Palaeoecological signatures of vegetation change induced by herbivory regime shifts on subantarctic Enderby Island

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ABSTRACT

The stratigraphic relationships of palaeoecological proxies and use of changepoint analyses to determine the cause and effect relationships between past events has allowed a better understanding of the relative contributions of humans and environmental drivers to Late Quaternary extinctions and of their effects on terrestrial ecosystems. Few studies, however, have validated these approaches at localities where past interactions between vegetation communities and large herbivores are well-documented. Here, we use a peat core from subantarctic Enderby Island to present the first study tracing the spores of dung fungi alongside pollen at a site where the history of mammalian herbivore introductions (and subsequent eradication), and their effects on the vegetation, are precisely known. We find a strong connection between spore influx rates of the dung-fungus *Sporormiella* and PCA axis 1 of the pollen assemblages, suggesting that past vegetation change caused by herbivore introductions and eradications at the core site can be readily deduced from the palaeoecological record. The response of the vegetation community to the removal of herbivores was so rapid, however, that a difference in timing between changepoints relating to specific pollen taxa, the overall pollen community, and the decline of *Sporormiella* spores, could not be resolved in our record, despite a sampling resolution of <5 years. We suggest that further case-studies, spanning different vegetation and herbivore communities, are required to provide increased confidence in inferences drawn about cause-and-effect relationships using proxy changepoint offsets in palaeoecological records.

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1. Introduction

The past 50,000 years has been a period of major environmental change across the globe (Barnosky et al., 2004; Burney and Flannery, 2005). Human dispersal, climate change, shifts in vegetation communities, altered fire frequencies and major faunal extinction events have all had (though not necessarily independently) significant consequences for global ecosystems and ecological processes over a geologically short time frame (Janzen and Martin, 1982; Barlow, 2002; Johnson, 2009; Levy, 2012; Cooper et al., 2015). By determining the cause and effect relationships between these events we can gain a better understanding of the relative contributions of humans and environmental drivers to Late Quaternary extinctions of megafauna (Barnosky et al., 2004; Cooper et al., 2015; Bartlett et al., in press), examine the effects that these extinctions had on terrestrial ecosystems, and better predict the potential consequences of future environmental change and re-wilding projects.

One way in which the cause and effect relationships between such past events can be inferred is by examining the sequence of changes in sedimentary proxies for each event. For example, within a sediment core, pollen assemblages (a proxy for vegetation community composition) can be stratigraphically connected with any number of other proxies, such as charcoal (a proxy for fire events), spores of dung-fungi (a proxy for the local density of large herbivores), or DNA of *Bacterioides* strain HF 183 (a proxy for the presence of local human populations) (Madeja et al., 2009, Madeja, 2015). Statistical methods for the detection of changepoints can then be used to determine when the trajectory of each proxy changes significantly, thereby allowing the relative timing of

changes between proxies to be inferred (e.g. Umbanhowar Jr. et al., 2006; Gill et al., 2012; Johnson et al., 2015).

Recently, the relative stratigraphic order of changes in palaeoecological proxies have been used to test whether vegetation changes apparently coincident with the extinction of large herbivores in North America and Australia actually occurred before (i.e. contributed to the extinctions; Stuart et al., 2004) or after (i.e. were a response to reduced herbivory; Gill et al., 2009; Rule et al., 2012; Johnson et al., 2015) the event. However, while the relationships between sedimentary dung-fungi spores and herbivores, and pollen and vegetation, have been clearly demonstrated, there are relatively few case-studies showing how observed historical interactions between vegetation communities and large herbivores are expressed in palaeoecological records. Dull (1999) attempted to do this by using radiometric dating to establish a chronology for a core, from which known ages of herbivore introductions/extirpations were identified within the stratigraphy and thereby compared against the pollen record. Unfortunately, due to the inherent uncertainties associated with age-depth models, this approach is less precise than the comparison of proxies in a stratigraphic sequence where leads/lags can be determined more clearly.

In this paper we examine the spores of dung fungi alongside pollen assemblages in a peat core taken from a subantarctic island in the southwest Pacific where the recent history of large herbivore introductions, their subsequent eradication less than 125 years later, and their effects on the vegetation are well-documented. Using ordination and changepoint analyses of the first detailed and radiocarbon dated palaeoecological record from this island, we aim to test how accurately the palaeoecological record reflects the true sequence of events, and thereby attempt to validate the approaches now being widely applied in Late Quaternary paleoecology.

