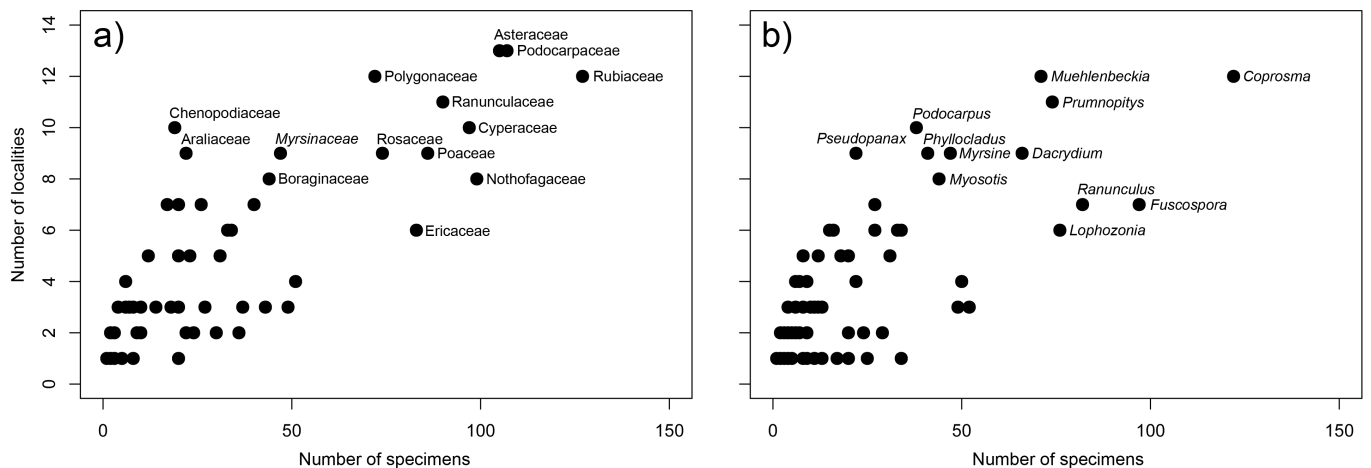
Figure 7. Frequency of occurrence of (a) plant families and (b) genera in moa gizzard and coprolite specimens. Taxon names are shown for those occurring at ≥8 different localities (16 in total) and/or ≥75 different specimens (181 in total).

Coprosma pollen in several soil profiles that coincided with the period after moa extinction. Together with *Myrsine*, which was one of the most frequently occurring plant genera in moa diet data (Fig. 7), these plant taxa contain high percentages of divaricating forms, suggesting that perhaps divarication did not reduce moa browse as has previously been suggested (e.g. Bond et al. 2004).

A range of other frequently occurring plant taxa were mainly found as pollen, and as taxa that produce large amounts of wind-dispersed pollen this may inflate their apparent importance in terms of moa diet. Such taxa include *Fuscospora*, *Dacrydium*, and *Podocarpus* (Fig. 7).

Surprisingly, the 19th century presumptions that moa were fern specialists are supported to some extent here. Ferns do appear frequently in the moa diet data: monolete spores (from ground ferns) occurred in 91 specimens from 7 localities, trilete spores 5 specimens from 2 localities. *Hypolepis* in two specimens from one locality, *Hymenophyllum* in 31 specimens from five localities, *Ophioglossum* in 49 specimens from three localities and *Cyathea* in 33 specimens from six localities. Moreover, *Polystichum* leaves were observed in moa gizzard content from Treasure Downs (Wood 2007a), and Wood & Wilmshurst (2017) observed increases in the abundance of ground fern spores in several soil profiles coinciding with the period after moa extinction. Only one genus of moa, *Emeus*, lacks any evidence for fern consumption (Fig. 6).

