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Do dung fungal spores make a good proxy for past distribution of large herbivores?

Ambroise G. Baker [a,*], Shonil A. Bhagwat [b], Katherine J. Willis [a,c]

[a] *Long-Term Ecology Laboratory, Biodiversity Institute, Oxford Martin School, Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS, United Kingdom*
[b] *School of Geography and the Environment, University of Oxford, Oxford OX1 3QY, United Kingdom*
[c] *Department of Biology, University of Bergen, N-5007 Bergen, Norway*

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ABSTRACT

The importance of herbivory as a long-term driver of ecosystem change is a topic that has been hotly debated over the past few years. An understanding of the interaction between herbivores and ecosystems is particularly important for conservation policies aimed at re-wilding. Dung fungal spores have been highlighted as an important potential proxy to reconstruct large herbivore densities across past landscapes. However, this proxy appears to have been used and interpreted in a variety of ways in addition to highly variable taxonomic identification of dung fungal spores. Here we review studies that have utilised fungal spore assemblages to assess past herbivore presence and test the validity of this method. We aim to determine whether there is a set of identifiable dung fungal spores that can unequivocally track variation of large herbivore activity through time and across regions. Our meta-analysis identifies: (1) spore types that are commonly found to be indicative of large herbivores and their geographical ranges, (2) linkages between these spores and their biological origin, and (3) the most appropriate quantitative method to express their abundance for comparisons through time and across sites.

1. Introduction

Large herbivores are increasingly accepted as playing an important role as ecosystem engineers across most of the Earth's biomes (Chase et al., 2000; Hopcraft et al., 2009; Estes et al., 2011; Griffiths et al., 2011). The disturbance regimes they create are often significant enough to modify vegetation structure and composition. Landscapes altered by domesticated and wild herbivores range from cultural landscapes such as the New Forest in the UK (Putman, 1986; Tubbs, 1986, 2001) through to wilderness area like the Serengeti in Tanzania (Sinclair and Norton-Griffiths, 1979; Sinclair and Arcese, 1995). In these herbivore-dominated ecosystems, grazing can represent one of the main drivers of disturbance along with fire regimes, human activity and climatic variability (Jeffers et al., 2012).

The past occurrence of large vertebrate herbivores and their impact on the Quaternary landscape has been traditionally studied on the basis of sub-fossilised bones recovered from places such as archaeological sites, caves, lacustrine and fluvial sediments. However these remains provide little opportunity to estimate distribution range, population size, or dates of exact colonisation/extinction events.

Obligate coprophilous fungi (hereafter referred to as dung fungi) provide a promising additional proxy to assess the past presence of large herbivore populations. These fungi strictly rely on terrestrial warm-blooded vertebrate such as elephants, deer, rabbits and larger birds to complete their life cycle. In fact their spores are ingested by herbivores while feeding on plants, survive digestion and then germinate in the dung where they are deposited (for dung fungi ecology and biology, see Bell, 1983, 2005; Dix and Webster, 1995). Fruiting bodies are produced after few to many days and, from those, spores are discharged to a distance of up to two metres (e.g. Ingold, 1971; Yafetto et al., 2008). Hence the underlying assumption is that the larger the herbivore biomass in an ecosystem, the larger is the fungal biomass, and the greater the quantity of spores produced. Following this line of reasoning, the abundance of these spores in Quaternary sediments is interpreted to infer the presence and abundance of large herbivores in the past (Davis, 1987; van Geel et al., 2003; Davis and Shafer, 2006). In fact, the utilisation of non-pollen palynomorphs such as dung fungal

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* Corresponding author. Tel.: +44 1865 2 81319.
E-mail address: ambroise.baker@zoo.ox.ac.uk (A.G. Baker).

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spores is a valuable complement to pollen analysis because fungal, algal, insect and other biological remains often provide proxies for environmental variables for which pollen alone is not informative (van Geel, 2001).

Dung spore presence, absence or abundance in sedimentary sequences have been used to determine dramatic wild herbivore population crashes during the late Quaternary in Madagascar (Burney et al., 2003), North America (Robinson et al., 2005; Davis and Shafer, 2006; Gill et al., 2009), New Zealand (Wood et al., 2011) and Australia (Rule et al., 2012). Fluctuations in domesticated herbivore populations have also been noted using dung spores in sedimentary sequences from the historic period in North America (Davis and Shafer, 2006) and Europe (e.g. Mazier et al., 2009).

In spite of an increasing number of studies (Fig. 1), there remain some concerns with regards to the methodology (see Raper and Bush, 2009; Feranec et al., 2011; Wood and Wilmshurst, 2011). In particular the potential weaknesses that have been highlighted include: complications related to local hydrology, problems with identification, lack of quantitative reconstructions and lack of understanding of the taphonomy (deposition and preservation in different environments). Despite these weaknesses, in practice it has been possible to demonstrate the worldwide impact of herbivory in ecosystems (Burney et al., 2003; Gill et al., 2009; Rule et al., 2012), supporting previous research in conservation biology, grazing ecology and palaeobiology (e.g. Owen-Smith, 1988; Vera, 2000; Johnson, 2009).

