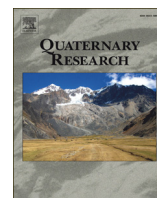


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## Calibrating the pollen signal in modern rodent middens from northern Chile to improve the interpretation of the late Quaternary midden record

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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.

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## 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).

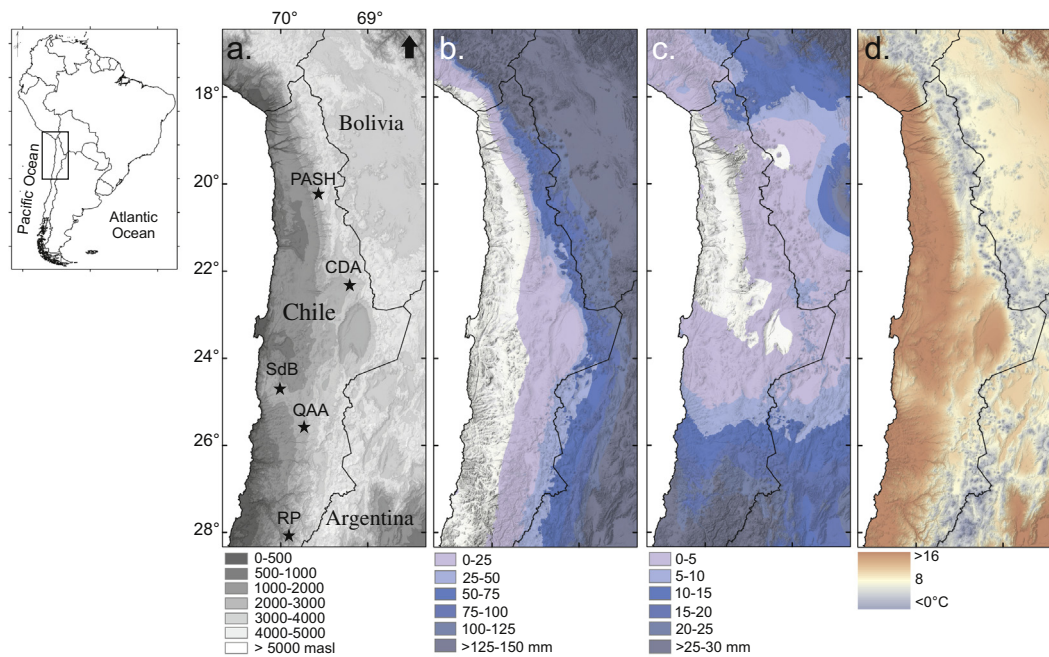
Due to the foraging behavior and range of most rodents, fossil middens are veritable “snapshots” of the composition of the vegetation surrounding the midden at different times in the past. Thus, the preserved plant fossils are a vital tool for reconstructing paleoecological and paleoclimatic histories 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 entomophilous 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  $^{14}\text{C}$  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

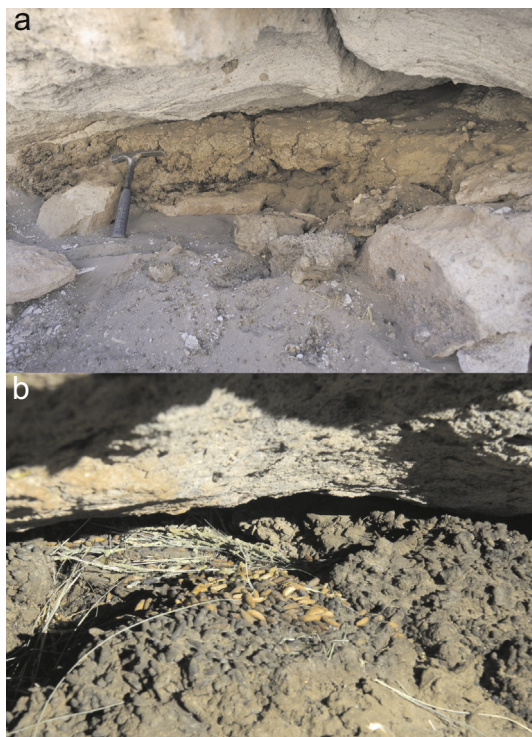


Fig. 2. Photographs of a. consolidated rodent midden and b. unconsolidated rodent midden.

leaf remains. However, taphonomic processes such as compaction during consolidation of the midden or hydration cycles of the rodent urine due to changing moisture conditions may have some effect on pollen spectra. To evaluate this possibility, we also compared pollen data from consolidated and unconsolidated modern middens. Finally, as rodent middens are biologically produced, there are concerns regarding the extent to which rodent behavior influences the pollen signal preserved within the middens. We evaluated the potential biasing of the pollen record by rodent diet by comparing pollen in fecal samples with pollen in the midden matrix from the same deposit.

### Modern setting

Hyperarid to semiarid climates are typical of northern Chile, which is located between 18° and 29°S and characterized by a steep west–east altitudinal gradient from sea level along the Pacific Ocean to the Andes (>6000 m asl) (Fig. 1a). The hyperarid part (18°–25°S) comprises the Atacama Desert, one of the driest deserts of the world, whereas the semiarid zone (25°–29°S) is a transitional zone between the Atacama and Mediterranean central Chile. At 25°S, the region features a precipitation-regime change from summer precipitation from the east, associated with the Easterlies, to winter rainfall from the southwest related to the southern Westerlies (Fig. 1b and c). Thus, north of 25°S precipitation occurs almost exclusively during the austral summer (>80% from December to March) when mid- and upper-level easterly winds bring moist air that feeds convective storms over the Altiplano and western Andes (Fig. 1b; e.g., Garreaud et al., 2003; Garreaud, 2009). In this area, moist air over the Pacific Ocean is limited laterally by the coastal topography, and vertically by a strong, persistent temperature inversion at about 800 m asl (Rutlland and Ulriksen, 1979). The inversion is maintained by large-scale subsidence over the subtropical southeast Pacific Ocean, leading to arid conditions over northern Chile (Garreaud et al., 2003). Because moisture is sourced to the east, annual (mainly austral

