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Sporormiella as a proxy for non-mammalian herbivores in island ecosystems

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ABSTRACT

Spores of the dung-fungi *Sporormiella* are routinely used as a proxy for past megaherbivore biomass and to pinpoint the timing of extinctions. Further ecological insight can also be gained into the impacts that followed initial human arrival in a region through correlation of spore abundance with other proxies (e.g. pollen, charcoal). Currently, the use of *Sporormiella* as a palaeoecological proxy has been restricted to landmasses where large-herbivore guilds are dominated by mammals. Here, we use New Zealand as a case study to show that the method can also be applied effectively to islands dominated by large avian herbivores. We examine 44 dung samples from 7 localities to show that *Sporormiella* spores were widely distributed in the dung of endemic avian herbivores (South Island takahe (*Porphyrio hochstetteri*), kakapo (*Strigops habroptilus*), and several species of extinct moa, identified by ancient DNA analysis). In addition, we show that *Sporormiella* spores in a forest soil core from the Murchison Mountains, South Island, accurately trace the post-settlement decline of native avian herbivores, and combined with high-resolution radiocarbon dating reveal severely reduced local herbivore populations by the late 17th Century AD. The spores also trace the subsequent spread of Red deer (*Cervus elaphus*) introduced to the area in the early 20th Century AD. Our results suggest *Sporormiella* spores may provide a useful new tool for examining extinctions on numerous islands where terrestrial herbivore guilds were dominated by birds or reptiles. Our findings also highlight the need to consider entire herbivore communities (including birds and reptiles) when examining Late Pleistocene continental *Sporormiella* records, where the focus has often been tracing the decline of populations of large mammals.

1. Introduction

The extinction of megafauna has been a widespread phenomenon across the world over the past 50,000 years (Burney and Flannery, 2005). The idea that fossil spores of the coprophilous ascomycete *Sporormiella* could be quantified in sediments and used as a proxy for past herbivore densities (Davis, 1987) has provided a novel tool for resolving the local timing of megafaunal extinctions. Since the late 1980s the technique, used in conjunction with other sedimentary proxies (pollen and charcoal), has also provided insights into the relative sequence of faunal extinctions, vegetation change, anthropogenically altered fire regimes, and livestock introductions (e.g. Davis, 1987; Burney et al., 2003; Innes and Blackford, 2003; Robinson et al., 2005; Davis and Shafer, 2006). These, and other studies, have demonstrated a strong relationship between *Sporormiella* spore abundance and the local population density of large herbivores. Spores are abundant in sediments associated with herbivore congregations, such as sheep corrals and dry rock shelters (Davis, 1987; Davis and Shafer, 2006). Further, a Late Pleistocene decline of *Sporormiella* spores in forest soil cores from across North America (e.g. Davis, 1987; Robinson et al., 2005; Davis and Shafer, 2006; Gill et al., 2009) appears to reflect a megafaunal extinction event that resulted in the loss of 75% of large mammals (Robinson and Burney, 2008). However, the application of *Sporormiella* to palaeoecological studies has been exclusively restricted to landmasses where large-herbivore guilds were dominated by mammals. Many islands across the world have native terrestrial faunas depauperate in mammals, in which birds and reptiles were the largest and dominant herbivores. *Sporormiella* has the potential to provide a useful tool for refining our understanding of Late Quaternary extinction events on such islands. Currently there are few reported instances of *Sporormiella* occurring in the dung of non-mammalian herbivores, but this is likely to be due to biased search effort.

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New Zealand provides an ideal context for investigating the reliability of *Sporormiella* in detecting the extinctions of non-mammalian herbivores. Before settlement by Polynesians around 1280 AD (Anderson, 1991; Higham et al., 1999; Wilmshurst et al., 2008), birds dominated the terrestrial vertebrate fauna, with mammals represented by just 3 species of bat (Worthy and Holdaway, 2002). The largest herbivores were 9 species of ratite moa (Aves: Dinornithiformes), weighing up to >240 kg (Bunce et al., 2003, 2009). Several other large avian herbivores were widespread, including flightless geese (up to 18 kg) (*Cnemiornis calcitrans*, *Cnemiornis gracilis*), a flightless, nocturnal parrot (kakapo (*Strigops habroptilus*)) (2.5 kg), and large flightless rails (South Island takahe (*Porphyrio hochstetterii*) and North Island takahe (*Porphyrio mantelli*)) (up to 4 kg). Several smaller species of herbivorous rail and waterfowl were also widespread (Worthy and Holdaway, 2002; Tennyson and Martinson, 2006; Lee et al., 2010). Hunting and habitat loss caused the rapid extinction of many of the largest of these birds following human arrival, with ongoing extinctions thereafter (Tennyson and Martinson, 2006). This is widely accepted and well-documented, supported by a combination of well-dated bones, eggshells, worked moa bone artefacts, and abundant evidence of over-exploitation in the form of bone-rich archaeological middens from the early settlement period (Anderson, 1989a; Holdaway and Jacomb, 2000; Holdaway et al., 2002; Worthy and Holdaway, 2002; Tennyson and Martinson, 2006). The chronology of mammalian herbivore introductions associated with European settlement is also well-documented in New Zealand (Thomson, 1922; King, 1990).

Here, we first test whether *Sporormiella* spores are present in the droppings of large, endemic, herbivorous birds. Second, we analyse *Sporormiella* spore abundance in a forest soil core from South Island, New Zealand, and discuss how accurately this reflects what is known about historic and prehistoric herbivore population changes.