The high occurrence frequency of *Muehlenbeckia* (Polygonaceae) in moa coprolites and gizzard content, represented by seeds, pollen and DNA, is also an interesting observation. This genus of lianoid plants appears to have been a favoured food of moa. Another genus of native lianoids, *Rubus* (bush lawyers), has been detected in the diet of every moa species examined (Fig. 6). The relatively frequent occurrence of mistletoe (Loranthaceae) pollen – resolved to *Peraxilla* by Wood et al. (2013b) – and DNA in moa coprolites from sites within beech forest – four from Takahe Valley (Horrocks et al. 2004), and six from Daley's Flat (Wood et al. 2013b) – is also worthy of note. At Daley's Flat coprolites containing mistletoe belonged to *Megalapteryx* and *Anomalopteryx*, and the Takahe Valley coprolites are likely from the former species; a coprolite from this site has been identified using DNA sequencing as being from *M. didinus* (see supporting information of Huynen

et al. 2010). These two species were browsers of short trees and shrubs in the forest understorey, suggesting that mistletoes may have formerly been more common at lower height tiers in the past and have now been largely removed at these levels by browsing ungulates. An alternative explanation is that moa ate the fallen flowers of the mistletoes, which can be locally abundant on the forest floor at certain times of the year. However, pollen was not abundant enough in any of the samples examined to suggest that flowers were being eaten en masse. Rather, consumption of nutrient-rich foliage that had fallen to the ground, and leaves growing on plants within the reach of the birds seem the most likely scenario.

Wood et al. (2017b) examined the degree of overlap between the diets of *D. robustus* and *M. didinus* with extant avian herbivore species currently in New Zealand. They found several moa-specific interactions (i.e. plant taxa that have not been recorded in the diets of other birds). These were mainly small shrubs, herbs and ferns (Wood et al. 2017a), including the herbs *Einadia*, *Myosotis*, *Ceratocephala* and *Myosurus*. The latter two of these are spring-annual herbs, which are discussed in the section below.

What plants did moa avoid eating?

Moa had diverse diets, consuming a wide range of plant taxa. However, by focussing only on the plants that moa ate we may be missing a vital part of the story, that is, which plants were avoided by moa? Understanding avoidance is a key piece of evidence for the co-evolution of defence traits against moa browsing in the New Zealand flora. However, assessing avoidance in extinct species, such as moa, is not a simple matter. It requires not only a comprehensive assessment of moa diet at a particular locality but also the plants that were available for those moa to consume (i.e. the contemporaneous composition of the local vegetation community). Our assessment focussed on three localities where these two types of data were available: Dart River Valley, Euphrates Cave/ Garibaldi Plateau and north Canterbury limestone areas. At these three localities, we resolved 25 plant species which we strongly suspect were growing in the presence of moa, but for which there was no evidence that moa ate them in any of the coprolite or gizzard content samples from throughout the South Island (Appendix S2).

Several orchids were present but appear to have not been eaten by moa (e.g. *Corybas trilobus*, *Microtis unifolia*, *Pterostylis montana* and *Thelymitra longifolia*). The near absence of orchids in moa diets (recorded only by 2 rbcL clones from one coprolite at Euphrates Cave) seems odd, given their ubiquity and apparently soft, edible foliage. Their rarity in moa diets may be due to their growth habit of many orchid species, having thin vertical stalks close to the ground, yet a number of plants with similar growth habits are found in moa diets (e.g. *Ophioglossum*, *Ceratocephala pungens*). However, reduced visual apparency may explain the lack of another species in moa diets, *Parsonsia heterophylla*, which can be locally common but whose thin branches and leaves may be difficult to see when it is climbing on a shrub. Another cluster of plant taxa that were absent from moa diets include small, long-leaved monocots, such as *Luzula banksiana*, *L. picta* (Juncaceae), *Arthropodium candidum* (Asparagaceae) and *Libertia ixioides* (Iridaceae). The tough leaves of these plants may have reduced the likelihood that moa would have eaten them. Also, worthy of note is the absence/rarity of plants with perceived defences against moa, including *Discaria toumatou* (spines), *Pseudowintera colorata* (mottled leaves and distasteful chemical compounds), *Sophora* (toxins) and *Kunzea* (*Leptospermum* is also very rare in moa diets; small, tough leaves, leaf volatiles and low-nutrient status). The absence of *Schefflera digitata* in moa diets is difficult to explain, as this plant is highly palatable and a preferred browse plant by deer (Forsyth et al. 2002), and another araliad genus (*Pseudopanax*) appears frequently in studies of moa diets.

