CLIMA Y VEGETACIÓN DEL DESIERTO DE ATACAMA DURANTE EL CUATERNARIO TARDÍO, II REGIÓN, CHILE

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RESUMEN

En esta tesis se presentan los resultados obtenidos utilizando un nuevo método paleoecológico diseñado específicamente para las regiones áridas del mundo: las paleomadrigueras de roedores. Estas madrigueras milenarias constituyen un verdadero archivo de cambio biológico y climático del paisaje del norte de Chile. En el primer capítulo de esta tesis se presentan los resultados de ocho transectos altitudinales, realizados en el norte de Chile entre 18° y 26° de latitud sur. Esto permite aclarar cuales son los controles climáticos actuales sobre la vegetación y su uso como análogo moderno. El segundo capítulo entrega los detalles del primer estudio chileno de paleomadrigueras, realizado sobre 49 muestras provenientes de la Segunda Región de Chile. Los resultados obtenidos indican que, para los últimos 45.000 años, la vegetación invadió amplias extensiones del desierto absoluto durante períodos breves de incremento de lluvia estival, entre 13.800-9500 y 7000-3000 años calendario atrás. El último capítulo aporta nuevos antecedentes obtenidos de 44 paleomadrigueras encontradas en la Cordillera Domeyko de la Segunda Región, entre 3100 y 3400 m de altitud. Las muestras detallan con precisión las fases húmedas descritas previamente. Los resultados obtenidos de ambos estudios discrepan de que es la insolación directa sobre Sudamérica lo que ha regulado la intensidad pasada de la circulación atmosférica sobre el Altiplano durante los últimos 22 mil años. En cambio, se propone que la circulación sobre los Andes Centrales, hoy en parte regulada por El Niño-Oscilación del Sur, fue afectada preferentemente por cambios en las temperaturas superficiales del Océano Pacífico tropical asociados a factores extra-regionales.

ABSTRACT

This thesis presents the results obtained from a new paleoecological method specifically designed for use in the arid regions of the world. Known as rodent middens, these constitute veritable archives of past biological and climatic change of the Atacama Desert of northern Chile. The first chapter of this thesis presents the results obtained from eight altitudinal surveys performed in northern Chile between 18° and 26° latitude south. The results from this study afford the basic modern analogue for interpreting the midden records and also provide considerable insight into what climatic controls affect plant distributions in the Atacama Desert today. In the second chapter I present the results from 49 middens collected from Chile's Second Region, the first such study in all of Chile. Results indicate that plants invaded considerable expansions of the desert for brief periods of increased summer rainfall during the past 45,000 years, radiocarbon dated between 13,800-9500 and 7000-3000 calendar years ago. The final chapter presents the results obtained from 44 rodent middens collected from the prepuna vegetation belt, between 3100-3400 m in elevation. The results from this study replicate and enhance our dating of the wet phases previously described. Results from both midden studies reject local insolation over South America as a major forcing factor of the intensity of atmospheric circulation over the central Andes for the past 22,000 years. This system today is partly affected by El Niño-Southern Oscillation, and we propose that sea surface temperatures changes of the tropical Pacific Ocean associated with extra-regional factors, are chiefly responsible for climate change over the central Andes.

INTRODUCCIÓN GENERAL

Quizás uno de los hallazgos más importantes de la investigación paleoclimática de las últimas décadas ha sido el descubrimiento de grandes fluctuaciones del clima global en escalas mileniales de tiempo (Clark et al., 1999). Estos cambios ocurrían a escalas de tiempo demasiado rápidos y no podían ser explicados por las hipótesis clásica basada en variaciones orbitales (Imbrie *et al.*, 1992) o por cambios en la circulación termohalina (Broecker, 1991; Broecker & Denton, 1990). Últimamente, se ha generado un gran debate en torno al rol que ha tenido el Océano Pacífico tropical como generador de grandes cambios climáticos globales a múltiples escalas temporales, ya sean estas a nivel intra- o interdecadales, o mileniales. Esta idea nació a partir de una nueva apreciación del creciente rol que tiene el fenómeno El Niño-Oscilación del Sur (ENOS) como motor de cambios climáticos a escala global (Cane & Clement, 1999). Esta hipótesis básicamente establece que son variaciones en la radiación solar sobre el Pacífico tropical las que inducen cambios no-lineales en el comportamiento de este, produciendo así cambios climáticos a escala milenial (Cane & Clement, 1999; Clement & Cane, 1999; Clement *et al.*, 1999).

