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REVIEW

Dung fungi as a proxy for megaherbivores: opportunities and limitations for archaeological applications

Angelina G. Perrotti[1] · **Eline van Asperen**[2,3]

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Abstract

The use of spores of coprophilous fungi from sedimentary sequences as proxy evidence for large herbivore abundance has garnered pronounced attention and scrutiny over the past three decades. In response to the rapid rate at which new information is being discovered on this topic, this paper presents a brief review of the archaeological applications so far, and outlines opportunities and limitations of using *Sporormiella* as a proxy for herbivore abundance. Specific archaeological uses of this proxy include understanding megaherbivore extinctions and human land use patterns such as pastoralism and agriculture. We analyse how dung fungal records are formed and review the mycological literature to outline factors affecting spore reproduction and preservation. These include how strongly each commonly used dung fungal taxon relies on dung as a substrate and environmental factors affecting dung fungal reproduction and coprophilous fungi deposition. Certain laboratory preparation techniques adversely affect spore representation on pollen slides. The methods of analysis and quantification of spore records also impact our understanding. We describe good practice to increase precision of analytical methods. Due to limitations imposed by some of these factors, it is possible that an absence of dung fungi from a palaeoecological record does not imply an absence of herbivores. However, consideration of these factors and inclusion of as wide a range of coprophilous spore records as possible increases the reliability of such inferences.

Keywords Coprophilous fungi · Sporormiella · Palynology · Megafaunal extinction · Pastoral activity · NPP

Introduction

The use of *Sporormiella* spores from sedimentary sequences as a proxy for large herbivore abundance has garnered pronounced attention and scrutiny over the past three decades. Since it was first proposed as a proxy for Pleistocene megaherbivore abundance in the 1980s (Davis 1987), increasing research has been devoted to developing sampling, recovery and quantification techniques, as well as understanding the applications and limitations of this method. In response to the rapid rate at which new information is being discovered on this topic, this paper presents a brief review of the archaeological applications so far, and outlines opportunities and limitations of using *Sporormiella* as a proxy for (mega) herbivore abundance.

Sporormiella is one of a number of genera of coprophilous fungi, also known as dung fungi. These are fungi that show a strong preference for (mainly herbivore) dung as their primary substrate. *Sporormiella* is one of many organisms that participate in the breakdown of herbivore dung after it is evacuated. This fungus belongs to a group of most commonly used fungal indicators of herbivore abundance, Ascomycota, which reproduce on the dung 2–4 weeks after it is deposited (e.g. Harper and Webster 1964). There are some indications that the spores produced by *Sporormiella* and similar genera need to pass through the digestive tract of an herbivore in order to activate germination, but evidence for this is limited (Janczewski 1871; Massee and Salmon 1902; Krug et al. 2004). Regardless of these uncertainties, the abundance of *Sporormiella* spores in sedimentary sequences has been demonstrated repeatedly to reflect herbivore abundance in both

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✉ Angelina G. Perrotti
Angelina.perrotti@tamu.edu

[1] Department of Anthropology, Texas A&M University, 340 Spence St, College Station, TX 77840, USA

[2] Department of Biosciences, Durham University, Dawson Building, South Road, Durham DH1 3LE, UK

[3] Department of Anthropology, Durham University, Dawson Building, South Road, Durham DH1 3LE, UK

modern (e.g. Parker and Williams 2012; Gill et al. 2013; Baker et al. 2016; Raczka et al. 2016) and ancient settings (e.g. Davis 1987; Burney et al. 2003; Davis and Shafer 2006; Gill et al. 2009; Doyen and Etienne 2017).

Applications for archaeologists

Dung fungal records are important datasets for archaeologists because of the frequency of interactions between ancient people and large herbivores. *Sporormiella* continues to be used as a proxy to detect declines in late Pleistocene megaherbivore communities (e.g. Davis 1987; Gill et al. 2009; Gill 2014; Johnson et al. 2015; Graham et al. 2016; Perrotti 2018). The North American extinction of over 30 species of large mammals at the end of Pleistocene is of particular interest to archaeologists because it roughly coincides with the earliest human colonization of the continent. The cause of these extinctions remains the subject of intense debate. Disagreement concerns the relative impacts of human hunting (Martin 1984; Alroy 2001; Surovell and Waguespack 2009; Frank et al. 2015; Surovell et al. 2016), climate change (Guthrie 1984; Grayson and Meltzer 2003), disease (MacPhee 1997) and a potential extraterrestrial impact (Firestone et al. 2007) on Pleistocene megafauna.

Because faunal remains are sparse and can be difficult to date, it is hard to establish extinction dates reliably. The use of the *Sporormiella* proxy allows researchers to fill in geographic gaps where there may be no dateable fauna. Since *Sporormiella* spores occur in the same deposits as pollen and plant macrofossils, patterns in their abundance can be linked directly with trends and changes in the vegetation record, as well as with absolute dates obtained for these deposits. The fungus has been found in sedimentary records across North America, and is aiding in the understanding of the timing and process of megafaunal extinction, and its effects on vegetation communities (Gill et al. 2009; Gill 2014; Perrotti 2018).

