



Using dung fungi to interpret decline and extinction of megaherbivores: problems and solutions



Chris N. Johnson^{a,*}, Susan Rule^b, Simon G. Haberle^b, Chris S.M. Turney^c,
A. Peter Kershaw^d, Barry W. Brook^a

^a University of Tasmania, School of Biological Sciences, Private Bag 55, Hobart, Tasmania 7001, Australia

^b The Australian National University, School of Culture, History and Language, Canberra, ACT 0200, Australia

^c Climate Change Research Centre, University of New South Wales, Sydney, NSW 2052, Australia

^d School of Geography & Environmental Science, Monash University, Clayton, Vic 3168, Australia

ARTICLE INFO

Article history:

Received 1 September 2014

Received in revised form

10 December 2014

Accepted 11 December 2014

Available online 14 January 2015

Keywords:

Megafaunal extinction

Trophic cascade

Pleistocene

Sporormiella

Podospora

Sordaria

Cercophora

Coniochaeta

ABSTRACT

Fungi which produce their spores on the dung of large herbivores show promise as indicators of the distribution and relative abundance of large herbivores in past environments. Recently, several studies have used counts of spores of such fungi, *Sporormiella* in particular, to resolve the timing and reveal the ecological consequences of extinction of Pleistocene megafauna. However, there are several problems in the interpretation of the dung-fungus proxy, relating mostly to taphonomic effects on spore accumulation. Here, we describe these problems and show how they can be solved, using new data from the Lynch's Crater site in northeastern Australia. Effects of variation in spore accumulation in relation to position in the sedimentary basin can be controlled by comparing cores from different locations; temporal variation in spore accumulation rates can be attributed to changes in herbivore populations, as distinct from time-varying taphonomic effects, by comparing trends in fungi exclusively associated with herbivore dung to trends for fungi that also sporulate on other substrates; effects of changing vegetation composition can be removed by measuring spore influx rates rather than expressing counts relative to the pollen sum. At Lynch's Crater, these approaches increase our confidence that a decline in dung fungi at ~40 ka indicates an unprecedented drop in biomass of large herbivores. We also show that before this decline, the biomass of large herbivores at this site was evidently similar to that in North America and western Europe.

Crown Copyright © 2014 Published by Elsevier Ltd. All rights reserved.

1. Introduction

During the late Quaternary, megafaunal species disappeared from most of the world's terrestrial ecosystems (Koch and Barnosky, 2006). These extinctions caused large reductions in biomass of vertebrate herbivores (Johnson, 2006; Barnosky, 2008). In turn, these reductions in herbivory might have triggered cascading effects on ecosystem structure and function, and fire behaviour (Johnson, 2009; Bond, 2010). However, understanding of the causes and environmental effects of the extinction of wild megaherbivores is strongly contested. One view is that these extinctions were caused by the arrival of humans both on continents and large islands. If so, major environmental changes might have

followed in their wake, as vegetation responded to reduced herbivory (Johnson, 2009). Others have argued that megafaunal extinctions were driven by climate-induced environmental change (Wroe et al., 2013). In that case the large-scale loss of herbivores should have followed vegetation change and would probably have been the culmination of gradual declines in abundance, and the impacts of extinction on ecosystem processes would have been far less significant.

Given that we are dealing with ecological events from prehistory, testing these contested scenarios depends crucially on our ability to reconstruct the time course of changes in megafaunal abundance and match these dynamics to other environmental trends and events. Chronologies of megafaunal extinction are mostly based on last-appearance dates of fossil and sub-fossil remains of the extinct animals, but inferences made directly from this evidence have serious limitations. Because fossils are so rare, and because their probability of preservation depends on many physical

* Corresponding author. Tel.: +61 (0)3 6226 6634.

E-mail address: c.n.johnson@utas.edu.au (C.N. Johnson).

factors unrelated to animal abundance, fossil data generally allow only the most tenuous conclusions about changes in abundance leading to extinction. The rarity of preserved and datable remains also means that the fossil record is discontinuous, containing many spatial and temporal gaps that make it difficult to infer time of extinction for species with sparse fossil data (Bradshaw et al., 2012; Alroy, 2014), or to test if extinction was synchronized among different species or across geographically separated sites (Signor and Lipps, 1982; Johnson et al., 2013). These problems mean that in most cases, chronologies based on fossil data cannot be aligned precisely with other higher-resolution records of environmental change such as ice or sediment cores.

Recently, there has been increasing interest in using spores of coprophilous fungi (hereafter, 'dung fungi') as a proxy indication of the past distribution and abundance of large vertebrate herbivores (Davis, 1987; Davis and Shafer, 2006; Baker et al., 2013). These fungi sporulate on the dung of vertebrate herbivores. Their spores may be ingested by herbivores along with vegetation, to pass through the animal's digestive tract and complete the fungus' life cycle, but many more are released into the environment and may accumulate in sediments (Feranec et al., 2011; Baker et al., 2013). Dung fungi have several useful features as proxies for herbivore activity.