Ecosystem functions provided by moa

Moa were the largest herbivores in New Zealand's terrestrial ecosystems at the time humans settled New Zealand, c. 750 years ago (Wilmshurst et al. 2008). Fossil evidence from the early Miocene Manuherikia Group lacustrine sediments in Central Otago suggest that their role as largest herbivores had been established by at least 20 million years ago (Tennyson et al. 2010), and it has been hypothesised that this niche may have been occupied by moa ancestors not long after the extinction of herbivorous dinosaurs (Mitchell et al. 2014). Having been the largest herbivores for such a long-time it might be expected that there has been some degree of co-evolution between plants and moa, and it has been suggested that a range of different plant traits could have evolved in response to moa browsing (Greenwood & Atkinson 1977; Atkinson & Greenwood 1989; Batcheler 1989). Coprolites and gizzard content may provide some insights into whether plants with such traits were browsed by moa, but cannot provide answers to these long-term evolutionary questions. However, coprolites and gizzard content can provide insights into the ecosystem processes that moa may have facilitated.

Pollination

There is no evidence to suggest that moa acted as pollinators. Consumption of flowers by moa is evident in some coprolites, which contain relatively high-levels of pollen from bird- or insect-pollinated flowers. Examples include *Phormium*, *Fuchsia*, and *Astelia* (Wood et al. 2012a). Even with wind-pollinated flowers, relative abundances of pollen types > 95% are likely to indicate consumption of flowers, an example being *Coprosma* (Wood et al. 2013b). Birds covered in pollen as a result of moving around and pushing through flowering plants, and their consumption of flowers may both have inadvertently transfered pollen (Wood et al. 2012c). However, feeding on flowers by moa was more likely to have been a destructive process and it is unlikely that moa were significant effective pollinators.

Propagule dispersal

Moa are likely to have played a major role in seed dispersal. Seeds are common in moa coprolites, and are often found intact (Wood et al. 2008). Carpenter et al. (2018a) compared the seeds present in moa gizzards and coprolites to show that large seeds (> 3.3 mm) appear to have been destroyed during passage through the digestive tract. This likely explains why there are no large anachronistic 'moa' fruits, such as those seen on other landmasses with extinct herbivores (Barlow 2000), and in extant associations such as with the southern cassowary (*Casuarius casuarius*) in the rainforests of north Queensland, Australia (Stocker & Irvine 1983). The largest fruit in the New Zealand flora can be dispersed by the extant kererū (*Hemiphaga novaeseelandiae*; Clout & Hay 1989) and probably other birds such as weka (*Gallirallus australis*; Carpenter et al 2018b). There is significant overlap between the identity of intact seeds from moa coprolites and those recorded in droppings of other native birds such as kea (*Nestor notabilis*; Young et al. 2012), kākāpō (*Strigops habroptilus*; Butler 2006) and forest passerines (Williams & Karl 1996), reflecting the generalist ecologies of New Zealand's birds. Therefore, while some plant species, especially herbs with small indehiscent fruits (Wood et al. 2013b), may have experienced reduced dispersal following moa extinction, this was likely supplemented to some extent by other bird species, and later by introduced birds and mammals (O'Donnell & Dilks 1994; Williams & Karl 1996; Lee et al. 2010). A group of plants whose seeds appear relatively frequently in coprolites from dryland Central Otago and which are now quite rare are the spring annual herbs including *Ceratocephala pungens* and *Myosurus minimus* (Wood et al. 2008). These plants may be declining as a result of reduced dispersal and habitat maintenance (soil scarification; cropping of taller plants) following the extinction of moa (Rogers & Overton 2007; Lee et al. 2010) but more work is required to demonstrate this conclusively.