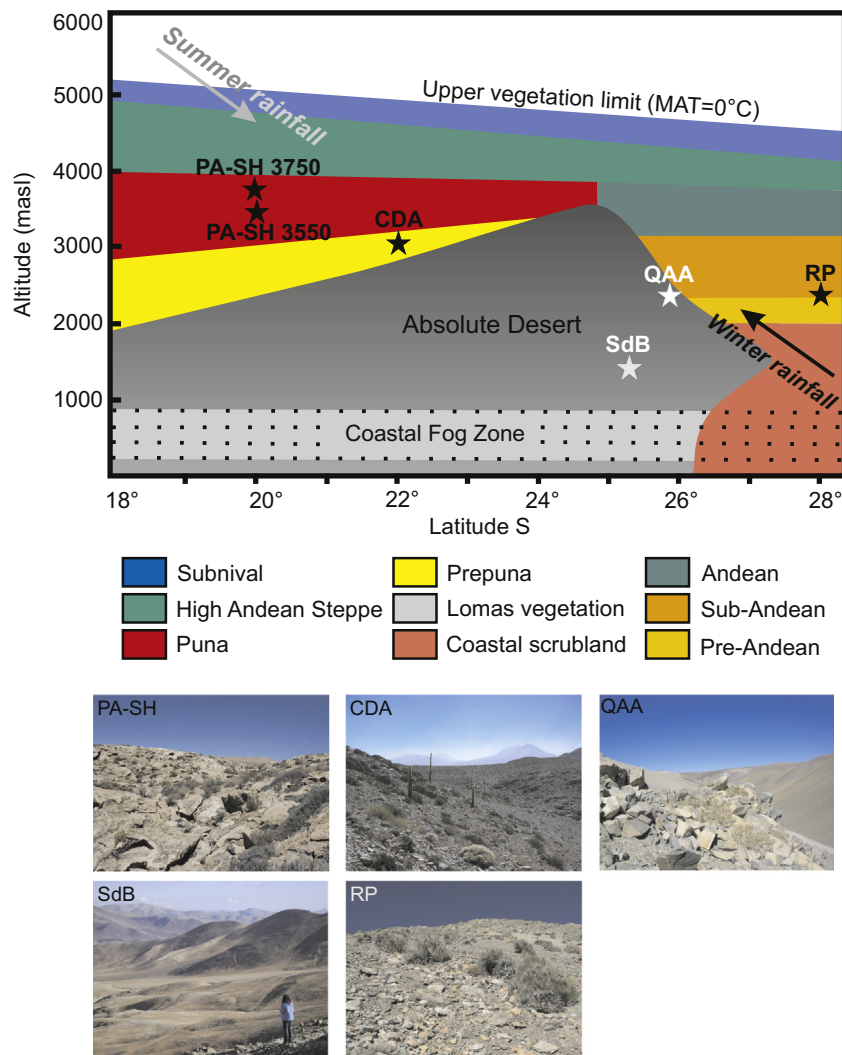
summer) precipitation amounts increase significantly from west to east, ranging from 50 to 150 mm along the western slope of the Andes (Fig. 1b). Between 25° and 29°S, precipitation occurs during the austral winter related to the northern expansion of the southern Westerlies (SW) (Fig. 1c). Low-pressure troughs and cut-off lows coming from the southwest bring winter storms that result in a decreasing precipitation gradient from southwest to northeast (50–2 mm) (Fig. 1c; Rutlland and Fuenzalida, 1991; Montecinos et al., 2000).

Vegetation patterns at the regional scale are determined mainly by precipitation, except at high elevations where temperature becomes the main limiting factor (Figs. 1d and 3). Vegetation patterns change northwards and southwards of 25°S, where the absolute desert penetrates into to its highest elevation in northern Chile (Fig. 3, Table 1).

From 18° to 25°S, three major ecosystems are present from west to east: (1) coastal Lomas, (2) Absolute desert, and (3) Andean vegetation (Fig. 3, Table 1). Lomas vegetation distribution is restricted to the coastal escarpment (between 300 and 800 m asl), where marine air flowing into the interior valleys is blocked by a thermal inversion, resulting in the condensation of fog at this altitude (Fig. 3). Lomas vegetation varies with latitude, from isolated communities of terrestrial *Tillandsia landbeckii* between 18° and 23°S to low-diversity vegetation including scattered individuals of *Eulychnia iquiquiensis*, *Copiapoa* spp., *Malesherbia tocopillana*, and *Nolana tocopillensis* between 23° and 25°S, and highly diverse shrublands (particularly of *Nolana* genera) and a pronounced number of endemics at 25°–26°S (Rundel et al., 1991; Schulz et al., 2011). Above 800 m asl (between 23°40' and 26°S), vegetation is scarce but hardy shrubs and annual herbs such as *Nolana leptophylla*, *Huidobria fruticosa*, and *Cistanthe* spp. are found along roads and on rocky hillslopes (Rundel et al., 1991; Marquet et al., 1998). The Absolute desert (900–2300/3100 m asl) is characterized by the complete absence of vegetation, but riparian vegetation, including *Nolana* spp., *Cistanthe* spp., *Atriplex atacamensis*, *Distichlis spicata*, and *Dinemandra ericoides*, is present in micro fog oases, groundwater oases, and perennial river valleys (Rundel et al., 1991) (Fig. 3).

Andean vegetation comprises four main vegetation belts distributed along the western slope of the Andes: Prepuna, Puna (locally known as Tolar), high Andean steppe, and Subnival (a high Andean formation) (Fig. 3). Located between the easternmost limit of the Absolute desert and 3100 m asl, the Prepuna is a xerophytic shrubland characterized by shrubs such as *Ambrosia artemisioides*, *Atriplex imbricata*, *Acantholippia deserticola*, *Solanum chilense*, and *Ephedra breana*, as well as annual herbs including *Tagetes multiflora*, *Cryptantha* spp., *Tiquilia atacamensis*, *Cistanthe* spp., *Cristaria* spp., *Tarasa operculata*, and some cactus species. The Puna (3100–3900 m asl) is a shrub formation dominated by *Fabiana ramulosa*, *Baccharis boliviensis*, *Diplostephium meyenii*, and *Ephedra breana*, along with grasses and different shrub genera such as *Senecio*, *Parastrephia*, and *Chuquiraga* toward its upper altitudinal limit. The high Andean steppe (3900–4400 m asl) is dominated by tussock grasses such as *Festuca orthophylla*, *F. chrysophylla*, *Stipa* spp., and *Deyeuxia* spp. Large cushion shrubs (*Azorella compacta* and *Pycnophyllum bryoides*), dwarf shrubs like *Mulinum crassifolium* and *Senecio* sp., and small rosettes such as *Chaetanthera* and *Lenzia* characterize the Subnival formation that extends up to 4800 m asl (Villagran et al., 1981, 1983; Arroyo et al., 1988).