Sin embargo, uno de los problemas para corroborar esta hipótesis ha sido la falta de registros paleoclimáticos con cronologías de alta resolución obtenidos en latitudes tropicales. Esto ha producido un sesgo y mayor dependencia sobre los registros polares de testigos de hielo, y en particular sobre el uso del gas metano presente en estos para inferir cambio climático en los trópicos a escala milenial (Chappellaz *et al*., 1990; Chappellaz *et al*., 1993; Severinghaus & Brook, 1999).

Los Andes centrales de Sudamérica han sido la excepción a este patrón. En esta región se han obtenido numerosos registros paleoclimáticos en los últimos años. Estos registros muestran numerosas coincidencias pero también muchos conflictos de interpretación y de fechado, como fue ampliamente debatido en un taller internacional dedicado al paleoclima de los Andes Centrales (http://wwwpaztcn.wr.usgs.gov/pcaw). En parte estos problemas surgen por una confusión de como las distintas variables climáticas, como temperatura, precipitación y evaporación, han afectado cada registro, ya sean estos de terrazas lacustres, de testigos de sales o de hielo, o fluctuaciones de glaciares tropicales. A su vez, la gran variabilidad regional del clima actual que existe sobre los Andes Centrales aporta otro nivel de complejidad sobre los intentos por mejorar la comprensión del paleoclima de esta región.

Una manera singular de abordar estos problemas es reconstruir un registro paleoclimático de cronología sólida que sea controlado en gran parte por una sola variable climática. Resulta paradójico entonces que en esta tesis se ha recurrido a uno de los lugares más áridos del mundo (Borgel, 1973; Caviedes, 1973) para documentar fluctuaciones de regímenes tropicales: el Desierto de Atacama. Para esto hemos recurrido a una técnica de reconstrucción paleoclimática desarrollada en el sur-oeste de los Estados Unidos (Betancourt *et al*., 1990), nunca antes aplicada en Chile, conocida como *paleomadrigueras de roedores*.

Este método está basado sobre la recolección de madrigueras de roedores abandonadas y preservadas en aleros y cuevas de zonas áridas. Dichas madrigueras contienen cuantioso material orgánico, ya sea de huesos, insectos, plumas, pelos y macrorrestos vegetales, todo encasillado en una pétrea matriz de orina cristalizada. En el norte de Chile, estas madrigueras son producidas por roedores habitantes de rocas, como la vizcacha (*Lagidium viscacia*), el lauchón orejudo (*Phyllotis* spp), la rata chinchilla (*Abrocoma cinerea*) y el ratón cola de pincel (*Octodontomys gliroides*) (Betancourt *et al.*, 2000; Betancourt & Saavedra, 2002). El método consiste en el fechado mediante radiocarbono (^{14}C), ya sea convencional o atómico (AMS), de las heces presentes en el depósito y el análisis de la composición vegetal de esta. La composición florística se obtiene entonces mediante la compilación de los macrorrestos presentes, material de cutículas presentes en las fecas y el polen presente en la matriz de orina. Los primeros dos métodos fueron empleados en esta tesis para reconstruir el paleoclima del Atacama. Cada madriguera con su fecha ^{14}C respectiva es un punto en el tiempo y el espacio y es solo con la recuperación de numerosos "puntos" en una región que se obtiene un cuadro general de como ha cambiado la vegetación, y por ende, el clima.

