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Late Pleistocene climate change, nutrient cycling, and the megafaunal extinctions in North America

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ABSTRACT

This study proposes an ecological mechanism for the terminal Pleistocene population collapse and subsequent extinction of North American megafauna. Observations of modern ecosystems indicate that feedback mechanisms between plant nutrient content, nitrogen cycling, and herbivore–plant interactions can vary between a nutrient accelerating mode favoring increased herbivore biomass and a nutrient decelerating mode characterized by reduced herbivore biomass. These alternate modes are determined largely by plant nitrogen content. Plant nitrogen content is known to be influenced by atmospheric CO_2 concentrations, temperature, and precipitation. It is argued that Lateglacial climate change, particularly increases in atmospheric CO_2, shifted herbivore–ecosystem dynamics from a nutrient accelerating mode to a nutrient decelerating mode at the end of the Pleistocene, leading to reduced megafaunal population densities. An examination of *Sporormiella* records – a proxy for megaherbivore biomass – indicates that megafaunal populations collapsed first in the east and later in the west, possibly reflecting regional differences in precipitation or vegetation structure. The fortuitous intersection of the climatically driven nitrogen sink, followed by any one or combination of subsequent anthropogenic, environmental, or extra-terrestrial mechanisms could explain why extinctions took place at the end of the Pleistocene rather than during previous glacial–interglacial cycles.

1. Introduction

The late Pleistocene of North America is characterized by the extinction of 36 genera of large mammals (Grayson, 1991, 2011; Barnosky et al., 2004; Grayson, 2007; Faith and Surovell, 2009). Six of these genera survived elsewhere, although within them some species were lost, and the majority became globally extinct. The losses were most severe for the largest taxa, with extinctions taking place across all genera larger than 1000 kg (e.g., *Mammuthus*, *Mammut*, *Glyptotherium*) and over half the genera between 32 and 1000 kg (Lyons et al., 2004a; Koch and Barnosky, 2006). Due to the limitations of the fossil record, the timing of the extinctions is debated (Grayson, 2001, 2007; Grayson and Meltzer, 2003; Fiedel and Haynes, 2004; Faith and Surovell, 2009; Fiedel, 2009). At least 16 genera are unequivocally known from the very latest Pleistocene (Grayson, 2007; Faith and Surovell, 2009; Fiedel, 2009), although the chronology is consistent with the synchronous loss of all 36 genera at the very end of the Pleistocene, between 12,000 and 10,000 ^{14}C yrs BP ($\sim$13,800 to 11,400 cal yrs BP) (Faith and Surovell, 2009).

At the same time that extinctions were taking place, there is evidence for dramatic shifts in the geographic range and composition of plant (Williams et al., 2001, 2004; Gill et al., 2009) and animal communities (FAUNMAP, 1994, 1996; Stafford et al., 1999), which includes non-analog communities (Williams et al., 2001; Gill et al., 2009), and increased biomass burning (Robinson et al., 2005; Gill et al., 2009; Marlon et al., 2009). This time period also encompasses the Younger Dryas cold interval (Alley, 2000; Rasmussen et al., 2006), the arrival of Clovis hunter–gatherers in North America (Meltzer, 2004; Waters and Stafford, 2007) and a proposed – although highly contested (Paquay et al., 2009; Surovell et al., 2009; Daulton et al., 2010; Haynes et al., 2010; Holliday and Meltzer, 2010; Scott et al., 2010) – extra-terrestrial impact event (Firestone et al., 2007; Kennett et al., 2008, 2009; Melott et al., 2010).