Although we have dealt so far only with plants in the diet of moa, it has been demonstrated through DNA analyses of moa coprolites that moa also ingested a range of different fungi, including representatives of *Cortinarius*, *Inocybe*, *Tomentella*, *Lepiota*, *Geastrum* and Lycoperdaceae (Boast et al. 2018). These fungal taxa appear relatively commonly in moa coprolites, occurring in 12 of the 19 (63.2%) specimens examined by Boast et al. (2018). *Cortinarius* and *Inocybe* are ectomycorrhizal species, and fruiting bodies of several species within *Cortinarius* are sequestrate and colourful; traits that have been suggested could be adaptations to enhance consumption and spore dispersal by birds or reptiles (Beever 1999; Beever & Lebel 2014). Although the results of Boast et al. (2018) provide an indication that moa could have been consumers and dispersers of key fungi such as ectomycorrhiza in New Zealand forests, confirmation of this must rely on the complementary identification of spores from within the same coprolites. This is because the fungal DNA could originate from ingestion of soil or plant matter containing hyphae of the fungi.

Nutrient cycling

Although moa did not change the total nutrient supply in terrestrial ecosystems (as seabirds do, for example), herbivory

and defecation by moa would have accelerated nutrient cycling rates, moved nutrients across the landscape, and concentrated nutrients where they defecated. However, demonstrating that these processes had a major influence on native vegetation communities is a challenging prospect. Tanentzap et al. (2013) used an experimental approach to test the potential effect of moa-derived nutrients on plants, applying hen (*Gallus gallus domesticus*) manure to experimental plots as an analogue for moa dung. In terms of nitrogen, the application rates used (100 kg N ha^{-1}) equated to 0.526–1.124 kg dry weight of moa dung m^{-2} (calculated using the %N values for moa coprolites provided by Tanentzap et al. 2013), cf. accumulation rates of < 0.00001 kg dry weight of cattle dung m^{-2} day^{-1} for rangelands (Tate et al. 2003). If moa dung was comparable to sheep dung and c. 60% water by weight (Araújo 2010), then this would translate to 1.3–2.8 kg m^{-2}. While such rates may have been achievable in discrete sites with a high frequency of moa occupation (e.g. rock shelters), they are exceedingly high compared to most natural situations. Moreover, in standardising for N application rates, the significantly higher phosphorus levels in the hen manure compared with moa coprolites meant that experimental P application rates were equivalent to 7–32 kg of moa dung m^{-2}. Despite these unrealistically high rates of application, which were acknowledged by the authors, native plant communities showed little response. Only fast-growing lianes (e.g. *Muehlenbeckia*) responded positively to the excessive nutrient application, along with non-native plant species that would not have co-occurred with moa.

Other roles of moa dung in the environment

Although the contribution of moa dung to nutrient cycling is unclear, it may have had other roles as food or habitat for different organisms within New Zealand's pre-human ecosystems. For example, coprophilous fungi such as *Sporormiella* are known to have grown on moa dung and used the incidental ingestion of their spores by moa as part of their life-cycle (Wood et al. 2011). New Zealand has 15 endemic species of dung beetle (Stavert et al. 2014a), and experimental work has shown that they tend to be generalist species attracted by a range of different compounds found in both carrion and dung (Stavert et al. 2014a; 2014b). With an attraction to a range of different dung from both native birds and introduced mammals (Stavert et al. 2014b), the relatively large dung of moa would likely have once contributed to the diet of New Zealand's dung beetle fauna (Stavert et al. 2014a). New Zealand also has several species of 'dung-mosses' (Splachnaceae) within the genus *Tayloria*. Dung mosses grow on animal dung and carcasses, and their spores are dispersed by flies moving between these habitats. While it seems probable that *Tayloria* would have grown on moa dung, evidence for this interaction will be difficult to find, as conditions suitable for moss growth are unlikely to favour the preservation of coprolites. Finally, moa dung may have acted as a reservoir of parasites within the environment (Wood et al. 2013a), which may have been transmitted to other moa and perhaps different bird species through the ingestion of infected faecal matter (e.g. Dolnik et al. 2010).