From 25° to 29°S, vegetation is characterized by coastal shrublands including *Echinopsis coquimbensis*, *Oxalis gigantea*, *Heliotropium stenophyllum*, and *Nolana* spp., and the presence of shrublands dominated by several species of *Adesmia* on the Andean slope (Fig. 3, Table 1). The pre-Andean belt (2000–2400 m asl) is characterized by *Ephedra breana*, *Lycium minutifolium*, *Gymnophyton flexuosum*, and *Adesmia pedicellata*, the sub-Andean belt (2400–3100 m asl) features *Adesmia hystrix* and *Adesmia aphylla*, and the Andean belt (3100–4000 m asl) is characterized by cushion shrubs of *Adesmia aegiceris*. Above 4000 m asl, the high Andean steppe and Subnival belts of similar composition to those described above (Andean vegetation) develop (Villagrán et al., 1983).



**Fig. 3.** Locations of rodent midden sites and latitudinal/elevational distribution of vegetation units and the Absolute desert in northern Chile (modified from Schmithüsen, 1956; Latorre et al., 2007). Photographs illustrate the landscape and environmental characteristics at each collection site (PASH, Pozo Almonte-Salar del Huasco; CDA, Cerros de Aiquina; QAA, Quebrada Agua Amarga; SdB, Sierra del Buitre; RP, Río Potrerillos).

## Material and methods

Vegetation data, soil-surface sediments, consolidated midden samples, and unconsolidated midden samples were collected at five sites: Pozo Almonte-Salar del Huasco (PASH), Cerros de Aiquina (CDA), Quebrada Agua Amarga (QAA), Sierra del Buitre (SdB), and Río Potrerillos (RP) (Fig. 1a, Table 2). These sites are located across different vegetation belts in northern Chile (20°–29°S; Fig. 3).

Vegetation census data for PASH 3750 and PASH 3550, and RP sites were taken from Collao-Alvarado et al. (2015) and Rozas (2012), respectively. Vegetation censuses at these sites and CDA were carried out following the methods outlined by McAuliffe (1990). No census was carried out at either SdB or QAA; the vegetation at both of these sites, located within the Absolute desert, is very sparse, with only single isolated individuals of some species. Thus, a floristic list better reflects the species present around these sites (Fig. 3, SdB and QAA photographs). Annual herbs or grasses may be under-represented or absent in the vegetation censuses or floristic lists, respectively, if the vegetation *relevés* were carried out during the dry season and/or dry years.

Soil-surface samples were collected at each site through the multi-sampling technique proposed by Adam and Merhinger (1975).

Unconsolidated rodent middens were sampled by using a spatula to collect equal proportions of plant macro-remains, sediment, and feces. Consolidated middens were extracted by using a hammer and chisel, cleaned in the field for surface contaminants, and considered as modern if their  $^{14}\text{C}$  age was younger than 200 years (Table 3). The age threshold was established at 200  $^{14}\text{C}$  yr BP because paleoecological research from northern Chile indicates that similar-to-modern vegetation was established by that time (e.g., Betancourt et al., 2000; Latorre et al., 2003; Maldonado et al., 2005). Thus, consolidated midden pollen assemblages should be comparable to soil-surface and unconsolidated midden pollen assemblages since they reflect the same vegetation. At the Sierra del Buitre site, midden SdB113E age was older than the established threshold (270  $^{14}\text{C}$  yr BP), but it was included since it was the only midden available for this site. The consolidated midden ages were calibrated using CALIB 7.0.2 (Stuiver et al., 2005) and CALIBomb (Reimer et al., 2004) (Table 3). Dates older than 100  $^{14}\text{C}$  years were calibrated with the Southern Hemisphere curve (SHCal13; Hogg et al., 2013) from CALIB 7.0.2, whereas those younger than 100  $^{14}\text{C}$  years were calibrated with the SHZ1-2 curve (Hogg et al., 2013) from CALIBomb.

Consolidated rodent midden samples were soaked in distilled water for 24–48 hours to dissolve urine (amberat). Then, both

**Table 1**

Summarized floristic list of vegetation units from northern Chile, including their life form, pollen type, and pollination syndrome (Faegri and van der Pijl, 1979).

Vegetation	Family	Species	Life form	Pollen type	Pollination syndrome		
					Anemophilous	Entomophilous	
Lomas	Bromeliaceae	<i>Tillandsia landbekii</i>	Epiphytic	<i>Tillandsia</i> type	?		
	Cactaceae	<i>Eulychnia iquiquensis</i>	Cactus	Cactaceae			
		<i>Copiapoa</i> spp.					X
	Malesherbiaceae	<i>Malesherbia tocopillana</i>	Herb	<i>Malesherbia</i> type			X
	Nolanaceae	<i>Nolana tocopillensis</i>	Herb	Nolanaceae/Solanaceae			X
		<i>Nolana leptophylla</i>	Herb				X
	Loasaceae	<i>Huidobria fruticosa</i>	Herb	Loasaceae		X	
	Portulacaceae	<i>Cistanthe</i> sp.	Herb	Portulacaceae		X	
Absolute desert	Nolanaceae	<i>Nolana</i> spp.	Herb	Nolanaceae/Solanaceae		X	
	Portulacaceae	<i>Cistanthe</i> spp.	Herb	Portulacaceae		X	
	Chenopodiaceae	<i>Atriplex atacamensis</i>	Shrub	Chenopodiaceae	X		
	Poaceae	<i>Distichlis spicata</i>	Grass	Poaceae	X		
	Malpighiaceae	<i>Dinemandra ericoides</i>	Herb	Malpighiaceae		X	
Prepuna	Asteraceae	<i>Ambrosia artemisioides</i>	Shrub	<i>Ambrosia</i> type	X		
	Chenopodiaceae	<i>Atriplex imbricata</i>	Shrub	Chenopodiaceae	X		
	Verbenaceae	<i>Acantholippia deserticola</i>	Shrub	Verbenaceae		X	
	Solanaceae	<i>Solanum chilense</i>	Shrub	Solanaceae		X	
	Ephedraceae	<i>Ephedra breana</i>	Shrub	<i>Ephedra</i>		X	
	Asteraceae	<i>Tagetes multiflora</i>	Herb	<i>Senecio</i> type	X	X	
	Boraginaceae	<i>Cryptantha</i> spp.	Herb	Boraginaceae		X	
		<i>Tiquilia atacamensis</i>	Herb				
	Portulacaceae	<i>Cistanthe</i> spp.	Herb	Portulacaceae		X	
	Malvaceae	<i>Cristaria</i> spp.	Herb	Malvaceae		X	
	<i>Tarasa operculata</i>	Herb					
Puna	Solanaceae	<i>Fabiana ramulosa</i>	Shrub	Solanaceae		X	
	Asteraceae	<i>Baccharis boliviensis</i>	Shrub	<i>Baccharis</i> type	X	X	
		<i>Diplostephium meyenii</i>	Shrub				
	Ephedraceae	<i>Ephedra breana</i>	Shrub	<i>Ephedra</i>	X		
	Asteraceae	<i>Senecio</i> spp.	Shrub	<i>Senecio/Parastrephia</i> type	X	X	
		<i>Parastrephia</i> spp.	Shrub				
	<i>Chuquiraga</i> spp.	Shrub	<i>Chuquiraga</i> type		X		
High Andean steppe	Poaceae	<i>Festuca orthophylla</i>	Grass	Poaceae	X		
		<i>Festuca chrysophylla</i>	Grass		X		
	Poaceae	<i>Stipa</i> spp.	Grass		X		
		<i>Deyeuxia</i> spp.	Grass		X		
Subnival	Apiaceae	<i>Azorella compacta</i>	Cushion shrub	<i>Azorella</i> type		X	
	Caryophyllaceae	<i>Pycnophyllum bryoides</i>	Cushion shrub	Caryophyllaceae		X	
	Asteraceae	<i>Chaetanthera</i> sp.	Rossete herb	<i>Proustia/Leucheria</i> type		X	
	Apiaceae	<i>Mulinum crassifolium</i>	Shrub	Apiaceae		X	
	Asteraceae	<i>Senecio</i> sp.	Shrub	<i>Senecio/Parastrephia</i> type	X	X	
	Montiaceae	<i>Lenzia</i> sp.	Rossete herb	Montiaceae		X	
Coastal scrubland	Cactaceae	<i>Echinopsis coquimbensis</i>	Cactus	Cactaceae		X	
	Oxalidaceae	<i>Oxalis gigantea</i>	Shrub	<i>Oxalis</i> type		X	
	Boraginaceae	<i>Heliotropium stenophyllum</i>	Shrub	<i>Heliotropium</i> type		X	
	Nolanaceae	<i>Nolana</i> spp.	Herb	Nolanaceae/Solanaceae		X	
Pre-Andean	Ephedraceae	<i>Ephedra breana</i>	Shrub	<i>Ephedra</i>	X		
	Solanaceae	<i>Lycium minutifolium</i>	Shrub	Solanaceae		X	
	Solanaceae	<i>Gymnophyton flexuosum</i>	Shrub	Solanaceae		X	
	Fabaceae	<i>Adesmia pedicellata</i>	Shrub	<i>Adesmia</i> type		X	
Sub-Andean	Fabaceae	<i>Adesmia hystrix</i>	Shrub	<i>Adesmia</i> type		X	
		<i>Adesmia aphylla</i>	Shrub				
Andean	Fabaceae	<i>Adesmia aegiceras</i>	Cushion shrub	<i>Adesmia</i> type		X	