To account for the massive loss of North America's Pleistocene megafauna (animals $>$ 44 kg), a number of hypothesis have been forwarded. These include human hunting pressure (Martin, 1967, 1984, 2005; Martin and Steadman, 1999; Alroy, 2001; Lyons et al., 2004a), environmental change (Graham and Lundelius, 1984; Guthrie, 1984; King and Saunders, 1984), or some combination of both (Barnosky et al., 2004). Alternative explanations include an extra-terrestrial impact (Firestone et al., 2007; Kennett et al., 2008,

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2009; Paquay et al., 2009; Surovell et al., 2009; Daulton et al., 2010; Haynes et al., 2010; Holliday and Meltzer, 2010; Melott et al., 2010; Scott et al., 2010), disease (MacPhee and Marx, 1997; Lyons et al., 2004b), or vegetation change stemming from the loss of keystone mega-herbivores (Owen-Smith, 1987). This study discusses how the interplay between Lateglacial climate change, nutrient cycling, and plant–herbivore interactions could have played a deciding role in the demise of North America's Pleistocene megafauna.

2. The late Pleistocene megafaunal population collapse

Davis (1987) demonstrated that *Sporormiella* dung fungal spores track herbivore abundances on the landscape. *Sporormiella* is a coprophilous fungus found only on the dung of herbivores (Ahmed and Cain, 1972). The spores are common on the dung of domestic herbivores and mega-herbivores (Ebersohn and Eicker, 1997) and are also known from the dung and gut contents of Pleistocene *Mammuthus* (Davis et al., 1984; Mead et al., 1986; van Geel et al., 2008). In pollen cores, *Sporormiella* abundances $<2\%$ of the arboreal pollen sum indicate the extinction (or population collapse) of megafauna during the terminal Pleistocene of North America (Davis, 1987; Robinson et al., 2005; Davis and Shafer, 2006; Gill et al., 2009) and the late Holocene of Madagascar (Burney et al., 2003).

Davis and Shafer (2006) review a number of terminal Pleistocene *Sporormiella* records from the western United States (Fig. 1, Table 1). Using *Sporormiella* as a proxy for megafaunal biomass, they show that megafaunal populations collapsed at roughly the same time that extinctions were taking place. The limiting radiocarbon dates for the *Sporormiella* decline ($<2\%$), meaning the dates after which *Sporormiella* is consistently below 2% of the arboreal pollen sum, are reported in Table 1 (2-sigma ranges) and illustrated in Fig. 2 as probability distributions. Radiocarbon dates are calibrated and probability distributions determined with OxCal 4.1 (Bronk Ramsey, 2009) using the IntCal09 calibration curve (Reimer et al., 2009). Across the western United States, the limiting radiocarbon dates for the megafaunal population decline coincide with the 13.8–11.4 cal ka BP extinctions window for North America's Pleistocene mammals (Faith and Surovell, 2009) (Fig. 2). Thus, population collapse and extinction are synchronous and coincide with the arrival of Clovis people (Meltzer, 2004; Waters and Stafford, 2007) and with changes in vegetation, temperature, and precipitation (Davis, 1999a,b; Davis and Shafer, 2006).

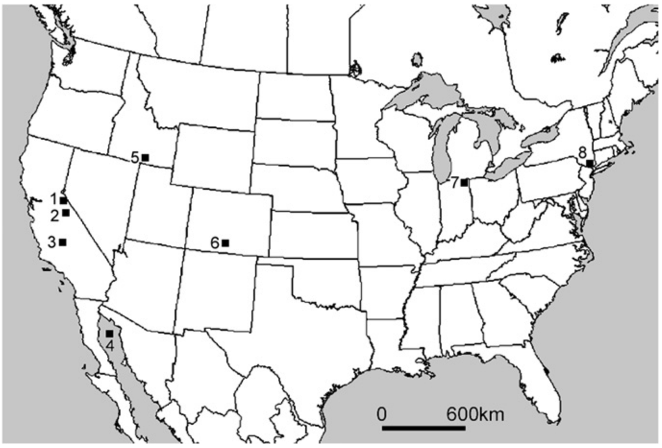

Fig. 1. Locations of late Pleistocene *Sporormiella* records referred to in the text: 1. Exchequer Meadow, CA; 2. Mono Lake, CA; 3. Tulare Lake, CA; 4. Wagner Basin, Gulf of California; 5. Lake Cleveland, ID; 6. Como Lake and Head Lake, CO; 7. Appleman Lake, IN; 8. Otisville, Binnewater Pond, Pawelski Farm, and Hyde Park, NY.