La Zona de Estudio

Sin ningún lugar a duda el Desierto de Atacama es uno de los ambientes más excepcionales en el mundo. Este desierto se extiende desde el norte de la costa peruana (5°S) a lo largo de la vertiente occidental de los Andes hasta la ciudad de Copiapó en territorio chileno (27°S). La escasez de precipitaciones ha generado un desierto 'absoluto' donde los valores de las coberturas de plantas vasculares son nulos (Villagrán *et al.*, 1983; Arroyo *et al.*, 1988) y ha producido un paisaje singular caracterizado por la práctica ausencia de procesos erosivos importantes (Alpers & Brimhall, 1988; Mortimer, 1980). Este último hecho, asociado a una tectónica activa, hace que la zona del Desierto de Atacama constituya uno de los relieves más extraordinarios del mundo: en menos de 300 km existen casi 15.000 m de desnivel entre la fosa marina de Atacama (-8066 m) y la cumbre del Volcán Llullaillaco (6723 m) en la Cordillera de los Andes (Abele, 1988).

Ubicada entre los 22° y los 24° de latitud sur, la zona de estudio de esta tesis corresponde al sector de máxima penetración de la aridez hacia el interior del Desierto de Atacama en el norte de Chile (Villagrán *et al.*, 1983). Esta área, ubicada al interior de la ciudad de Calama y el Salar de Atacama, representa en parte a las vertientes oriental y occidental de la Cordillera de Domeyko y a la vertiente occidental de la Cordillera de los Andes. La aridez extrema favorece la preservación de vastas extensiones de ignimbritas volcánicas formadas durante el Mio-Plioceno, a lo largo de gran parte de la zona e interrumpidas por quebradas profundas y serranías locales de rocas Paleozoicas y Mesozoicas, como la Serranía de Tuina y los Cerros de Aiquina - Minta (Abele, 1988; Marinovic & Lahsen, 1984). A su vez, el área comprende el límite septentrional de la Cordillera Domeyko, un gran macizo de rocas sedimentarias Paleozoicas a Oligocénicas, en su mayoría marinas o volcano-siliciclásticas y delimitadas por fallas inversas en su vertiente occidental y fallas normales en su vertiente oriental. Las alturas promedio de esta Cordillera van desde los 3500 a 4000 m con su punto más alto en el Cerro Quimal (4500 m.). Domos volcánicos y estratovolcanes, cuyas edades van desde el Plioceno hasta el Holoceno, constituyen las cimas más altas de la Cordillera de los Andes y gran parte de ellas sobrepasan los 5500 m en altura (Marinovic & Lahsen, 1984).

Uno de los objetivos principales de esta tesis fue documentar la migración de plantas hacia el Desierto. Sobre la base de la composición, fisionomía, y cobertura vegetal, la vegetación de los Andes del Norte Grande de Chile (18°-27° S) ha sido dividida tradicionalmente en tres pisos o zonas: el piso Prepuneño, que comienza a los 2700-2800 m y se extiende hasta los 3100-3500 m; la Puna o Tolar, que va desde los 3100-3500 hasta los 3900-4000 m; y la estepa Altoandina, cuyo comienzo oscila entre los 3900-4000 m y termina donde cesa la cobertura vegetal, a los 4500-4800 m (Villagrán *et al.*, 1981). Considerando estos antecedentes, un énfasis particular fue puesto en las zonas rocosas presentes en torno al límite sensible inferior de la vegetación desde los 2500 m hasta los 3100 m. Sobre la base de estos resultados se ponen a prueba las distintas hipótesis paleoclimáticas que han sido propuestas para el último ciclo glacial-interglacial en los Andes Centrales.

A continuación sigue la hipótesis general de la tesis seguido de las hipótesis específicas de trabajo.

Hipótesis general

"Si la vegetación del Desierto de Atacama (22°-24°S) se vió afectada por las profundas transformaciones climáticas asociadas al último ciclo glacial/interglacial, entonces:

a) en períodos más húmedos que el régimen climático actual, la mayor humedad efectiva disponible en el ambiente indujo a las especies de plantas zonales presentes en los pisos Prepuneño y de Tolar a expandir sus rangos de distribución altitudinal y en un descenso del límite inferior de la vegetación hacia el desierto absoluto. A su vez, la especies del Altoandino se desplazaron desde zonas de mayor altitud hacia zonas de menor altitud. Esto se expresaría en la obtención de 'middens' con vegetación Altoandina y de Tolar en el Prepuneño o desierto absoluto.