If humans are unequivocally tied to megaherbivore extinction, it is possible that the timing of local extinctions could be used as a signal of human colonization in different regions, particularly when complemented with archaeological evidence. Studies incorporating *Sporormiella* in western North America are rare, but declines in *Sporormiella* coincide with generally accepted dates of human colonization in the northeastern United States (Davis and Shafer 2006; Gill et al. 2009; Gill 2014). However, the *Sporormiella* record and archaeological evidence from Page-Ladson, Florida (Halligan et al. 2016; Perrotti 2018) indicate that humans and megaherbivores coexisted in the region for ~ 2,000 years. Fiedel (2018) suggests that *Sporormiella* may not be a reliable indicator of megaherbivore extinction in eastern North America because current *Sporormiella* records (i.e. Gill et al. 2009; Gill 2014) point to a decline in megaherbivores around 14,800 BP, while some mammoth remains in the region are dated to as late as ~ 12,000 BP. Furthermore, it is unclear whether absence of spores is equally informative as spore presence (e.g. see below for factors other than herbivore abundance influencing fungal growth, and thus, potential spore presence; see also Raper and Bush 2009; Jones et al. 2017). However, researchers using *Sporormiella* as a proxy for large herbivore abundance acknowledge that declines in *Sporormiella* do not necessarily indicate a complete extinction of all megaherbivores; but rather, a functional decline in grazing pressure that represents shrinking herbivore populations relegated to patchy environments prior to extinction (Gill et al. 2009, 2012). Nonetheless, because of the discrepancies between regions and the inconclusive evidence for a human driven extinction of North American megafauna, at present *Sporormiella* or other coprophilous fungi cannot be used as a proxy for human activity and migration in this region (Fiedel 2018).

Human colonization seems to coincide with a decline in coprophilous fungi in other parts of the globe, including Australia (Rule et al. 2012; van der Kaars et al. 2017), New Zealand (Wood et al. 2011) and Madagascar (Burney et al. 2003). In some cases, the initial fungal spore decline is followed by an increase after the introduction of domesticated animals (Burney et al. 2003; Davis and Shafer 2006; Graham et al. 2016) or other non-native herbivores (Wood et al. 2011).

Additionally, many archaeologists use *Sporormiella* and other coprophilous fungi as markers of pastoral and other human land use activities across Europe, Africa and Asia (van Geel et al. 2003; Miehe et al. 2009; Lehmkuhl et al. 2011; Felauer et al. 2012; Ahlborn et al. 2015; Shumilovskikh et al. 2016a, b, 2017; Ghosh et al. 2017; Szymanski 2017). Coprophilous ascomycetes other than *Sporormiella* have also been verified to reflect pastoral activities in mountainous, pasture-woodland landscapes (Cugny et al. 2010), in upland grasslands and bogs (Feeser and O'Connell 2010) and in boreal forest (Kamerling et al. 2017). Evidence of direct domestication of herbivores in the pre-Columbian Americas is rare. However, dung fungi could potentially be used to provide more information about communal hunting in the Great Basin region of North America, where pronghorn and mountain sheep were rounded up and potentially kept in pens constructed of stone and brush (Hockett 2005; Hockett and Murphy 2009).

Opportunities and limitations

Dung fungus reproduction

Interpreting the abundance of spores of coprophilous fungi in a sedimentary record requires an understanding of the different factors influencing fungal reproduction. *Sporormiella* is strongly coprophilous and is observed almost entirely in association with herbivore dung (Doveri 2007, p 613). Gelorini et al. (2011) emphasized that only genera that are obligate to herbivore dung, such as *Sporormiella* and *Podospora*, could serve as a reliable signal of herbivore presence. However, the precise lifecycle and substrate preferences remain ambiguous for even the most commonly noted spores of coprophilous fungi (Table 1). *Apiosordaria* and *Coniochaeta* are two taxa that are often taken to indicate herbivore presence but have recently been found to be poor indicators of herbivore abundance (Baker et al. 2013; Doyen and Etienne 2017). This is not surprising, since the mycological literature indicates they primarily grow in soil (Bell 1983, p 33; Krug et al. 1983; Doveri 2007, p 760; Guarro et al. 2012, pp 47–51, 118). Other commonly observed semi-coprophilous ascomycetes such as *Cercophora* and *Sordaria* are also found on other organic substrates, such as plant debris, decaying wood, or soil, with some frequency (Bell 1983, pp 36, 40; Hanlin 1990; Doveri 2007, pp 826, 847; Kruys and Wedin 2009; Guarro et al. 2012, pp 111, 383). Newcombe et al. (2016) found evidence that *Sordaria, Preussia* and even *Sporormiella* may be epiphytic and concluded that the presence of these spores is not undisputable evidence of herbivore abundance. Because herbivore dung consists largely of partly digested plant remains, the ability of some dung fungi to opportunistically grow on plants is not surprising. However, coprophilous fungal taxa *Sporormiella* and *Podospora*, as well as a number of less common taxa such as *Ascodesmis, Arnium, Bombardioidea, Delitschia* and *Trichodelitschia*, have a strong preference for dung as a substrate and therefore typically reflect the presence of large herbivores. Despite its strong preference for dung as a substrate, caution still must be applied when observing *Sporormiella* in sediment samples, as *Sporormiella* spores can be indistinguishable from the spores of *Preussia* (Cain 1961; Barr 2000; Kruys and Wedin 2009). Though these two fungi are closely related, only *Sporormiella* depends on dung as a growth substrate (von Arx and van der Aa 1987).

Even if spores of coprophilous fungi may not necessarily have to pass through the gut of an herbivore to complete reproduction, many fungal spores are consumed and move through the digestive system. After consumption by an herbivore, spores of coprophilous fungi are expelled with the dung after which they germinate and propel spores away from the dung. The spores typically adhere to nearby vegetation and are inadvertently consumed along with the vegetation. After passing through the digestive tract, the spores are expelled along with the dung to complete the lifecycle again (Fig. 1).