Building on previous research, here we review studies that have utilised dung fungal spore assemblages to assess past herbivore presence or those that have tested the validity of this method. Our aim was to determine whether there is a set of identifiable dung fungal spores that can unequivocally track variation of large herbivore activity through time and across regions. Specifically, we review (1) spore types that have been found, in practice, to be indicative of large herbivores and their geographical ranges, (2) linkages between these spores and their biological origin, and (3) the most appropriate quantitative method to express their abundance for comparisons through time and between sites. We then discuss the future potential of this method for reconstruction of large herbivore past populations.

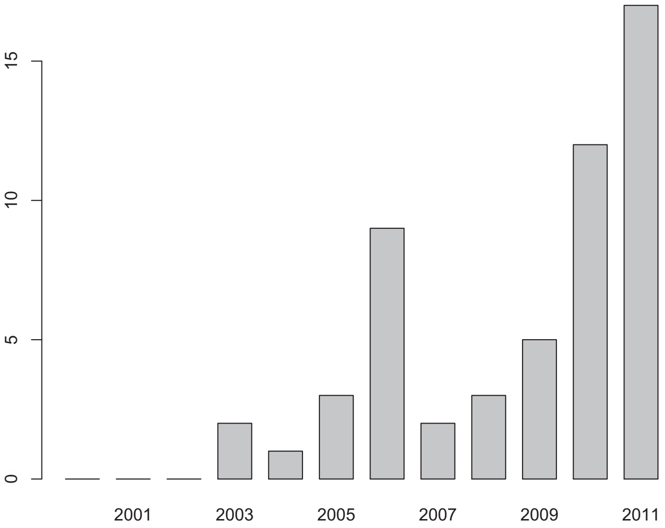

Fig. 1. Number of published articles using coprophilous organism as a proxy for large herbivore. Publications selected from Reuters' ISI Web of knowledge using the key words "coprophilous" or "*Sporormiella*".

2. Which spores provide unequivocal evidence of the presence of large herbivores?

2.1. What fungal spore types are commonly recorded, on what basis and where

Spore types that are found to be indicative of large herbivores are listed in Table 1 and their geographical ranges are mapped in Fig. 2.

A total of 33 fungal spore types identified in the published palynological literature are related to large herbivore activity (Table 1). This list includes types that have been identified as confirmed bioindicators (e.g. *Sporormiella*-type and *Sordaria*-type) and potential indicators in need of further research (e.g. *Arnium*-type and *Trichodelitschia*-type).

Many of those types have been the subject of validation studies (e.g. Davis and Shafer, 2006; Raper and Bush, 2009; Cugny et al., 2010). These studies seek empirical evidence from modern and ancient sediments that show whether a spore type is consistently found in greater abundances in situations where herbivory is also known to be higher. Such evidence is necessary in order to demonstrate the applicability of dung fungal spores to palaeoenvironmental reconstructions. However, they do not provide any information regarding the process explaining the relationship between a spore type and herbivory. In addition, they rely on an accurate measurement of herbivore densities and on quantitative estimate of the distance fungal spores can travel.

Spore types supported by empirical evidence are listed in Table 2. Six of these fungal types were found several times to indicate herbivore activity. Of these, *Sporormiella*- and *Apiosordaria*-type show consistently positive evidence. For the remaining four types, *Sordaria*- and *Podospora*-, *Chaetomium*- and *Cercophora*-type, the positive association with herbivory has been questioned on at least one occasion each (van Geel et al., 2003; Blackford and Innes, 2006; van Geel and Aptroot, 2006; Cugny et al., 2010; Ejarque et al., 2011; Parker and Williams, 2011).

Other spore types that are promising, but whose occurrence in sediments has been studied even less well are: *Coniochaeta*-, *Arnium*-, *Delitschia*-, *Trichodelitschia*-, *Microthyrium*-, *Anthostomella fuegiana*-type and a series of unidentified types (see Table 2). These fungal spores were not linked to herbivory in more than one study and therefore need further research. Other spore types were not reported to have been associated with high herbivore densities. Noteworthy, however, are the identifiable eggs of various parasitic worms regularly observed in archaeological deposits (see references in Chaves et al., 2006) and in particular those of *Trichuris ovis*, recorded by Ejarque et al. (2011) within a sedimentary archive. Although this type of microfossil deserves to be the subject of further research, it is beyond the scope of this paper.

Validation studies that aim to establish association between fungal spores and herbivores are mapped on Fig. 2A. They are mostly restricted to North America and Europe, and one to New Zealand. This strongly contrasts with the worldwide distribution of palaeoenvironmental reconstructions using these same spore types (Fig. 2B). In fact, the map of Fig. 2B shows that fungal spores have been identified in sedimentary archives and interpreted as indicative of herbivory from most biomes and continents on Earth, from the tropics (e.g. Mumbi et al., 2008) to the arctic (e.g. Gauthier et al., 2010). Despite this variety of locations, North America and Europe show a much greater density of studies than the rest of the World. In particular, not a single published dung fungal spore record was found from Southern Asia.

In addition, the number of spore types assumed to indicate large herbivore activity varies greatly between palaeoecological studies and regions of the world. Fig. 2B shows that records from the United