First, their spores are abundant and are continually generated through the life of the animal hosting the fungi. Therefore, they provide what is effectively a continuous signal of herbivore presence. Second, spore production should increase proportionally with biomass of dung, which in turn reflects abundance and biomass of dung-producing herbivores. It follows that changes in spore counts should indicate variation in herbivore biomass (although the quantitative relationship between spore counts and absolute herbivore biomass is unknown). Several studies have demonstrated positive relationships between abundance of spores of dung fungi and local abundance of large herbivores, such as sheep, deer, cattle and bison, in contemporary settings (Davis and Shafer, 2006; Raper and Bush, 2009; Wood et al., 2011; Parker and Williams, 2012; Etienne et al., 2013; Gill et al., 2013). Third, many taxa of obligately coprophilous fungi have cosmopolitan distributions and occur in many herbivore species. This means the dung-fungus proxy should be useful in many different environments and indicate total activity of vertebrate herbivores, which is a useful quantity for interpretation of herbivore impact on vegetation. Fourth, although dung fungi are associated with small as well as large vertebrate herbivores, large herbivores evidently make proportionally greater contributions to the production of spores (Feranec et al., 2011; Gill et al., 2013). There could be several reasons for this: being bulk feeders on low-quality vegetation, large herbivores typically have large gut capacity relative to body size and produce large volumes of dung; they also produce large dung boluses, which tend to dry out and break down more slowly than the dung of small herbivores, and might therefore better accommodate the life cycles of dung fungi. The dung fungus proxy is therefore particularly valuable for tracking changes in populations of megaherbivores and larger domestic livestock. Finally, spores of dung fungi disperse locally and accumulate in sediments that also preserve other environmental proxies, especially pollen grains to indicate dominant vegetation types and charcoal particles as indicators of fire activity. The co-occurrence of these diverse ecological indicators means that records of herbivore biomass can be aligned exactly with changes in vegetation, fire, and other states and processes indicated by the composition of sediments (Gill et al., 2012), and strong inferences can be made even when absolute chronologies are imprecise (Rule et al., 2012). In short, all of these records can be analysed simultaneously at fine temporal resolutions relevant to the operation of ecological processes, provided that sediments can be sampled at sufficiently

high density and that stratigraphic integrity of the enclosing sediments remains intact.

For these reasons, spores of dung fungi are becoming widely used to interpret dynamics of mega-herbivores in the late Quaternary (Davis, 1987; Davis and Shafer, 2006; Jeffers et al., 2011, 2012; Baker et al., 2013), and to reconstruct changes in the densities and distribution of domestic livestock during the Holocene (Mazier et al., 2009; Cugny et al., 2010; Schofield and Edwards, 2011). Studies using the dung fungus *Sporormiella* in Madagascar, New Zealand, North America and Australia have been especially valuable in revealing the fine temporal structure of megafaunal extinction in relation to other environmental shifts, and so indicating mechanisms that might (or could not) have been involved (Burney et al., 2003; Robinson et al., 2005; Gill et al., 2009, 2012; Wood et al., 2011; Rule et al., 2012). For example, the studies in the north-eastern USA (Robinson et al., 2005; Gill et al., 2009, 2012) and at Lynch's Crater in northeast Australia (Rule et al., 2012) suggest that declines of large herbivores were completed within periods of approximately one thousand years, and were closely followed—rather than preceded—by elevated fire and shifts in vegetation type. The Lynch's Crater study in Australia also showed that before its abrupt decline about 40,000 years ago, herbivore biomass had been unaffected by large shifts in climate through the Last Glacial cycle (Rule et al., 2012). If correct, these results make it clear that mega-herbivore extinction was not caused by environmental change, but that the consequent loss of large-herbivore biomass and associated cropping and trampling probably triggered major ecosystem shifts, including increased fire and alteration of vegetation state. However, there remain unresolved problems in interpretation of the dung-fungus proxy, which must be addressed before these interpretations can be accepted.

2. Problems in using the dung-fungus proxy

A primary challenge is to clarify the taxonomy of dung fungi, and resolve their biological affinities to make it clear which taxa are dependent solely on dung—and therefore are useful specific indicators of large-herbivore biomass, independent of other environmental factors—and which others also use substrates other than dung. Baker et al. (2013) show that there is a set of fungal taxa, identifiable by spore type, that occur only on the dung of vertebrate herbivores and which therefore ought to be useful in tracking large-herbivore populations. However, interpretation of the relationship of these fungi to herbivore abundance and biomass is complicated by further problems. These relate to taphonomy, especially the potentially confounding effects of hydrological conditions, and to the use of relative rather than absolute measures to describe variation in abundance of dung fungi, as explained below.

Spores of dung fungi are initially discharged over short distances, typically two metres or less (Baker et al., 2013). In some taxa, such as *Sporormiella*, the spores stick together in gelatinous masses and adhere to vegetation. This promotes ingestion of spores by herbivores, but reduces secondary transport. Gill et al. (2013) in North America show that concentrations of *Sporormiella* spores are most closely related to activity of bison over distances of 25 m or less. Further, Wood and Wilmshurst (2012) argue that local moisture conditions affect spore production, because sporulation may be prevented either when dung dries out completely or is continuously saturated. These factors can cause high local and temporal variability in production and accumulation of spores for reasons unrelated to dung availability. Such effects ought to be reduced for spore counts from lake and wetland sediments, because transportation of spores by water and their deposition in lake basins would tend to even out fine-scale spatial heterogeneity in spore abundance in the source region. However, Baker et al. (2013) point

Download English Version:

<https://daneshyari.com/en/article/4735898>

Download Persian Version:

<https://daneshyari.com/article/4735898>

[Daneshyari.com](https://daneshyari.com)