Extensive research exists on the fungal community composition of different types of herbivore dung (e.g. Wicklow et al. 1980; Piontelli et al. 1981; Ebersohn and Eicker 1992; Richardson 2001; Nyberg and Persson 2002; Mungai et al. 2011, 2012; van Asperen 2017). Often, a few species are abundant, alongside a large number of rare species (Ebersohn and Eicker 1992; Richardson 2001; Nyberg and Persson 2002; Krug et al. 2004). Most coprophilous fungi occur on a wide range of dung types (Richardson 1972, 2001; Angel and Wicklow 1983), but many genera show a

Table 1 Substrates of commonly encountered spores of coprophilous fungi in sedimentary sequences

Genus	Substrate
Ascodesmis	Primarily herbivore and carnivore dung; occasionally soil or decaying vegetation (Doveri 2007, p 492; Guarro et al. 2012, p 79)
Apiosordaria	Primarily soil; occasionally dung (Krug et al. 1983; Guarro et al. 2012, pp 47–51)
Arnium	Primarily dung; occasionally soil (Bell 1983, p 46; Doveri 2007, p 872; Guarro et al. 2012, p 59)
Bombardioidea	Exclusively dung (Bell 1983, p 49; Doveri 2007, p 870)
Cercophora	Primarily decaying wood and vegetation; occasionally charcoal, soil and dung (Bell 1983, p 40; Doveri 2007, p 847; Hanlin 1990, pp 46–47; Guarro et al. 2012, p 111)
Chaetomium	Primarily decaying vegetation; also dung, soil, and a range of other organic substrates (Bell 1983, p 33; Doveri 2007, p 760; Guarro et al. 2012, p 118)
Coniochaeta	Primarily soil; also dung and decaying wood (Bell 1983, p 39; Hanlin 1990; Doveri 2007, p 810; Guarro et al. 2012, pp 132–142)
Delitschia	Almost exclusively herbivore dung; occasionally soil and decaying wood (Bell 1983, p 51; Guarro et al. 2012, p 159)
Podospora	Almost exclusively herbivore dung; occasionally soil (Bell 1983, p 14; Doveri 2007, p 905; Guarro et al. 2012, p 340; Schlütz and Shumilovskikh 2017)
Sordaria	Almost exclusively herbivore and omnivore dung; occasionally soil or vegetation (Bell 1983, p 36; Doveri 2007, p 826; Guarro et al. 2012, p 383)
Sporormiella	Mostly (75%) herbivore dung; occasionally decaying wood or soil (Doveri 2007, p 613); NB closely similar to the soil-inhabiting genus *Preussia*
Trichodelitschia	Exclusively dung (Bell 1983, p 51)

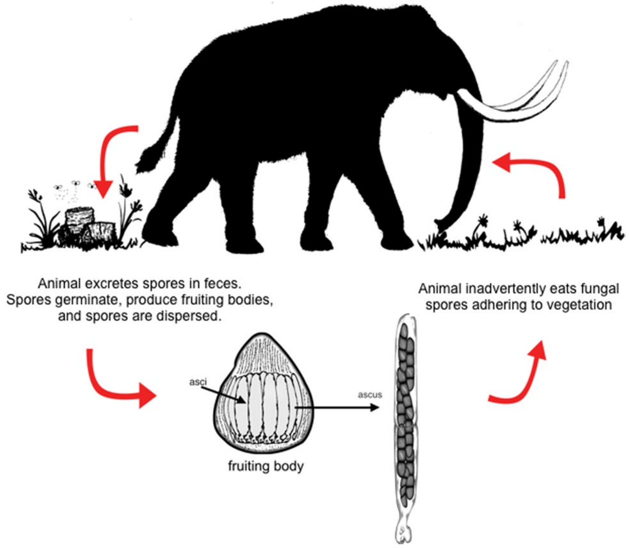

Fig. 1 A generalized depiction of the lifecycle of *Sporormiella*. The spores are inadvertently consumed and pass through the herbivore's gut and are then discharged as a part of the faeces. Although some spores may be carried away by water or work their way into terrestrial sediments, many germinate in the faeces and the mycelium produces the perithecia (or fruiting bodies). These perithecia contain the individual ascospores. Figure courtesy of Chase W. Beck

preference for certain types of dung. While these genera also occur on other dung types, they occur more often and more abundantly on their preferred dung type (Lundqvist 1972; Richardson 1972, 2001; Bell 2005; van Asperen 2017).

Spores of coprophilous fungi are typically a very local indicator of herbivore dung (Graf and Chmura 2006) due to their short dispersal distances (Ingold and Hadland 1959; Ingold 1961; Trail 2007; Yafetto et al. 2008). They can become airborne, but are likely deposited within 100 m of the dung source (Gill et al. 2013). However, it is possible to get a more regional assemblage of dung fungi if water is present because spores can enter a river, pond, or lake via slopewash. The spores tend to settle out fairly rapidly (Raczka et al. 2016), so spore concentration declines toward the centre of lakes and ponds (Raper and Bush 2009). This discrepancy could be addressed by analysing multiple cores from various locations within the same site. Overall, spores within smaller bodies of water are more likely to reflect herbivore abundance (Johnson et al. 2015).