In the lower Hudson Valley of New York (Fig. 1), Robinson et al. (2005) demonstrate that megafaunal populations collapsed many centuries in advance of the extinction event (Fig. 2, Table 1). At four localities (Otisville, Hyde Park, Binnewater Pond, and Pawelski Farm), the onset of the megafaunal population decline predates the Younger Dryas (at 12.9 cal ka BP) and the limiting radiocarbon dates for the *Sporormiella* decline are associated with the onset of the Bølling–Allerød interstadial or slightly after (Fig. 2). However, extinct megafauna (e.g., *Castoroides* and *Mammut*) are securely dated to the very latest Pleistocene in nearby localities (Steadman et al., 1997; Robinson et al., 2005; Faith and Surovell, 2009), indicating that population collapse preceded the actual extinction event. The timing of the population decline is of particular interest in that it predates a number of possible extinction mechanisms, including Younger Dryas climate change, the arrival of Clovis people in North America, and the proposed extra-terrestrial impact event.

Consistent with the record from New York, Gill et al. (2009) present *Sporormiella* records from a sediment core recovered from Appleman Lake, Indiana (Fig. 1), showing a pronounced decline in megafaunal populations during the Bølling–Allerød interstadial from 14.8 to 13.7 cal ka BP (Figs. 2, 3). Once again, this decline precedes the extinction for many taxa (Figs. 2, 3). For example, *Cervalces*, *Megalonyx*, and *Mammut* are securely dated to the latest Pleistocene in nearby localities (Schubert et al., 2004; Faith and Surovell, 2009), indicating a population collapse well before the extinction event. Together with the evidence from New York, the Appleman Lake core suggests that megafaunal population collapsed earlier in eastern North America than in the west (Fig. 2, Table 1). This implies a possible longitudinal gradient or east–west dichotomy underlying the timing of the megafaunal population collapse, whereas the extinctions appear to have been synchronous across the continent (Faith and Surovell, 2009).

Both at Appleman Lake and to a lesser extent in the Hudson River Valley, the timing of the decline in megafaunal populations predates major turnover in the pollen assemblages (Robinson et al., 2005; Gill et al., 2009). This is particularly clear at Appleman Lake (Fig. 3) and may suggest that climate-driven changes in vegetation structure are unable to explain the megafaunal decline. For example, *Picea* (spruce) remained the dominant contributor to the pollen assemblage and pollen turnover was relatively low during the megafaunal population collapse (Fig. 3). Only after the megafaunal decline is there evidence for major turnover in the pollen assemblage, which includes increasingly non-analog floral communities and a transition from *Picea* to *Pinus* (pine) and later, *Quercus* (oak) as the dominant contributors to the pollen assemblage (Gill et al., 2009; Fig. 3). If climate change played a role in the megafaunal decline, then it did not operate through vegetation-related habitat change. However, this does not preclude the role of climate change as an important contributor to the megafaunal population decline. It is this possibility that I turn to below.

3. Nutrient cycling in modern ecosystems & Lateglacial climate change

Modern ecosystems are characterized by dynamic feedback mechanisms between herbivores, plant tissue chemistry, and nutrient (nitrogen) cycling (Pastor et al., 2006). As reviewed by Pastor et al. (2006), ecosystems are broadly characterized by two primary modes of herbivore–ecosystem interactions, termed nutrient accelerating or nutrient decelerating modes (Fig. 4) (Ritchie et al., 1998). Theoretical and empirical evidence suggests that the distinction between these modes depends on forage nitrogen content (Pastor et al., 2006).

When plant nitrogen content is high ($>1.5\%$), mammalian herbivores excrete nitrogen in urea in order to remove excess