consolidated and unconsolidated rodent midden samples were sieved through a 120- $\mu$ m mesh to separate macro- (plant, seeds, feces, etc.) and micro-remains (midden matrix). A 1-cm<sup>3</sup> aliquot of feces and matrix sample from each midden was separated for pollen analysis and processed following standard methods for pollen extraction (Faegri and Iversen, 1989). Pollen sums included a minimum of 300 grains. Pollen identification was based on the reference collection of Laboratorio de Paleoecología y Paleoclima (CEAZA; Centro de Estudios Avanzados en Zonas Áridas) and published atlases (Heusser, 1971; Markgraf and D'Antoni, 1978). Pollen percentages were calculated and plotted using TGView 1.7.16 (Grimm, 2011).

Correspondence analysis, including soil-surface and midden matrix samples from PASH, CDA, SdB, QAA, and RP, was performed and plotted with MVSP 3.13b (Multi-Variate Statistical Package). The data were transformed by applying a log-ratio transformation to eliminate the dependence of percentage data (Aitchison, 1986).

Non-metric multidimensional scaling (NMDS) analysis, including midden matrix and midden feces samples from the RP and CDA sites, was performed and plotted with the Vegan package (Oksanen et al., 2013) of the R Statistical Environment (R Core Team, 2014). These sites were selected since both have an appropriate number of samples (compared to the number of variables) to obtain robust results with this type of multivariate analysis.

**Table 2**  
Sites and kind of samples included in this study.

Site	Kind of sample	Name
Pozo Almonte-Salar del Huasco 3750	Surface	LLP3750
	Unconsolidated midden	SH 22
	Unconsolidated midden	ACT17
	Consolidated midden	SH 119
	Consolidated midden	SH 116
Pozo Almonte-Salar del Huasco 3550	Surface	LLP3550
	Unconsolidated midden	ACT 1
	Unconsolidated midden	ACT 2
	Consolidated midden	SH 161-2A
	Consolidated midden	SH 164
Cerros de Aiquina	Surface	LLP 15
	Surface	LLP 17
	Surface	LLP 20
	Unconsolidated midden	CDA 03
	Unconsolidated midden	CDA 16
	Unconsolidated midden	CDA 18
	Unconsolidated midden	CDA 19
	Consolidated midden	CDA 592
	Consolidated midden	CDA 517A
Sierra del Buitre	Surface	LLP22
	Unconsolidated midden	SdB 21
	Consolidated midden	SdB 113E
Quebrada Agua Amarga	Surface	LLP 22
	Unconsolidated midden	QAA 60
	Consolidated midden	QAA 20E
Río Potrerillos	Surface	LLP131
	Surface	LLP133
	Surface	LLP133
	Unconsolidated midden	RP131
	Unconsolidated midden	RP 133
	Unconsolidated midden	RP 134
	Consolidated midden	RP 107
Consolidated midden	RP 130A	

## Results and discussion

### Vegetation

The vegetation census data used in our analyses reflect the variations in composition and cover of the plant communities at these study sites in northern Chile (Fig. 4). A shrub-dominated community including *Adesmia* spp., *Baccharis boliviensis*, *Parastrephia* spp., and grasses, with a total vegetation cover of 22.3%, is present at PASH 3750 (Fig. 4a). Vegetation at PASH 3550 has similar total cover values (23.9%) but different composition; it is dominated by shrubs such as *Fabiana densa*, *Adesmia histrix*, *Baccharis boliviensis*, *Senecio* spp., and *Parastrephia quadrangularis* (Fig. 4b). CDA features a more diverse shrub community dominated by *Ambrosia artemisioides*, *Fabiana ramulosa*, and *Ephedra breana*, along with grasses, herbs, and cacti such as *Maihueiopsis camachoii* and *Echinopsis atacamensis*; total vegetation cover is 34.8% (Fig. 4c). RP has a lower total vegetation cover (8.22%), with plant communities dominated by *Ephedra breana* and *Adesmia aphylla*, with lesser amounts of *Senecio* spp., *Gymnophyton*

*flexuosum*, and *Lycium* spp. (Fig. 4d). The floristic list for QAA includes shrubs such as *Adesmia* spp. and *Ephedra breana* and annual herbs such as *Salpiglossis* spp., *Cistanthe* spp. and *Atriplex* spp. At SdB, isolated individuals of *Nolana* spp., *Cistanthe* spp., and *Cristaria* spp. were found.