Environmental factors

Dung fungi have species or genera-specific responses to microenvironmental factors that affect the success of reproduction (Dix and Webster 1995). These species-specific responses to environmental changes could potentially encourage or limit growth of a particular fungal type, which leads to a fluctuation in spore abundance that is not actually representative of megafaunal activity. In part, this issue can be ameliorated by completing a comprehensive palynological study, including multiple coprophilous fungal taxa.

Presence, abundance and succession of specific fungal genera and species on dung incubated in the laboratory is known to differ from that on dung in field conditions (Harper and Webster 1964; Angel and Wicklow 1983; Richardson 2001). Laboratory conditions are highly artificial, with relatively constant temperatures and humidity. In contrast, under field conditions, temperatures are generally lower and display daily fluctuations, and waterlogging and precipitation vary in frequency and intensity. Although the growth of dung fungi in the laboratory cannot be used as a direct analogue to fungal growth in nature, research suggests that coprophilous ascomycetes are not as successful when temperature or relative humidity becomes too high or too low (Asina et al. 1977; Kuthubutheen and Webster 1986a). The effects of low relative humidity can be compounded by competition between ascomycetes (Kuthubutheen and Webster 1986b). Soil hydrology is also likely to affect spore reproduction (Wood and Wilmshurst 2013).

Although at varying levels of success, spores can often germinate across a wide range of temperatures. For example, Asina et al. (1977) found that three *Sporormiella* species could germinate at temperatures within a range of 10–30 °C, although the range of temperatures at which germination was maximal was smaller (a range of 5–15 °C). Dung fungal development is generally slower at lower temperatures, and although the abundant genera tend to be present across a range of temperatures, they produce fewer fruiting bodies at lower temperatures (Wicklow and Moore 1974; Krug et al. 2004). However, dung could provide warmer conditions than are prevalent in the surrounding environment as long as decomposing organisms are still capable of growth (Webster 1970; Lundqvist 1972).

Most dung fungi germinate, grow and produce fruiting bodies more slowly when water availability is low, and fruit for a shorter period of time, although some species produce fruiting bodies more quickly (Dickinson and Underhay 1977; Harrower and Nagy 1979; Kuthubutheen and Webster 1986a, b). Dickinson and Underhay (1977) suggest that the rapid decline in water content common in the warm and/or dry season soon inhibits fungal growth, whereas in the cold and/or wet season, growth may be limited or slowed by high water content. Kuthubutheen and Webster (1986b) found that *Sporormiella* was the most tolerant of low water availability of the genera they tested, which included *Podospora*. The interaction between the effects of temperature and moisture availability on dung fungal growth leads to higher dung fungal diversity during the wetter, cooler season in temperate latitudes than in the warmer, drier season (Wicklow 1992; Richardson 2001; Krug et al. 2004; van Asperen 2017). Although winter temperatures are lower, this temperature drop presents a stress factor which may have the effect of reducing the reproductive fitness of dominant species, thereby releasing less-specialized, more stress-tolerant species. In contrast, in summer the primary factor is the lower substrate humidity negatively affecting germination rate (Harrower and Nagy 1979; Kuthubutheen and Webster 1986a, b).

Dung type and animal behaviour may also affect the durability of the dung resource. Some animals defecate in latrines to which they return regularly, leading to large accumulations of dung material. Larger dung pats are less susceptible to desiccation, while clusters of pellets create a wider range of microhabitats but are more prone to desiccation (Beynon 2012). Salt from urine may also inhibit sporulation (Schlütz and Shumilovskikh 2017). Furthermore, dietary diversity and the quality of the vegetation consumed also leads to dung with different characteristics. For example, moisture and nitrogen content of dung of a range of herbivores in South Africa was found to be correlated with the amount of precipitation in the 2–6 weeks before sample collection (Edwards 1991). Dung from cattle feeding on the new growth of grass in spring in temperate climates generally has a higher moisture content than later in the growth season (Greenham 1972; van Asperen personal observation).

Another factor that may reduce the number of fruiting bodies produced and the duration of fruiting is competition between ascomycetes (Lussenhop and Wicklow 1985; Kuthubutheen and Webster 1986b). *Sporormiella* species often appear relatively late in the incubation period (Angel and Wicklow 1983), so perhaps they are more easily outcompeted by genera that appear earlier when environmental factors favour those genera.

In addition to direct effects of environmental factors, in temperate latitudes the activity of other dung-inhabiting species, in particular dung beetles (both adults and larvae) and fly larvae, is much higher in wet and warm conditions than in dry or cool conditions (Davis 1994). In North Carolina, beetle activity greatly diminished at temperatures below 10 °C, as well as in dry, hot conditions or very wet spells (Bertone et al. 2005). Further north, in the more continental climates of Alberta and Michigan, beetle activity extended from early March to late November, with the main period of activity ranging from May to July (Floate and Gill 1998; Kadiri et al. 2014; Wassmer 2014).