b) en los períodos más secos que el régimen climático actual los indicadores en 'middens' mostrarían vegetación prepuneña en altitudes más altas que las que corresponden hoy en día (sobre 3200-3300 m); además, se esperaría escasez o absoluta falta de 'middens' correspondientes al piso Prepuneño en las altitudes características de ese piso en el presente (2700-3200 m), debido a la baja bioproductividad del ambiente causado por la migración hacia mayores altitudes del límite inferior de la vegetación y/o la extinción (regional o local) de las especies estresadas de este piso."

Cabe destacar la posibilidad de múltiples escenarios posibles al conjugar las variables climáticas de precipitación y temperatura. No obstante, los gradientes vegetacionales actuales en el Desierto de Atacama parecen estar controlados principalmente por la cantidad de precipitación y humedad efectiva y en menor medida por gradientes de temperatura (Arroyo *et al.*, 1988)

Hipótesis específicas

1) "Las fases húmedas y frías propuestas para el Pleistoceno tardío, tales como las fases 'Minchin' (>35-23 ^{14}C kyr) (*kyr*: miles de años antes de 1950) y 'Tauca' (entre los 16-11,5 kyr calendario) pueden ser puestas a prueba mediante la evidencia arrojada por los 'middens' ya que deberían producir el desplazamiento de especies altoandinas y del tolar hacia menores altitudes y la colonización vegetacional de zonas del actual desierto absoluto."

2) "A su vez, las fases de mayor aridez propuestas a partir de registros geológicos y arqueológicos para el Desierto de Atacama (percibido como el "silencio arqueológico" entre los 9 y 3,8 kyr calendario) determinaron la restricción y/o la extinción de las especies presentes actualmente en el límite inferior de la vegetación (piso prepuneño). Luego, habría ausencia o escasez de middens en las altitudes desérticas durante esas fases, mientras que depósitos a mayores altitudes tendrán especies pertenecientes a pisos inferiores."

3) "La etapa húmeda y cálida de la fase "Tauca" (Clapperton, 1993; Clapperton *et al.*, 1997; Grosjean, 1994; Grosjean & Nuñez, 1994) entre los 11,5 y 9 kyr calendario, debió producir dinámicas diferentes en las respuestas de la vegetación. Esto se vería reflejado en la expansión de todos los pisos vegetacionales tanto hacia mayores como hacia menores altitudes durante las etapas húmedo/cálidas, hecho que se vería reflejado en 'middens' de las altitudes respectivas."

Sobre la estructura de esta tesis

Esta tesis consta de tres publicaciones (enviadas o por enviar a revistas especializadas de habla inglesa) divididos en capítulos respectivos. Los métodos, resultados y conclusiones de esta tesis se encuentran en estos tres capítulos.

El primer capítulo es titulado "A natural experiment revisited: latitudinal and altitudinal plant diversity/productivity gradients in the Atacama Desert and Pacific slope of the Central Andes" y fue escrito por Claudio Latorre, Carolina Villagrán, Antonio Maldonado y Julio L. Betancourt. El manuscrito fue elaborado para ser enviado a la revista "*Global Ecology & Biogeography*". Este capítulo aborda un problema crítico en cualquier estudio paleoecológico: el análogo moderno. ¿Como se distribuye la vegetación actual en la vertiente andina del norte de Chile? ¿Cuales son sus controles climáticos? ¿Cuales son las principales hipótesis biogeográficas postuladas para el origen de esta flora singular? Estas son preguntas que el primer capítulo intenta responder.