2. Study site and methods

2.1. Study site

Our peat core (Landcare Research core X13/81a) was collected from behind the dunes at sea level on Sandy Bay, Enderby Island (50° 29′ 55.87″ S, 166° 17′ 2.26″ E) in December 2013 (Fig. 1) using a hand operated D-section corer. Enderby Island (700 ha) is the northernmost island of the subantarctic Auckland Island archipelago. Although there is a detailed post-glacial history of vegetation change from the Auckland Islands (McGlone et al., 2000, 2010; McGlone, 2002; Wilmshurst et al., 2015), the only pollen identified from Enderby Island includes spot samples from lake silts sandwiched between two possible Pleistocene-era tills (Fleming et al., 1976; McGlone, 2002). A midden containing stone tools and animal bones provides evidence for pre-European Polynesian settlement at Sandy Bay, but this was likely only of short duration (Anderson, 2005). Enderby Island was unsettled when it was first seen by Europeans in 1806. A number of shipwrecks and unsuccessful attempts at settling the island during the 19th Century saw a range of different mammal species being introduced (Taylor, 1971). The chronology of the mammalian herbivore introductions and eradications on Enderby Island is well documented (Taylor, 1971). Species introduced to the island included rabbits (*Oryctolagus cuniculus*), pigs (*Sus scrofa*), sheep (*Ovis aries*), cattle (*Bos taurus*) and goats (*Capra hircus*). Although 660 sheep were introduced to the island between 1850 and 1851 (Dingwall, 2009), rabbits and cattle had the longest persistence of any mammalian herbivores introduced to the island. Cattle (80 individuals) were introduced in 1850 (Dingwall, 2009) (although these only lasted a few years, and a persistent population of cattle were not introduced until 1894; Taylor, 1971) and a significant population of rabbits was first

established in 1865. The extermination of rabbits and cattle from Enderby Island for conservation purposes was completed in 1993 (Torr, 2002). Just prior to their extermination, rabbit densities of >35 individuals per hectare were recorded around Sandy Bay (Torr, 2002), and the cattle population consisted of 40—50 individuals, most of which were bulls (Department of Conservation (1998)). Rabbits and cattle had major impacts on the bird and vegetation communities at Sandy Bay, through processes including soil disturbance, grazing and destabilisation of the dunes, and these have been detailed by several authors during the 20th Century (e.g. Cockayne, 1904; Aston, 1912; Godley, 1965; Taylor, 1971). Moreover, the extermination of these mammals in 1993 led to a release of herbivory pressure and saw rapid changes in the vegetation communities at Sandy Bay (Torr, 2002).

2.2. Age-depth model

Subsamples of bulk peat (spanning 1 cm intervals) were taken from eight locations through the peat sequence and submitted to the Waikato Radiocarbon Dating Laboratory for accelerator mass spectrometry dating. Samples were prepared by washing in hot HCl, rinsing, then treated with multiple hot NaOH washes. The fraction that was insoluble in NaOH was again treated with hot HCl, filtered, rinsed and dried.

We created age-depth models for the Sandy Bay core using the P_sequence function of OxCal 4.2 (Bronk Ramsey, 2008). All modelled age ranges are reported in calibrated years AD. Radiocarbon ages were calibrated using the SHCal 13 calibration dataset (Hogg et al., 2013). Modern radiocarbon ages (i.e., post 1950 AD) were calibrated in Calibomb (http://calib.qub.ac.uk/CALIBomb; accessed Sept. 2015); using the SHCAL 13 and SHZ1-2 bomb extension zone options.

2.3. Palynology

Standard volumes of peat (1 mL) were taken from the peat core and processed by washing in hot KOH for 10 min followed by a wash in HCl, acetolysis, flotation of pollen and spores using lithium polytungstate (specific gravity 2.2), staining with fuchsin-red, and mounting on glass microscope slides in glycerol jelly. Samples were spiked with spores of exotic *Lycopodium* to allow pollen and spore concentrations to be quantified. A minimum of 200 pollen grains were identified on each slide (except for three slides with low concentration where a minimum of 80 grains were identified). Identifications were based on a reference collection of pollen grains made from herbarium specimens held at Landcare Research, Lincoln, New Zealand, and using pollen and spore identification keys (Large and Braggins, 1991; Moar, 1993). Pollen nomenclature follows Moar et al. (2011). The pollen concentrations in the Sandy Bay peat core varied markedly between the lower and upper portions of the sequence (≥ 56 and ≤ 54 cm). A minimum of 433,816 grains/mL was recorded before this zone, and maximum of 187,198 grains/mL afterwards. However, changes in pollen influx were ruled out as a cause because the composition of pollen assemblages did not vary dramatically across this zone. Accordingly, the most likely explanation of this change in pollen concentration is a change in deposition rate. Therefore, we created separate age-depth models for the bottom (using radiocarbon dates at 80 cm, 74 cm, 70 cm, 69 cm and 67 cm depths) and top (using radiocarbon dates at 56 cm, 30 cm and 16 cm, constrained by a collection year of 2013) of the sequence. The final age-depth model was created by linear interpolation between the modelled 95.4% confidence ranges for each dated horizon.

For charcoal analysis, standard volumes of peat (2.5 mL) were bleached and passed through 250 μm and 125 μm mesh sieves. The