Besides potential direct consumption of dung fungi, the grazing activity of these insects has several adverse effects on dung fungal growth: it reduces the amount of dung available for growth, it disrupts fungal hyphae, and it fragments the dung (Lussenhop et al. 1980; Wicklow and Yocom 1982). Fragmentation makes the dung more susceptible to moisture loss, and also removes the competitive advantage of fungal hyphal growth compared to bacterial growth (Lussenhop et al. 1980). Lussenhop et al. (1980) found that the presence of dung beetles reduced dung fungal hyphal density, especially at lower moisture content, but this did not lead to lower rates of fruiting and increased dung fungal diversity, possibly by dispersing the fungi more widely. Wicklow and Yocom (1982) observed that the presence of fly larvae reduced the species diversity of dung fungi. However, they note that *Sporormiella* abundance was not significantly affected, whereas there was a small negative effect on *Podospora* and *Sordaria*. In another study, species diversity was not affected, but there was a highly significant 68% reduction in spore production in the presence of fly larvae (Lussenhop and Wicklow 1985). A study in a savanna environment in Nigeria found that during the dry season, cattle dung was broken down by insects (primarily termites), whereas in the wet season, when termites were absent, dung breakdown was almost entirely due to fungal activity (Omaliko 1981).

Incorporation of fungal spores into sedimentary records

Local hydrology has the potential to produce fluctuations in a spore record that are not representative of herbivore abundance at the site. Wood and Wilmshurst (2013) demonstrated that spore fluctuations can correlate with changes in local hydrology. However, these correlations were not consistent. Two bogs demonstrated an increase in *Sporormiella* when water levels were at their peak, while one bog exhibited an increase in *Sporormiella* while water levels were lower than usual. Because the apparent correlations are not consistent between the sites, it is possible that the changes in local hydrology could be affecting herbivore behaviour. Depending on local conditions, animals could be preferentially utilizing the site based on water availability, or in contrast may be avoiding it when water levels are too high due to decreased ground stability. Similarly, Ponel et al. (2011) interpreted the coprophilous fungi record at a site in the French Alps as reflecting taphonomic processes. Due to hydrological factors, spores of coprophilous fungi were almost completely absent in the lower, lacustrine part of the record, whilst the presence of dung was attested by an abundance of dung beetle remains. In contrast, spores of coprophilous fungi became more abundant and dung beetles declined as the lake infilled and transitioned into a peat bog, as herbivores were able to graze within the bog.

Rainfall and the degree of storminess at a site can also affect a dung fungal record. Spores can be flushed into waterways, and if the faecal material is washed away soon after it is deposited, the fungus may not have sufficient time to reproduce and deposit higher numbers of fungal spores into a record. Finally, high energy depositional environments could potentially transport spores further than lower energy systems. In these types of environments, the fungal spore record could be more regional than expected, given the local nature of spore deposition. However, to date there has been little research into the role of these factors in the deposition of spores of coprophilous fungi in sedimentary records.

Laboratory recovery

Spores of coprophilous fungi and other non-pollen palynomorphs are generally extracted from palaeoecological samples along with pollen, usually using the 'standard' pollen preparation method (Fægri and Iversen 1989; Moore et al. 1991). However, a range of alternative preparation techniques are also available. Several studies have tested the effect of a number of chemicals and preparation techniques on the survival and preservation of fungal remains.

Clarke (1994) processed samples from a variety of substrates with three different techniques:

a. Boiling in KOH (potassium hydroxide), sieving (150 µm mesh), HF (hydrofluoric acid), acetolysis, mounting using TBA (tertiary butyl alcohol) (similar to the 'standard' pollen preparation method; Fægri and Iversen 1989; Moore et al. 1991);
b. boiling in NH_4OH (ammonium hydroxide), sieving (150 and 10 µm mesh), swirling, mounting using TBA;
c. boiling in KOH, sieving (150 µm mesh), heavy liquid separation with $ZnCl_2$ (zinc chloride), mounting using TBA.

Her results indicated that small round to oval fungal spores behave in a similar way as pollen in terms of survival. Treatment A led to a loss of large, buoyant forms, whilst these were the only forms consistently present in samples treated with method B. Thick-walled forms were lost in treatment C. None of the treatments led to significant preservation issues.

In a study focusing specifically on spores of coprophilous fungi recovered from dung samples incubated in the lab, van Asperen et al. (2016) tested five preparation methods:

A. Boiling in NaOH (sodium hydroxide), sieving (125 and 6 µm mesh), treatment with HCl (hydrochloric acid), acetolysis, mounting using TBA.
B1. boiling in NaOH, sieving, treatment with HCl, mounting using TBA.
B2. boiling in KOH, sieving, treatment with HCl, mounting using TBA.
C. boiling in KOH, sieving, density separation by swirling, treatment with HCl, mounting using TBA.
D. sieving, mounting using TBA.

This allowed them to tease out the effects of the different chemicals used in standard pollen preparation procedures on coprophilous fungi recovery and preservation. The use of corrosive chemicals, such as NaOH, KOH and acetolysis, led to a significant loss of hyaline spores (e.g. *Cheilymenia, Coprotus, Iodophanus, Peziza* and immature *Cercophora* spores), as well as spores that lose their epispores over time (e.g. *Ascobolus* and *Saccobolus*). Such spores are unlikely to be preserved in sediments, but since these spores dominate certain dung types (Lundqvist 1972; Richardson 1972), this can significantly bias spore counts. Hyaline appendages were also lost (*Sordaria* and *Cercophora*/*Podospora*). Spores with thicker, pigmented spore walls (e.g. *Sordaria, Sporormiella* and *Cercophora*/*Podospora*, as well as basidiomycete spores) were more resistant to chemical degradation. *Sordaria* spores deteriorated and *Sporormiella* spores tended to swell when acetolysis was used. All spores that were large enough to be retained in the mesh were recovered when samples were sieved but not submitted to any other treatment. This includes the vulnerable spores that were lost when chemicals were used. Spores small enough to pass through the mesh (e.g. small basidiomycete spores and single cells of *Saccobolus*) were lost, which is significant considering that *Sporormiella* spores often break up into their constituent cells (Ahmed and Cain 1972). The single cells of some *Sporormiella* species are so small that they would not be retained in a 10 or 6 µm mesh, leading to a potential loss of information.