El segundo capítulo es titulado "Vegetation Invasions into Absolute Desert: A 45,000-Yr Rodent Midden Record from the Calama-Salar de Atacama Basins, Northern Chile (22-24°S)" y fue escrito por Claudio Latorre, Julio L. Betancourt, Kate A. Rylander, y Jay Quade. Este manuscrito se encuentra publicado en la revista "*Geological Society of America Bulletin*". En este capítulo, se abordó el estudio de las paleomadrigueras de manera específica, y se discuten los métodos exhaustivamente como a su vez los primeros resultados para un registro de este tipo en Sudamérica. Los resultados aportados por este estudio corroboran la presencia de una gran fase húmeda al final del Pleistoceno en el Atacama, precisamente fechada entre 13.800 y 9.500 años calendario antes del presente. Otros resultados fueron provocativos para la comunidad paleoclimática de los Andes Centrales ya que señalan la posible existencia de una fase húmeda durante el Holoceno medio, asociado a mayor actividad del Océano Pacífico.

El tercer y último capítulo titulado "A vegetation history from the arid prepuna of northern Chile (22-23°S) over the last 13,500 years " fue escrito por Claudio Latorre, Julio L. Betancourt, Kate A. Rylander, Jay Quade y Oscar Matthei. Este manuscrito, actualmente en prensa en "*Palaeogeography, Palaeoclimatology, Palaeoecology*" replica los resultados principales del estudio presentando en el capítulo dos. Además, aporta nuevos datos de paleomadrigueras para enfrentar una de las partes más débiles del capítulo anterior, esto es la presencia de un Holoceno medio más húmedo de lo que se pensaba.

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Capítulo 1:

“A natural experiment revisited: latitudinal and altitudinal plant diversity/productivity gradients in the Atacama Desert and Pacific slope of the Central Andes”

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ABSTRACT

Using simple climatic parameters to infer productivity, we have documented patterns of local species richness, percent cover and species distributions along altitudinal and latitudinal gradients across the Atacama Desert and adjacent Andes of northern Chile. A plethora of studies have documented the relationship between productivity and species richness. Most of these studies indicate either positive linear or unimodal relationships, depending on scale. Here we present evidence from eight altitudinal vegetation surveys from latitudes along the Andes Cordillera of northern Chile to the point that productivity gradients are clearly driving local species richness and percent cover. Productivity, as established by available moisture and mean annual temperature, is highest at intermediate elevations. All of our transects displayed maximum percent cover and local species richness between 3500-4000 m in elevation depending on latitude. Thus most species trade off higher rainfall available at higher altitudes for more mesic temperatures. But as aridity increases with latitude, local species richness declines and plants are forced upslope were they encounter less productive conditions. The result is that at the hyperarid core region of the Atacama, between 24-26° S latitude, percent cover drops by an order of magnitude and local richness is seven-fold reduced when compared to transects further north.

A flurry of recent paleoclimate literature also allows us to adventure several hypotheses as to what has regulated the distribution of the Andean flora in northern Chile during the past. Clearly, increases in precipitation associated with intensified monsoonal conditions during glacial to interglacial transitions have affected this flora differently than those associated with northward expansions of the westerlies during full glacial periods.

Keywords: phytogeography, Atacama Desert, northern Chile, Andes Cordillera, paleoecology, historical biogeography, log-series survey method, arid diagonal.

INTRODUCTION

As human-induced extinctions become more widespread, ecologists are racing to elucidate the links that exist between ecosystem properties such as productivity and biological diversity. An ever increasing body of literature has documented the strong positive relationship between productivity (the rate of conversion of resources to biomass from solar energy per unit area per unit time) and species richness (see Waide *et al.*, 1999 for a recent review). The relationship seems to be scale dependent, with unimodal patterns on local scales and linear patterns on regional scales (Waide *et al.*, 1999; Chase & Leibold, 2002). The literature on land plant diversity, however, has mostly concentrated on humid environments rather than deserts (Currie & Paquin, 1987; Huston, 1994; Tilman *et al.*, 1996; Tilman *et al.*, 1997). What research exists for arid enviroments has mostly been conducted in hot lowland deserts (Whittaker & Niering, 1965, 1975; Webb *et al.*, 1983; Bowers *et al.*, 2002). This research has demonstrated that in hot deserts productivity is highly variable in space and time and positively correlated with moisture availability (Waide *et al.*, 1999). Almost nothing is known about how this pattern might develop in high-altitude cold deserts. One advantage of working in such extreme environments is that biotic interactions (such as interspecific competition), which may possibly confound the relationship between productivity and diversity in very productive environments, are often neglible.