Ecological replacement

Can the ecological roles left vacant following the extinction of moa be filled by other species? Based on evidence from gizzard content and coprolites, the two main roles of moa within ecosystems appear to have been herbivory and seed dispersal. We can explore each of these separately.

It is clear that moa dispersed seeds of a wide range of plants. Although dispersal distances were unlikely to have been as far as for volant birds, moa may still have ranged over several kilometres. However, although the extinction of moa may have led to reduced seed dispersal for some plants, there appear to be no instances of plants that relied on moa solely for their dispersal. Seed dispersal is commonly facilitated by New Zealand fauna, and the seed dispersal roles once provided by moa continue to be performed by extant native bird species, such as kererū, kea, tuī (*Prosthemadera novaeseelandiae*), silvereye (*Zosterops lateralis*) weka, waterfowl, reptiles (Kelly et al. 2010; Wotton et al. 2016), invertebrates (Duthie et al. 2006), and also some introduced species, e.g. blackbird (*Turdus merula*; Kelly et al. 2010).

Herbivory was another ecological process performed by moa. In non-forest habitats extant grazing birds may provide some degree of surrogacy for moa, and in fact may have been the main herbivores in such plant communities even in the presence of moa. For example, waterfowl alone can provide sufficient grazing pressure to maintain species-rich native wetland turf communities (Lee et al. 2010; Korsten et al. 2013). Perhaps the most important herbivore niche left vacant following the extinction of moa was that of a browser of forest understorey trees and shrubs. While native fauna such as kereru and kōkako consume leaves of forest trees to some extent, they do not browse twigs and leaves in the understorey in the same way that some moa species once did. As the largest herbivores in New Zealand forests during the post-European era, deer (Cervidae) are a favourite 'moa substitute' candidate for filling this forest understorey browser role. Caughley (1983) was perhaps the first to posit that the open-understorey forests created and maintained by deer may have appeared similar to those in which moa browsed hundreds of years ago. At a broad scale this seems like a sensible idea, as deer certainly do fill the niche of a forest understorey browser. Yet the comparison does not hold up under closer scrutiny. Aside from the obvious mammal v. bird difference, deer are completely different animals to moa, from their teeth and hooves to their higher population densities and fecundity. Accordingly, their ecological impacts appear to far exceed those of moa. Any notion that deer and moa had comparable effects on native ecosystems has been comprehensively dismissed based on multiple lines of evidence, including an assessment of differences in soil compaction, a direct comparison of the content of moa coprolites and deer faeces, and pollen analysis of forest soil cores to examine vegetation responses to moa extinction (Atkinson & Greenwood 1989; Caughley 1989; Duncan & Holdaway 1989; Forsyth et al. 2010; Tanentzap et al. 2013; Wood & Wilmshurst 2017; 2019; Wood et al. 2008; 2012a; 2013b). Visions of extant large ratite species such as, emu (*Dromaius novaehollandiae*) or ostrich (*Struthio camelus*), being introduced to New Zealand to fill the ecological niches of moa (Nicholls 2006; Bond et al. 2004) are also misguided. Again, while these species may perform some of the seed dispersal once provided by moa, they cannot fulfil the role of a large avian tree and shrub browser that is now missing from New Zealand ecosystems. Differences in feeding capabilities means that extant large ratites could not consume enough nutrition to survive if feeding on many of the divaricating understorey shrubs once consumed by moa (Bond et al. 2004).