Local vegetation data at the different sites match the vegetation patterns described at the regional scale (Fig. 3). Thus, PASH 3750 and PASH 3550 plant communities resemble the Puna shrub community, with the presence of grasses at the highest site (PASH 3750) consistent with its location near the transition to the high Andean steppe. In addition, the CDA vegetation census reflects the Prepuna xerophytic shrubland characterized by the presence of *Ambrosia artemisioides*, *Atriplex imbricata*, *Ephedra breana*, *Criptantha diffusa*, and *Tarasa* spp. and RP data resemble the Pre-Andean belt vegetation dominated by *Ephedra breana*, *Lycium minutifolium*, and *Adesmia pedicellata*. Similarly, the floristic composition of SdB and QAA resembles the vegetation associated with perennial river valleys within the Absolute desert. The vegetation census for QAA yielded unexpected results, including the presence of shrubs such as *Adesmia* spp. and *Ephedra breana* from the Pre-Andean belt. This is probably related to the close location of QAA to the transition between the Absolute desert and this vegetation belt (Fig. 3).

### Pollen–vegetation relationships

The modern pollen assemblages in soil-surface samples, consolidated middens, and unconsolidated middens from northern Chile (Fig. 5) feature key similarities and differences that provide insights into pollen–vegetation relationships and important taphonomic processes.

Pollen assemblages from the different types of samples reflect the different vegetation units from northern Chile where they were collected (Fig. 5). The pollen spectra from the PASH sites resemble the local vegetation and the broader Puna vegetation belt. PASH 3750 pollen assemblages are dominated by shrub pollen types such as *Baccharis* type (20–60%), and also feature *Senecio/Parastrephia* (5–40%), Fabaceae (<40%), and herbaceous pollen types including Chenopodiaceae (<25%) and grasses (Poaceae <10%). PASH 3550 pollen assemblages are similarly dominated by shrub pollen types such as *Senecio/Parastrephia* (5–70%), along with *Baccharis* type (5–55%), Solanaceae (<20%), Fabaceae (<40%), and herbs like Brassicaceae (<25%) and Chenopodiaceae (<45%).

The presence of grass in pollen assemblages from PASH 3750 is consistent with its proximity to the Puna–High Andean steppe transition. On the other hand, the presence of Chenopodiaceae and Brassicaceae in pollen assemblages from both PASH sites (Fig. 5) does not match the local vegetation censuses (Fig. 4). Both of these pollen types represent plants found in the Prepuna belt or in perennial springs in northern Chile, and both are anemophilous and high pollen producers. Thus, the presence of both pollen types in PASH samples may be attributed to medium- to long-distance pollen transport (1 to >10 km) from the Prepuna belt and/or perennial springs located close to the sites.

CDA pollen assemblages reflect both the local vegetation census data (Fig. 4) and the Prepuna vegetation type. These spectra are co-dominated by *Ephedra* (80–2%), *Ambrosia* type (60–2%), and Chenopodiaceae

**Table 3**  
<sup>14</sup>C and calibrated dates for consolidated rodent middens used in this study.

Site	Midden code	<sup>14</sup> C age	Calibrated age	Laboratory code
Pozo Almonte-Salar del Huasco	SH 119	Modern	–	UGAMS-6368
	SH 116	70 ± 30	AD 1878–1934	UGAMS-6365
	SH 161-2A	80 ± 25	AD 1878–1933	UGAMS-9272
	SH 164	90 ± 30	AD 1877–1950	UGAMS-9265
	SdB 113E	270 ± 15	AD 1655	UCIAMS 123273
Quebrada Agua Amarga	QAA 20E	150 ± 40	AD 1838	CAMS-133240
Río Potrerillos	RP 107	200 ± 25	AD 1758	UGAMS-3161
	RP 130A	130 ± 25	AD 1859	UGAMS-3158
	CDA 592	Modern	–	UGAMS-8972
Cerros de Aiquina	CDA 517A	Modern	–	UGAMS-8965