The Pacific slope of the central Andes and adjacent Atacama Desert (Fig. 1.1) provide a suitable testing ground for these hypotheses in cold desert environments. Here, plant cover is very low (<25%), interspecific competition is often neglible (Armesto & Villagrán, 1987) and thus can offer helpful insights into the nature of the productivity-biodiversity relationship. In the design of this particular 'natural experiment', hyperaridity at low elevations gives way to extreme cold at high elevations and exacts a double filter on species distribution and diversity. Latitude imposes a secondary control, with aridity at equivalent elevations increasing southward to a maximum in the transition between summer and winter rainfall regimes between 24-26° S.

The sharp latitudinal and altitudinal climatic gradients of the Atacama have proven fertile testing ground for numerous biogeographic and ecologic hypotheses. These range from the historical development of its flora (Villagrán *et al.*, 1983; Arroyo *et al.*, 1988), to the predominance of endemics and life-form distribution (Arroyo *et al.*, 1988; Arroyo *et al.*, 1998), nutrient recycling (Ehleringer *et al.*, 1992) and the relationship between species richness, altitude, and precipitation along riparian habitats (Gutierrez *et al.*, 1998).

All these previous studies imply that aridity gradients would seem to be responsible for patterns in vegetation cover, species richness and the overall distribution of vegetation belts. The conventional wisdom is that peak diversity and maximum total cover should occur at intermediate elevations, where both cold and dryness are less severe. Although precipitation in the Atacama increases with elevation (Fig. 1.2), decreasing temperatures set a limit on productivity, which thus peaks at intermediate elevations. The sparse temperature and precipitation records available for northern Chile indicate that the elevation of the intersection between mean annual rainfall and mean annual temperature increases with latitude (Fig. 1.2). This implies that peak productivity should also increase in altitude with increasing latitude as well. Overall total productivity should also decrease, as the increase in altitude entails a drop in temperature as well. Here, we present patterns of species richness, percent cover values and plant distributions from the Pacific slope of the Andes to test these hypotheses and offer further insight into the productivity-biodiversity debate. We also discuss the past enviromental history of this cold desert and its possible impact on the distribution of the modern day floras in the light of recent paleoecological evidence for past climate change (Betancourt *et al.*, 2000; Latorre *et al.*, 2002a; Latorre *et al.*, 2002b).

Overview of the phytogeography of the central Andes

Located along the Pacific margin of South America and extending some 7,500 km (65° in latitude), the Andes Cordillera spans both the northern and southern tropics and reaches south to Tierra del Fuego. Over 900 km wide at its central portion, with altitudes surpassing 6000 m, it is a region of diverse climate and biota. The Andes have had a long history of profound geologic change since their origin back in the Mesozoic (Zeil, 1979). In particular, the central and northern Andes had only attained half of their present altitude 10 million years ago; their role as a formidable barrier to atmospheric circulation and biological dispersal is thus a relatively recent feature of the South American continent (Gregory-Wodzicki, 2000).

The Andean orography establishes a strong west-east rainfall gradient across South America. South of 26° latitude the western Andean front receives more precipitation than the eastern slope, the product of the increased influence of the westerly (extratropical) rainfall belt. Whereas the westerlies are highly seasonal in the mediterranean climate zone of central Chile, their influence becomes much more permanent south of 38° latitude where precipitation occurs year-round (Schwerdtfeger, 1976). The combined effect of these two major circulation systems, coupled with the orographic rainshadow of the Andes, produces a belt of semiarid to arid climates and vegetation that crosses the continent (called the 'arid diagonal') from the Pacific coast south of the Equator, across the central Andes, and down to the Atlantic Ocean through Argentine Patagonia. Maximum aridity, or the core region, of this diagonal is centered along the Andes between 24-26° S (Garleff *et al.*, 1991).