In addition to seed dispersal and herbivory, moa likely also played a relatively minor role in a number of other ecosystem processes, and some of these may also be being replaced by

extant species. For example, it is possible that the dung of ungulate herbivores may be replacing some of the roles of moa dung. This has been demonstrated for fungal habitat (Wood et al. 2011), but more research is required on aspects such as their contribution to invertebrate foodwebs and nutrient cycling. However, through an increased understanding of moa diversity, diets and ecology, it is now clear that no single extant species can completely fill the niches left vacant by moa (Wood et al. 2013b). This is perhaps not surprising, given that moa were c. 60 million years evolutionarily distinct from their nearest living relatives; the comparatively small and volant tinamou (Aves: Tinamidae) of South America (Mitchell et al. 2014).

Future directions

That coprolites and gizzard content samples have now been found for all six genera of moa is quite remarkable. The ecology of fauna that became extinct following initial human settlement is perhaps better resolved in New Zealand than on any other landmass globally. The relatively recent human settlement, a temperate climate and geologically dynamic landscape with many deposits suitable for preserving palaeofaunal remains (e.g. caves, spring-bogs) and a long history of palaeofaunal studies have contributed towards this understanding. However, before we can achieve a more complete understanding of the diets and ecology of our largest herbivores, there are still some major gaps.

First, coprolites/gizzard content samples are only known from 6 of the 9 moa species. There is still no direct evidence of diet for *P. australis*, Mantell's moa (*Pachyornis geranoides*) and North Island giant moa (*Dinornis novaezealandiae*). Based on similarity in habitat preferences and morphology it could be assumed that *D. novaezealandiae* might have had a broadly similar diet to *D. robustus*. However, *P. australis* was unique in that it had a highly-restricted distribution and appears to have been a specialist of subalpine habitat. Moreover, samples from *P. geranoides*, the moa species with the smallest body size, mean of 27 kg (Tennyson & Martinson 2006), would undoubtedly provide interesting insights into the breadth of moa diets. The lack of samples from *D. novaezealandiae* and *P. geranoides* reflect the fact that no moa coprolites or gizzard content samples have yet been found in the North Island. Given the high diversity of plants restricted to the North Island, the discovery of such samples has the potential to greatly expand the number of plant taxa known to have been eaten by moa, which despite the wealth of data summarized in this paper has not yet reached an asymptote (Fig. 3).

Second, there is a bias in the number of samples from those moa species for which coprolites/gizzard content remains have been found. *Dinornis robustus* and *M. didinus* numerically dominate studied samples, while just a handful of samples from *E. crassus* and *E. curtus* means that the full dietary breadth of these species is obscure. Additional samples from these species, and additional samples from all species from more localities, will help resolve the degree of diet overlap between moa species and lead to a better understanding of niche partitioning.

Finally, although moa played an important ecological role as New Zealand's largest terrestrial herbivores, they were still just one part of a diverse avifauna. Coprolites of a variety of shapes and sizes, likely representing a range of different faunal species, have been recovered alongside moa coprolites (Wood & Wilmshurst 2014). Applying the techniques learnt through the study of moa diets to coprolites of other prehistoric bird species, such as kākāpō (e.g. Horrocks

et al. 2008; Wood et al. 2012c; Boast et al. 2018), will help to broaden our understanding of New Zealand's pre-human ecosystems, former animal-plant interactions, and the legacy of avian extinctions (Lee et al. 2010).

Acknowledgements

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Supplementary material

Additional supporting information may be found in the supplementary material file for this article:

Appendix S1. Moa herbivory database.

Appendix S2. Native plant species present at ≥ two of three localities (Dart River, Garibaldi Plateau and North Canterbury limestone areas) but which were absent from moa gizzard content / coprolite specimens at those localities, and for which their genera have not been recorded in moa diets from elsewhere.

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