Other alternative pollen preparation techniques are also available, although these have not been tested explicitly on spores of coprophilous fungi. Riding and Kyffin-Hughes (2004) used a treatment with sodium hexametaphosphate followed by density separation by means of swirling and centrifuging. With this simple method, they achieved equal or better palynomorph recovery than with the standard preparation method for most lithologies, although they did not test their method on sediments high in organic material.

Given the clear adverse effect of some of the chemicals used in standard pollen preparation methods on coprophilous fungi recovery and preservation, it is highly advisable to test and use alternative, non-chemical, techniques wherever possible (cf. van Asperen et al. 2016).

Analysis and quantification

Typically, spores of coprophilous fungi are counted alongside pollen. In some environments, however, it may be beneficial to count spores in relation to tracer spores. Etienne and Jouffrey-Bapicot (2014) suggest counting 300–350 *Lycopodium* tracer spores to obtain an accurate evaluation of *Sporormiella* in a sample, but the number of tracer spores and sample sizes in this study were not reported. The amount of tracer spores counted should depend on the environment, the size of the sample, the concentration of pollen within a sample, and how many tracer spores are added.

Examining pollen samples for spores of coprophilous fungi using different approaches can produce discrepancy in results between sites. The threshold for "background" levels of spores of coprophilous fungi has been consistently suggested to be below 2% of the total pollen assemblage in various modern environments (Gill et al. 2013; Baker et al. 2016; Raczka et al. 2016). It was first suggested by Davis (1987), in his work in (mostly arid) western North America, that functional extinction of megaherbivores can be observed when fungal spores fall below 2% of the total pollen assemblage (TPA). However, it is not likely that this threshold can truly be extrapolated between sites and environments. In the southeastern United States, for example, two different methods for quantifying spores of coprophilous fungi may have yielded differing results. To our knowledge, recent research at Cupola Pond, Missouri (Jones et al. 2017) and Page-Ladson, Florida (Perrotti 2018) are the only two published palynological studies that attempt to incorporate spores of coprophilous fungi within the analysis from that region. These sites are similar in age and both occur within spring-fed ponds in areas with carbonate rich bedrock. In contrast to Page-Ladson, no evidence of *Sporormiella* spores were found in pollen samples at Cupola Pond, leading Jones et al. (2017) to conclude that herbivory was not a key factor in ecosystem regulation around the site. The discrepancy between the observations of dung fungi at Cupola Pond and Page-Ladson deserves further exploration.

Though late Pleistocene vegetation at the two locations does differ, the inconsistency in fungal spore records may have resulted from differences in noting and quantifying spores of coprophilous fungi. Perrotti et al. (2018) counted spores of coprophilous fungi separately from pollen rather than noting them only when encountered during pollen counting. Most North American coprophilous fungi studies, including that by Jones et al. (2017), have used the latter method (Davis 1987; Davis and Shafer 2006; Gill et al. 2009). At Page-Ladson, Florida, *Sporormiella* spores never constitute more than 2% of the TPA (Perrotti 2018) due to a high concentration of arboreal pollen at the site. If *Sporormiella* was tallied as a percentage of that total pollen assemblage, spores of coprophilous fungi would have been far less represented than those from arid environments as in the desert west, where this method was first conceived. Pollen concentrations at Cupola Pond (Jones et al. 2017) are similar to those at Page-Ladson, suggesting that a different method of searching for spores of coprophilous fungi may have resulted in the recovery of more spores.

Analysing and quantifying spores of coprophilous fungi as %TPA can also produce fluctuations within a spore record that are not representative of herbivore abundance. This method is vulnerable to fluctuations in pollen accumulation rates. In sediments with high pollen concentrations, fungal spores are often represented by lower %TPA values. Parker and Williams (2012) found a negative relationship between mean annual precipitation and spore abundance in lake-centre sediments that they attributed to a higher influx of arboreal pollen during wet years, which would drive down relative *Sporormiella* abundance. Wood and Wilmshurst (2013) confirm that *Sporormiella* as %TPA is subject to fluctuations in pollen accumulation that may skew spore data, even when the spores are being consistently deposited. Moreover, in contrast to the sporopollenin walls of pollen grains, the cell walls of fungal spores are composed mainly of chitin and glucans (Deacon 2006), and therefore will degrade in response to different environmental factors.

Furthermore, expressing fungal spore presence as %TPA can mask low spore counts, making it difficult to assess the reliability of the conclusions drawn from such percentages. In pollen analyses, it is common, for instance, to count up to 200–400 pollen grains. In such assemblages, the 2% TPA "background" level of fungal spore presence translates into 4–8 spores counted, with each 1% increase representing 2–4 extra spores counted. In most cases, even where herbivores are present, the coprophilous fungi counts are not higher than 10% TPA, with counts for most Pleistocene (predating megafaunal extinctions) samples below 5% (e.g. Davis and Shafer 2006; Parker and Williams 2012; Gill et al. 2013; Johnson et al. 2015). Such low spore count fluctuations are unlikely to be statistically significant and should be interpreted with caution.