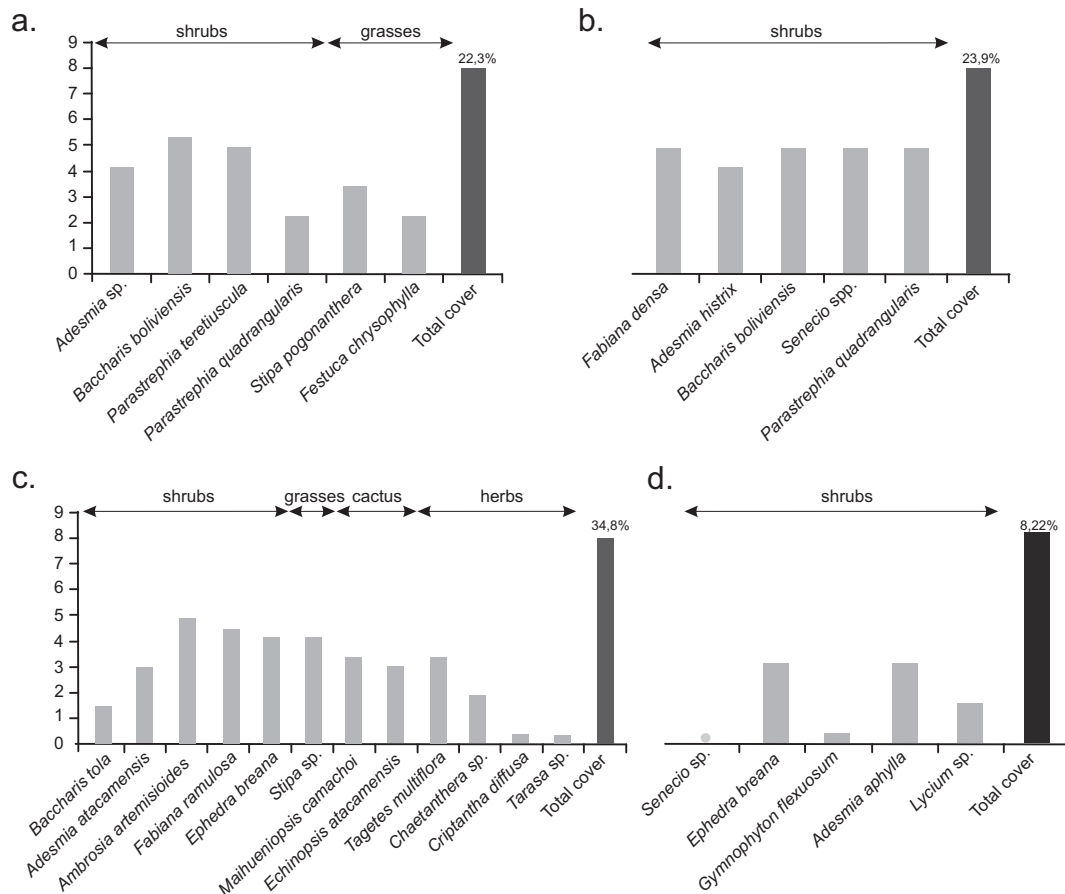


Fig. 4. Relative abundance of different vegetation types at the study sites: a. PASH 3750; b. PASH 3550; c. CDA; and d. RP.

(70–2%), with lesser amounts of Fabaceae (45–2%), *Senecio/Parastrephia* type (35–3%), *Baccharis* type (<20%), *Proustia/Leucheria* type (<20%), and *Krameria* (<25%) (Fig. 5). Similar to PASH, Chenopodiaceae pollen is present in CDA assemblages, even though no plants belonging to this family were found in the vegetation censuses. The presence of Chenopodiaceae may be attributable to nearby patches of *Atriplex imbricata*, one of the typical shrubs of the Prepuna belt.

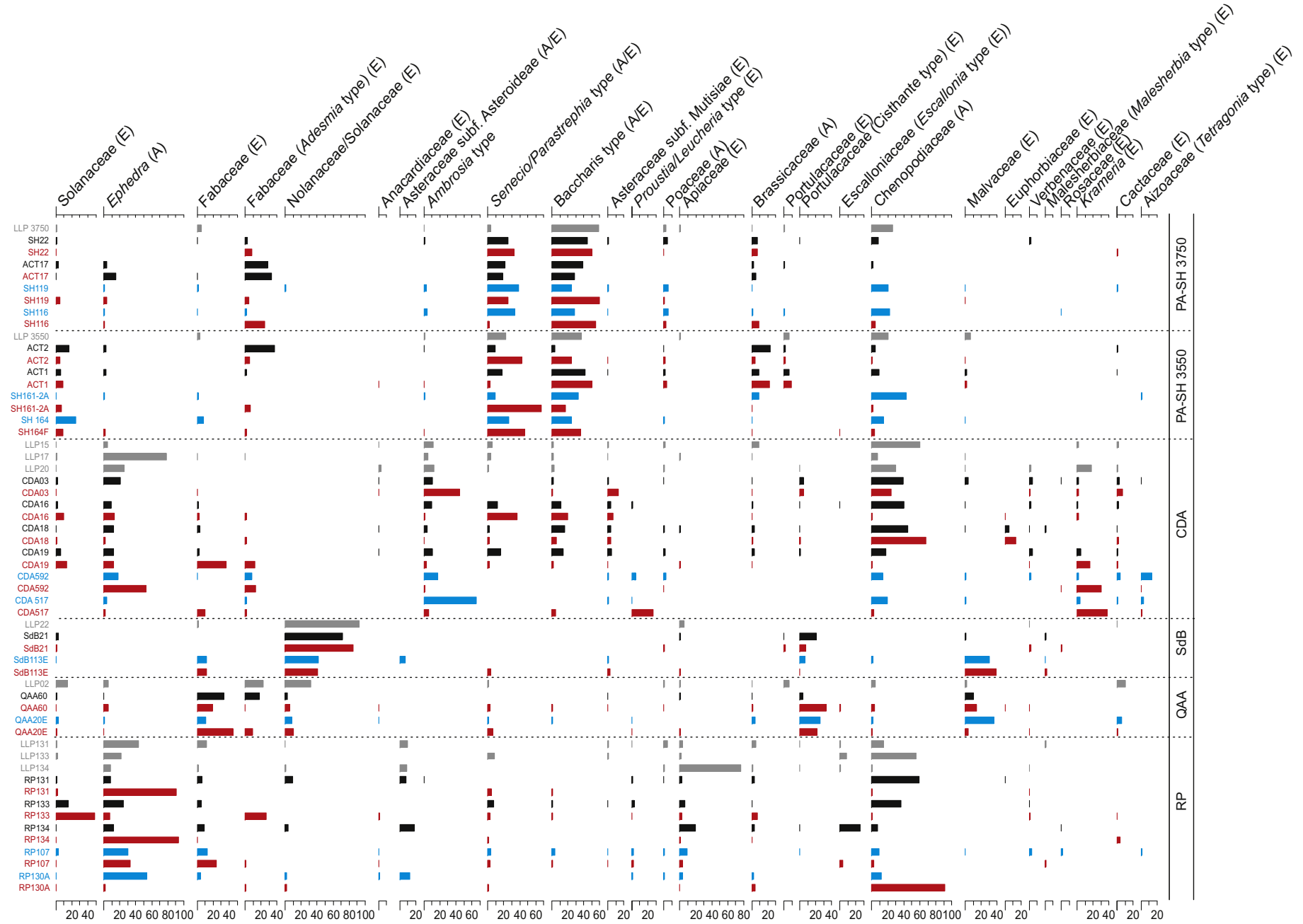
High percentages of Nolanaceae/Solanaceae (90–40%) and low percentages of Fabaceae (<10%), Portulacaceae (<10%), and Malvaceae (<40%) characterize SdB pollen assemblages (Fig. 5), reflecting riparian vegetation (i.e. in local springs) within the Absolute desert. QAA pollen assemblages feature Fabaceae (50–20%), Nolanaceae/Solanaceae (30–5%), Portulacaceae (35–5%), Malvaceae (40–5%), and Cactaceae (<10%) (Fig. 5). These pollen assemblages represent the vegetation of perennial river valleys within the Absolute desert associated with Pre-Andean *Adesmia* spp. dominated shrub communities.

RP pollen assemblages are dominated by *Ephedra* (90–10%) and Chenopodiaceae (90–2%), along with Solanaceae (40–2%), Fabaceae (<25%), Asteraceae subf. Asteroideae (<20%), Apiaceae (80–2%), and Escalloniaceae (*Escallonia* type; <25%) (Fig. 5). These pollen assemblages reflect the local vegetation (Fig. 4) as well as the pre-Andean vegetation belt. The presence of *Escallonia*-type pollen in RP assemblages is inconsistent with vegetation censuses and descriptions. However, *Escallonia pulvurulenta* is distributed in this area in azonal plant communities along small canyons, so *Escallonia*-type pollen may have been transported from such populations.

