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Calibrating the pollen signal in modern rodent middens from northern Chile to improve the interpretation of the late Quaternary midden record

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ABSTRACT

The use of rodent middens from northern Chile as paleoecological archives has at times been questioned due to concerns about their biogenic origin and the degree to which their record represents vegetation composition rather than rodent habits. To address such concerns, we carried out a modern calibration study to assess the representation of vegetation by pollen records from rodent middens. We compared vegetation censuses with soil-surface and midden (matrix and feces) pollen samples from sites between 21° and 28°S. The results show that (1) the pollen signal from the midden matrix provides a more realistic reflection of local vegetation than soil-surface samples due to the pollen-deposition processes that occur in middens; and (2) in contrast to feces pollen assemblages, which feature some biases, rodent dietary habits do not seem to influence midden matrix pollen assemblages, probably because midden agents are dietary generalists. Our finding that modern pollen data from rodent middens reflect vegetation patterns confirms the reliability of midden pollen records as paleoecological archives in northern Chile.

Introduction

Rodent middens are complex accumulations of local vegetation, nesting materials, insect remains, bones, sediment, and feces preserved underneath rock slabs and within caves (Betancourt et al., 1990, 2000; Betancourt and Saavedra, 2002). Four families of rodents (Abrocomidae, Chichillidae, Muridae, and Octodontidae) are known "midden agents" or builders of these urine-hardened deposits in the arid and semiarid regions of northern Chile (Fig. 1) (Latorre et al., 2002, 2003).

Due to the foraging behavior and range of most rodents, fossil middens are veritable "snapshots" of the composition of the vegetation surrounding the midden at different times in the past. Thus, the preserved plant fossils are a vital tool for reconstructing paleoecological and paleoclimatic histories over the last 50,000 yr (e.g., Betancourt et al., 2000; Latorre et al., 2002, 2003). The vast majority of published analyses of rodent middens in northern Chile are based on the study of midden plant macrofossil content (see Latorre et al., 2005, 2007 for reviews). The analysis of pollen in middens is less common than macrofossil studies, even though this method has proven its potential to infer the history of vegetation and precipitation dynamics (Maldonado et al., 2005; Díaz et al., 2012; Rozas, 2012; Mujica et al., 2015).

Despite its initial success, the analysis of pollen in rodent middens from northern Chile has been questioned as a viable paleoecological tool due to concerns regarding (1) the biogenic origin of the middens, and particularly, the degree to which their record actually represents past vegetation rather than rodent habits; (2) the temporal resolution afforded by the middens, with samples possibly representing years to decades; and (3) their discontinuous deposition (e.g., Grosjean et al., 2003). The temporal scale and discontinuous nature of rodent middens are inherent characteristics that need to be taken into account when interpreting midden records. However, the development of calibration studies that test the way in which vegetation is reflected in rodent middens, and whether rodent habits bias that representation, would help us determine what level of detail is achievable with such records. In turn, this better understanding of the pollen–vegetation relationship would improve the precision of reconstructions of past environments and climates in northern Chile.

One of the specific challenges of interpreting midden-derived pollen records is the unclear meaning of multivariate assemblage data. For example, fossil pollen assemblages from rodent middens in northern Chile have been interpreted solely using soil-surface pollen assemblages (e.g., Maldonado et al., 2005; Rozas, 2012). However, a more suitable modern analog should consider the many different taphonomic processes that could affect pollen incorporation and preservation for soil-surface versus midden samples. To date, there are no studies that have addressed these issues directly in South American rodent middens. Maldonado et al. (2005) argue that, similar to the North American *Neotoma* middens, pollen reaches the middens primarily through the

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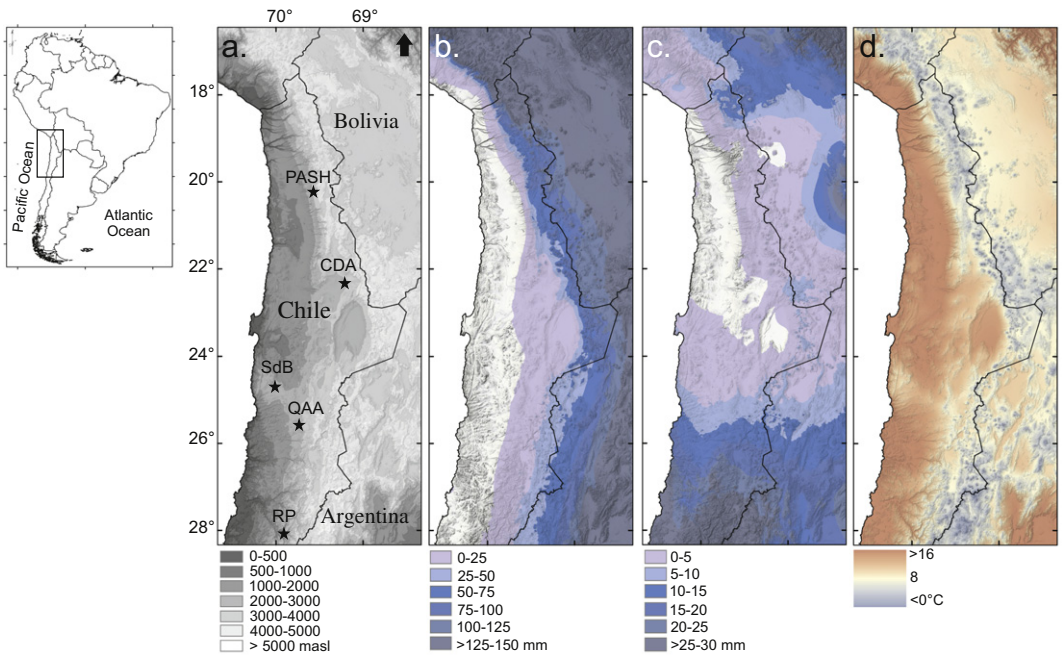