Whenever possible, reporting coprophilous fungi abundance using both accumulation or concentration and %TPA could be beneficial. Total pollen production will vary greatly between different ecosystems and fungal spores and pollen have differing reproductive strategies and cell wall compositions, so future studies should avoid quantifying spores solely as %TPA. Calculating spore accumulation requires a well-dated core but can be a useful illustration of how changes in sediment deposition at a site can affect the accumulation of fungal spores (Fig. 2).

Current limitations

Typically, North American researchers focus on *Sporormiella* as an indicator of megaherbivore abundance without including other coprophilous fungi. Perhaps due to its distinct morphology or presence in many North American pollen samples, it has become the sole taxon reported in many studies (Gill et al. 2009; Gill 2014; Halligan et al. 2016; Perrotti 2018). Though *Sporormiella* alone has been used as a proxy for herbivore abundance, it is becoming more apparent that noting other coprophilous fungi can increase the robustness of interpretations regarding megaherbivore abundance (Fig. 3).

Johnson et al. (2015) found that the commonly encountered coprophilous and semi-coprophilous ascomycetes

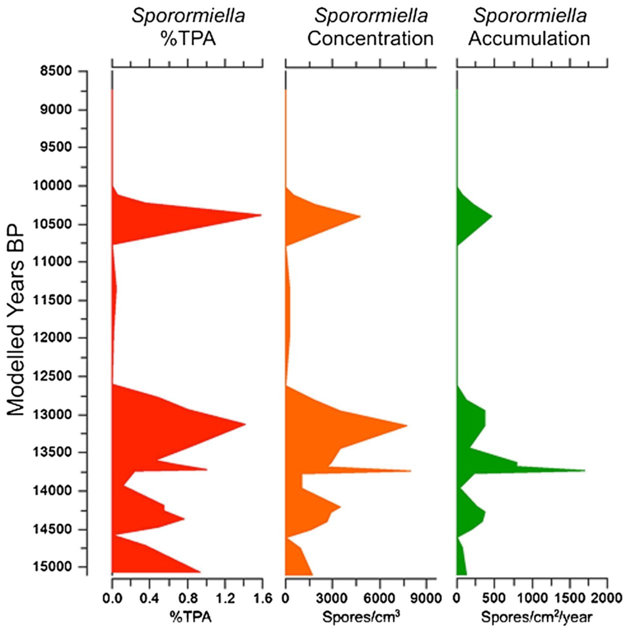

Fig. 2 *Sporormiella* data from Page-Ladson, Florida (Halligan et al. 2016; Perrotti 2018). Spore accumulation is the most accurate way to understand coprophilous fungi abundance in a sedimentary record

Cercophora, Coniochaeta, Podospora and *Sordaria* contributed to a better overall understanding of dung fungal abundance. In addition, van Asperen (2017) notes that *Sporormiella* can be rare on the dung of some modern large herbivores whilst other coprophilous fungi are found in abundance. Therefore, a lack of *Sporormiella* in sediments does not always indicate that herbivores were not present at the site, and as a consequence, counting *Sporormiella* only may prevent the recognition of herbivore presence. Incorporating all dung fungal counts better indicates herbivore presence and abundance (Johnson et al. 2015; Baker et al. 2016; van Asperen et al. 2016; van Asperen 2017), but the dependence on dung of each taxon must be considered (Table 1).

In addition to a lack of herbivore activity, an absence of dung fungi at a site may be the result of a number of factors. First, as previously discussed, little is known about the environmental preferences of each dung fungus and the effect of varying environmental conditions on dung fungal reproduction and dispersal. More research is needed on the topic. Second, most dung fungi inhabit many different types of herbivore dung, with many genera also utilizing other substrates. It is possible that noting particular species of fungi that are associated with dung of specific animal species could contribute to the understanding of extinctions.