Correspondence analysis (Fig. 6a) shows that samples from each study site group together, regardless of the sample type (soil-surface or midden matrix), thus supporting the vegetation–pollen relationships described above. Samples from PASH are mainly defined by Puna shrub

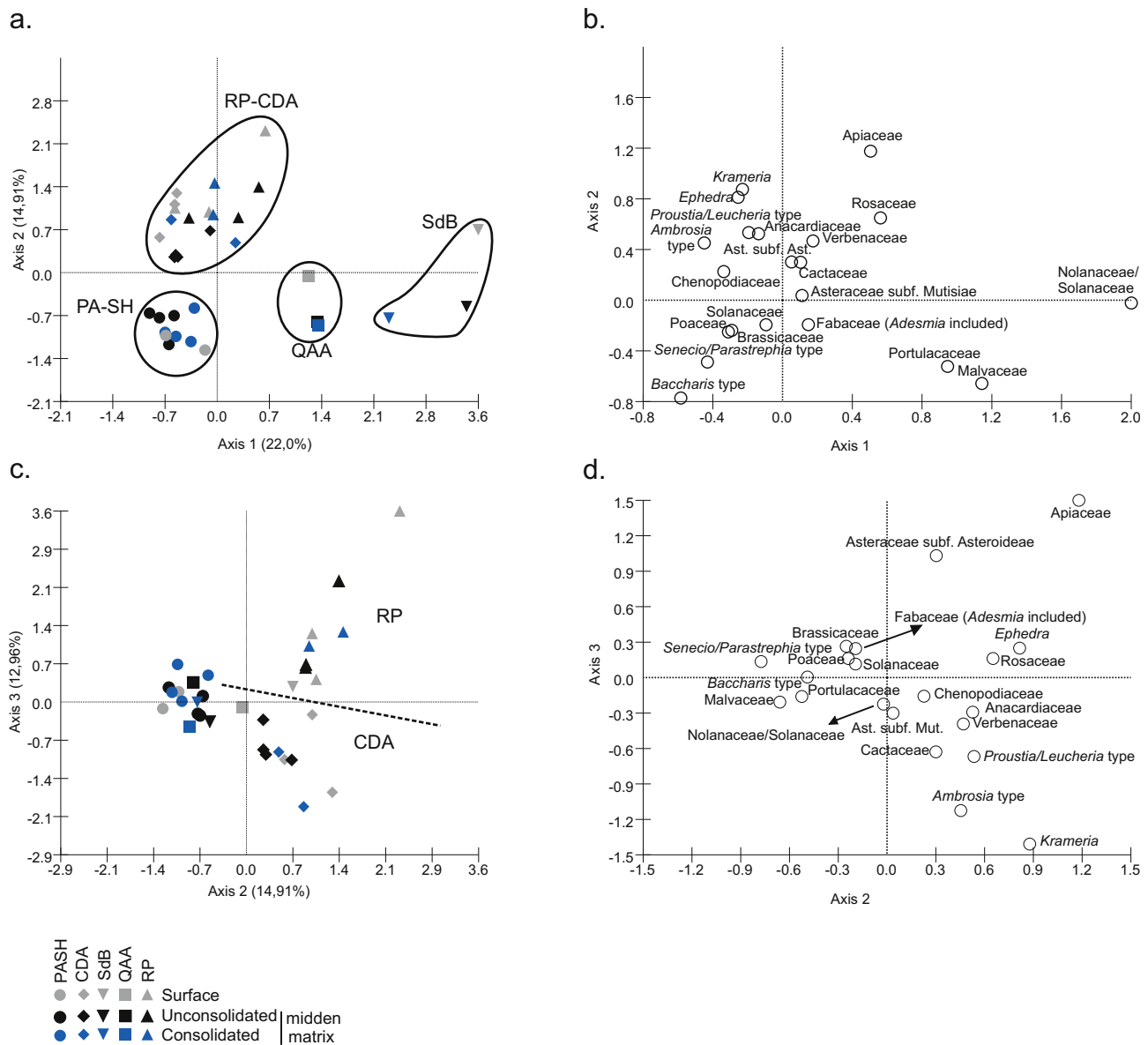
pollen types such as *Senecio/Parastrephia* and *Baccharis* types, whereas those from SdB and QAA are defined by riparian herb pollen types, including Nolanaceae/Solanaceae, Portulacaceae, and Malvaceae along Axis 1 (accounting for 22% of the total variance) (Fig. 6a,b). CDA and RP samples are separated along Axis 3 (accounting for 12.96% of the total variance) according to the abundance of Prepuna shrubs (*Ambrosia* type, *Protustia/Leucheria* type, and *Krameria*) and Pre-Andean belt shrubs (*Ephedra*, Asteraceae subf. Asteroideae, and Apiaceae), respectively (Fig. 6c, d). Overall, the modern pollen data reflect the various vegetation belts, but differences among sample types are also evident. In CDA and RP, anemophilous taxa (Table 1), such as *Ephedra* and Chenopodiaceae, are over-represented in soil-surface pollen assemblages (Fig. 5), which is not surprising given that the main (if not exclusive) source of pollen is air-borne deposition. Compared to soil-surface samples, consolidated and unconsolidated midden matrix pollen assemblages provide a more realistic picture of local vegetation, with both anemophilous and entomophilous species represented. This is likely because middens receive pollen from both airfall deposition (mainly anemophilous taxa) and biotic deposition (attached to fur, paws, or the plant remains gathered by rodents; mainly entomophilous, but with some anemophilous taxa) (Fig. 5). Because many of the plant species in desert areas, such as northern Chile, are entomophilous (e.g., Fabaceae, Solanaceae, *Proustia/Leucheria* type, Malvaceae, and Cactaceae; Table 1), the use of midden pollen assemblages seems to be advantageous, as they appear to produce a better sampling of the local vegetation and regional vegetation. This interpretation is consistent with the findings of King and Van Devender (1977) and Davis and Anderson (1987) in their analyses of *Neotoma* middens.

Furthermore, both consolidated and unconsolidated midden matrix pollen assemblages appear to reflect vegetation composition without major differences (Fig. 6), suggesting that the taphonomical processes



**Fig. 5.** Pollen diagram (percentages) of soil-surface (gray), consolidated midden matrix (blue), unconsolidated midden matrix (black), and feces from both kind of middens (red). Samples are arranged according to the collection sites and the different kind of samples can be identified by their color. General pollination syndrome of plants: (E) = entomophilous, (A) = anemophilous (Faegri and van der Pijl, 1979). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)





**Fig. 6.** Correspondence analysis for soil-surface, consolidated, and unconsolidated midden matrix samples; a. and c. plots show the sample ordination whereas b. and d. plots show the species ordination.

related to the consolidation or hydration cycles of the midden do not affect the pollen signal. This result suggests that pollen samples from unconsolidated middens are appropriate for use as modern analogs for fossil-pollen samples.