Fig. 1. Maps of northern Chile showing: a. locations of rodent midden sites included in the present study; b. summer precipitation; c. winter precipitation; and d. mean annual temperature. Climate data were taken from Pliscoff et al. (2014).

air and on the plant material that rodents bring to their nests, but lesser amounts of pollen may be incorporated through fecal pellets and by transport on animal pelts (Davis and Anderson, 1987).

The implications of these taphonomic issues are critical for establishing whether midden pollen assemblages represent vegetation at the local spatial scale (like the macrofossil record), at the regional scale, or at both spatial scales. This issue spans continents, as the spatial scale of pollen preserved in *Neotoma* middens from North America (King and Van Devender, 1977; Thompson, 1985; Davis and Anderson, 1987) and in *Hyrax* middens from southern Africa has also been the subject of discussion (Scott et al., 2004; Gil-Romera et al., 2007). Some researchers suggest that pollen data from rodent middens reflect vegetation at both local and regional scales (King and Van Devender, 1977; Davis and Anderson, 1987), whereas others argue that such records represent local vegetation patterns (Thompson, 1985; Gil-Romera et al., 2007).

In this study, we explore the way in which pollen in modern rodent middens from northern Chile reflects vegetation composition, with the goal of improving the interpretation of fossil midden pollen records. We attempt to answer the following questions: (1) Do modern rodent midden pollen samples and soil-surface pollen samples represent vegetation similarly? What spatial scale do these data reflect, and are anemophilous and enthomophilous plants either over- or under-represented? (2) Is the rodent midden pollen signal influenced by rodent behavior? (3) Are modern unconsolidated rodent middens suitable for use in a modern pollen–vegetation training data set for northern Chile?

Methodological reasoning

To date, fossil–pollen assemblages from rodent middens in northern Chile have been interpreted using soil-surface pollen assemblages (e.g., Maldonado et al., 2005; Rozas, 2012). Pollen–vegetation calibration studies carried out across the world have demonstrated that pollen assemblages from soil-surface samples represent vegetation at local and regional scales (e.g., Prentice et al., 1987; Jackson, 1990; Anupama et al., 2000; Walker, 2000; Gajewski et al., 2002; Markgraf et al., 2002). Such studies performed in Peru, Bolivia, and Chile have demonstrated that present-day vegetation patterns are reflected by soil-surface pollen samples (Weng et al., 2004; Maldonado et al., 2005; Reese and Liu, 2005; Kuentz et al., 2007; Ortuño et al., 2011).

Birks and Gordon (1985) suggests that in paleoecological reconstructions, the modern calibration data set should come from a sedimentary environment that is similar to the fossil data set. Following this recommendation, new (and existing) paleoecological information from northern Chile based on the rodent midden pollen record should be interpreted by comparing these results to modern pollen data from rodent middens, thus improving the quality and precision of these interpretations. Birks' point is particularly important considering the different pollen-depositional processes in soils and middens in northern Chile. Pollen reaches the soil surface by wind (airfall deposition) or by falling directly from plants to the soil surface (gravity deposition). On the other hand, pollen could reach a midden by airfall deposition, attached to the plant parts that rodents gather and take into the midden, attached to the fur and paws of the rodent, or within rodent feces.

To better understand these depositional processes with the broader goal of improving our understanding of past ecological and climatic changes in northern Chile, this study explores the way in which modern pollen assemblages preserved in rodent middens reflect vegetation. We carried out vegetation censuses and analyses of pollen in soil-surface and midden samples. The vegetation data were compared qualitatively with both types of pollen data; quantitative analyses would be complicated by the non-linear relationships between plant and pollen abundances. We also compared the pollen data from soil-surface and middens samples to explore potential differences in vegetation representation.

Because fossil rodent middens are urine-hardened (consolidated) deposits, the ideal approach for creating a modern pollen data set would be through the analysis of consolidated modern rodent middens (Fig. 2a). However, the development of this type of calibration data set would require a huge sampling effort, not to mention the ^{14}C dating of the midden deposits that would be needed to confirm that they are indeed modern. One solution is the use of unconsolidated middens (Fig. 2b) as a potential alternative. These are much easier to find and collect than consolidated midden deposits, and they are readily identified as modern because of the presence of fresh feces and chlorophyll in