2. Study sites and methods

2.1. Avian herbivore dung

Forty-four samples of dung from at least 6 species of endemic large avian herbivores (South Island takahe, kakapo and 4 species of extinct moa) were analysed for *Sporormiella* spores. We examined existing palynological slides prepared from fresh faecal boli of takahe ($n = 6$) collected from near Lake Eyles in the Chesterburn area of the Murchison Mountains (Fig. 1) during late summer (February) (Wilmshurst, 2003), and subsamples taken from the interior of moa coprolites from a wide range of sites from the southern South Island, New Zealand: Daley's Flat, Dart River Valley, West Otago ($n = 20$); Takahe Valley rock shelter, Murchison Mountains ($n = 2$); Earnscleugh Cave, Central Otago ($n = 1$); and Shepherd's Creek rock shelter, North Otago ($n = 1$) (Fig. 1). The depositors of the specimens from Dart River Valley and Earnscleugh Cave were identified using ancient DNA (Wood et al., 2008), and included 4 species: South Island giant moa (*Dinornis robustus*), heavy-footed moa (*Pachyornis elephantopus*), upland moa (*Megalapteryx didinus*) and coastal moa (*Euryapteryx curtus*). The other 3 coprolites were identified as moa based on size and morphological similarity to specimens identified by DNA (Wood et al., 2008). We also prepared samples of kakapo coprolites from Cobb Valley, North-West Nelson ($n = 6$), and Honeycomb Hill Cave, north Westland (n = 8), South Island, New Zealand (Fig. 1). Kakapo coprolites occur throughout cave systems in the northwest region of the South Island (Horrocks et al., 2008).

The samples of bird dung represent potential feeding in a variety of habitat types, from sub-alpine grassland to lowland forest and shrubland. Details of climate and vegetation for each site are described below.

The Chesterburn stream (fresh takahe boli site) flows from glaciated cirque basins (c. 1020 m altitude at Lake Eyles) to Lake Te Anau (210 m altitude), and the catchment receives approximately 5000 mm annual rainfall (Wilmshurst, 2003). Soils are typically thin and peaty, overlying gneiss bedrock. The forest in the catchment is dominated by silver beech (*Nothofagus menziesii*), with sub-alpine *Chionochloa* grasslands above the treeline (Wilmshurst, 2003).

Takahe Valley has a similar climate and vegetation, but also has significant outcrops of Tertiary marine limestone, which forms rock shelters at the east end of the valley.

In contrast, Shepherd's Creek and Earnscleugh Cave are located east of the Southern Alps in the Otago region (Fig. 1), within the semi-arid dryland rainshadow zone (Rogers et al., 2005). The zone has experienced significant ecological modification since human

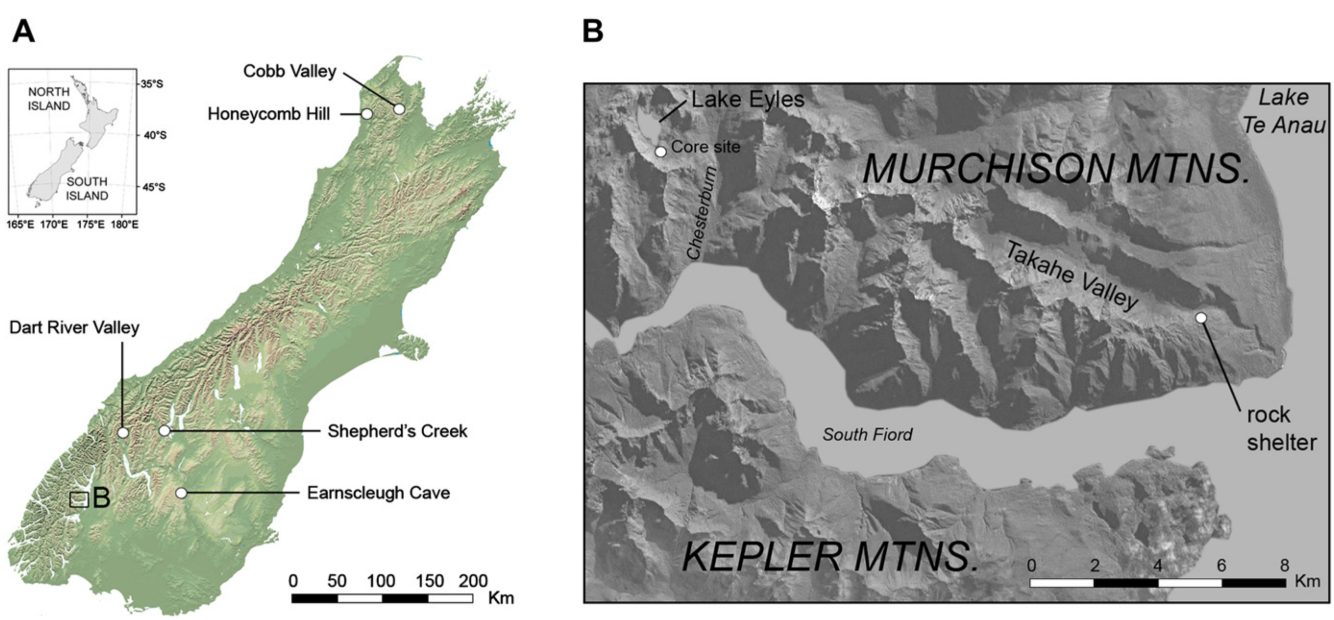

Fig. 1. Location of study sites on (A) South Island, New Zealand, and (B) expanded view of Murchison Mountains area.