Pollen assemblages from rodent midden feces also reflect the composition of the surrounding vegetation, although in some ways they differ from the midden matrix samples (Fig. 5). Non-metric multidimensional scaling analysis of midden matrix and midden feces samples from RP (Stress = 0.18; Fig. 7a) and CDA (Stress = 0.10; Fig. 7b) show that both unconsolidated and consolidated midden matrix samples tend to group in the central area of the graph, whereas feces samples occur in more distal positions. This pattern appears to be driven by relatively high abundances of Chenopodiaceae, Anacardiaceae, Fabaceae (*Adesmia* type), and *Ephedra* at RP and higher values of *Ambrosia* type, *Senecio* type, Euphorbiaceae, *Proustia/Leucheria* type, Fabaceae, *Ephedra*, and *Krameria* at CDA. The distal ordination of the feces samples (Fig. 7a,b) indicates that those pollen assemblages contain over-representations of certain pollen types (regardless of whether they are entomophilous or anemophilous; Table 1) that are likely due to rodent consumption habits. The fact that midden-building rodents from northern Chile are dietary generalists

(Spotorno et al., 1998; Cortés et al., 2002; Latorre et al., 2002) produces an adequate sampling of local vegetation, but also introduces some biases because of the differential consumption of particular species and/or plant parts (e.g., flowers vs. leaves/stems). Thus, matrix pollen assemblages are preferable to those from feces for use as modern analogs, as they do not appear to feature the over-representation of certain taxa due to rodent dietary habits.

## Conclusions

Our analyses of pollen assemblages from modern rodent middens in northern Chile show that (1) the pollen signal from midden matrix provides a more realistic reflection of local vegetation than soil-surface samples because the complementary mechanisms of pollen deposition in middens (airfall and biotic) reflect both anemophilous and entomophilous plants; (2) there appear to be no differences in pollen assemblages from consolidated versus unconsolidated middens, suggesting that taphonomical processes related to the consolidation of the midden or hydration cycles do not affect the pollen signal; and (3) in contrast to feces pollen assemblages, rodent dietary habits do not seem to influence

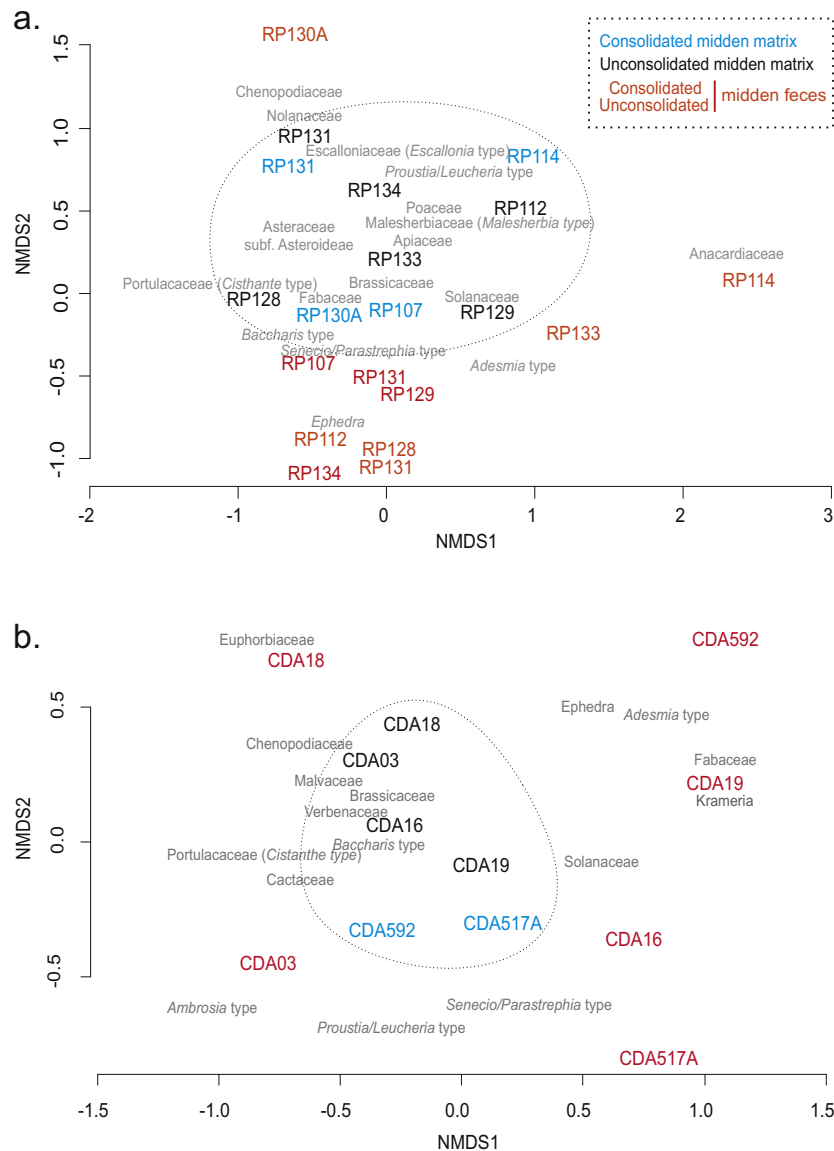


Fig. 7. Non-metric multidimensional scaling analysis for pollen assemblages from midden matrix and feces from a. Río Potrerillos (RP) and b. Cerros de Aiquina (CDA).

midden matrix pollen assemblages, presumably because midden agents in northern Chile are dietary generalists.

Taken together, these results demonstrate that pollen assemblages preserved in the matrix of rodent middens provide a balanced and robust reflection of plant communities at local and regional scales. Our finding that such pollen records represent vegetation patterns rather than rodent habits is of particular importance, as most evidence for past ecological and climatic change in northern Chile is based on these archives. This study illustrates the potential for the development of a robust, regional vegetation–pollen–climate calibration set that represents as many ecological and climatic scenarios as possible. Intensive sampling of unconsolidated middens along summer and winter precipitation gradients and the mean annual temperature gradient (Fig. 2b, c, d) at different latitudes across northern Chile would provide a modern pollen data set that could be applied to fossil records to further improve our understanding of past environmental change in this region.

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