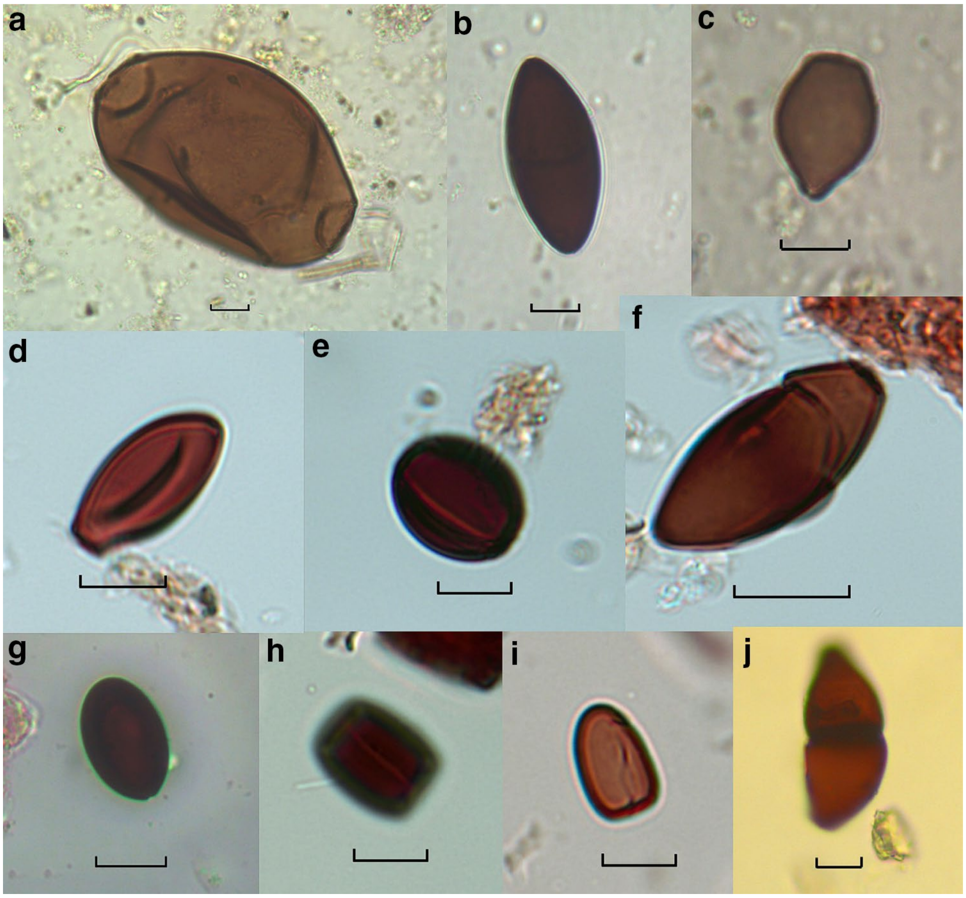

Fig. 3 Commonly encountered coprophilous and semi-coprophilous fungi. **a** *Arnium* sp. (from modern context—pollen trap); **b** *Arnium imitans* (from modern context—pollen trap); **c** *Apiosordaria* sp. (from modern context—pollen trap); **d** *Cercophora* sp. (from Pleistocene sediment), **e** *Coniochaeta* sp. (from Pleistocene sediment); **f** *Podosopora* sp. (from Pleistocene sediment); **g** *Sordaria* sp. (from modern context—directly from dung); **h, i** *Sporormiella* sp. (from Pleistocene sediment); **j** *Trichodelitschia* sp. (from modern context—soil)

However, species-level dung fungus identification relies on the fruiting body in addition to the spores. Though van Geel et al. (2011) recovered complete fruiting bodies from inside a mammoth dung ball, fruiting bodies are rarely preserved in sediment samples and would typically be destroyed during laboratory procedures. Third, little is known about how spores preserve. It is widely assumed that they are more durable than pollen because of their thick, chitinous walls and frequent presence in pollen samples exhibiting poor pollen preservation. Spores of many fungi can remain in soil for extended periods in a dormant state (Lockwood 1977; Deacon 2006). Fourth, because spores of coprophilous fungi typically represent a very local proxy due to their limited dispersal distances, it is likely not possible to draw any conclusions regarding the demise of wide-ranging megafauna from spore abundance in one location alone. Finally, hydrological factors also influence where spores, if present in the environment, ultimately enter the palaeoecological record. For example, spores of coprophilous fungi from cores taken in lakes at different distances from the shoreline (Raper and Bush 2009) or from the nearest stream discharge (Etienne et al. 2013) show different relationships to animal abundance in the area around the lake.

Because of the factors discussed above, it is possible that an absence of dung fungi from a palaeoecological record may not always indicate a decline in herbivores. However, by understanding the past environment, particularly in regard to hydrologic factors, more weight can be placed on the interpretation of the abundance or lack of spores of coprophilous fungi. Overall, the effects of these factors on spore records may be minimized with the incorporation of multiple fungal taxa. Ultimately, spores of coprophilous fungi alone likely cannot be used to infer an absence of herbivores. When using spores to infer extinction or regional disappearance of large herbivores, it is best practice to utilize this proxy alongside other lines of evidence, such as faunal remains or macrofossils from herbivore dung (i.e. Halligan et al. 2016; Perrotti 2018).

Future directions and conclusions

The methods for analysis and research of analogues for the interpretation of dung fungal records are improving, but additional research is still needed. First, more modern experiments need to be conducted to understand the relationship between dung fungal abundance, herd size, and other geographical and environmental factors. Much research has been devoted to this topic recently and studies have established correlations between cattle (Wood and Wilmhurst 2013) and bison (Gill et al. 2013) herd size and *Sporormiella* abundance. Baker et al.'s (2016) informative study conducted in The Netherlands was an excellent demonstration of the correlation between spore accumulation, taphonomic processes and herd size, but more studies incorporating a wider variety of large herbivores would be valuable. Because spore reproduction and deposition differ between environments, a wider array of modern environments should also be explored. If a clearer correlation between coprophilous fungi abundance and herbivore diversity and abundance could be established, dung fungal data could be incorporated into dynamic vegetation models, strengthening our interpretation of the effects of grazing on vegetation systems.

Second, still more research is needed on laboratory recovery and identification of spores of coprophilous fungi. Certain laboratory recovery procedures can alter the size of dung fungi, further inhibiting species identification (van Asperen et al. 2016). Minimizing harsh chemical extraction procedures could be made possible by the implementation of techniques such as sonication-assisted sieving through <5 micron mesh (i.e. Perrotti et al. 2018). Regardless, more research is needed on the effects of standard palynological procedures on the recovery of spores of coprophilous fungi. By developing more standardized processing and extraction, comparisons between studies would be made easier.

Although additional research is still needed before researchers can fully rely on the application of dung fungi to questions raised in archaeology, we believe that this type of research has proven its potential as a valuable tool for understanding past herbivore abundances. Thorough consideration of the limitations of the method, particularly through engagement with the mycological literature, as well as through carefully designed actualistic experiments, greatly increases the reliability and applicability of dung fungal data to archaeology.

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