To date, the best known examples of this close-knit interaction between abiotic factors and Andean vegetation are embodied by the various classification schemes for vegetation zonation (Czajka, 1968; Graf, 1986; Hueck & Seibert, 1972; Troll, 1959). Thus along both slopes of the Andes along the equator we find that tropical rainforest dominates below 1000 m, and is succeeded by Andean evergreen forests up to 3000 m. This formation then grades through strings of cloud forests into the Andean belts dominated by shrubs and perennial herbs known as the subpáramo, páramo and subnival which continue towards the upper vegetation limit located at approximately 5000 m. In contrast, the pronounced east-west asymmetry and different floristic composition of the central Andes interrupts this biogeographic pattern, and delineates the singularity of the Puna Province within the Andean-Patagonian Dominion (Cabrera, 1968; Cabrera &

Willink, 1980). Whereas the eastern Cordillera maintains a similar vegetation belt distribution to that seen further north, the Altiplano and the western Cordillera is dominated by semi-deserts and arid steppe that constitute what has been termed the Puna Formation (Cabrera, 1968; Ruthsatz, 1977). On the Pacific slope of the Andes, an impoverished vegetation grades into hyperarid desert: the Atacama Desert of southern Peru and northern Chile. The presence of absolute desert, defined by the general absence of vascular plants (Becerra & Faúndez, 2001) here marks the western limit of the Andean Puna floras (Fig. 1.1).

Climate and Origin of the Atacama Desert

The climate of the Atacama Desert, possibly one of the driest places on Earth, is due to several factors, which include the pronounced orographic rainfall shadow caused by the Andean massif, low sea surface temperatures off the coast due to the north flowing Humboldt Current, and the subsidence of air masses associated with the subtropical High known as the South Pacific Anticyclone (SPA) (Borgel, 1973; Caviedes, 1973; Ruttlant *et al.*, 1998). Precipitation along the western Andean slope (18-24° S latitude) results mostly from convective air masses that cross the Andean crest bringing moisture laden air across the Altiplano and ultimately from the Amazon Basin. The intensity of summer convection over the central Andes is strongly linked to an upper tropospheric feature known as the Bolivian High which during favorable years is capable of interrupting west to east zonal flow in the upper troposphere enabling moisture transport across the Altiplano (Aceituno & Montecinos, 1993; Lenters & Cook, 1995, 1997; Garreaud *et al.*, 2002). Thus, mean annual precipitation is greatest at 18°

and drops off sharply with decreasing altitude and gradually with increasing latitude (Fig. 1.2). Summer convective cloudiness decreases along these gradients as well and practically disappears south of 23° latitude, delimiting a region that is practically without precipitation (Arroyo et al., 1988). This region of maximum hyperaridity extends south to approximately 26° latitude where precipitation increases abruptly due to more frequent incursions of winter stormfronts associated with the westerly rainfall belt. Infrequent snowfall events associated with cut-off lows can reach as far north as southern Perú, and have been underestimated in local precipitation records (Vuille & Baumgartner, 1993; Vuille & Ammann, 1997; Ammann *et al.*, 2001). The low relative moisture content of the atmosphere, however, produces direct sublimation of the snowpack back into the atmosphere generating little soil infiltration and runoff (Vuille & Ammann, 1997).

Few temperature records are available from northern Chile. The few records available indicate large variations in daily temperatures of up to 30° C at Canchones (900 masl- Rundel *et al.*, 1991) but little variation in mean annual temperature between 21-24° S latitude (Fig. 1.2). Also, the low moisture content of the atmosphere generates a constant adiabatic lapse rate of 6.5° per 1000 m. These two features of the temperature regime in northern Chile should simplify interpretation of vegetation gradients with elevation, a fact pointed out previously by Arroyo *et al.* (1988).

Arid conditions in the Atacama Desert are of ancient origin and probably date back to the late Eocene (Mortimer, 1973, 1980; Ericksen, 1981, 1983). Hyperaridity has been present in the central Atacama for at least the last 15 million years, based on reduced erosion rates and supergene copper enrichment (Alpers & Brimhall, 1988).

Hyperaridity was in part generated by the Andean orogeny, which doubled the average elevation of the central Andes during the past 10 million years (Gregory-Wodzicki, 2000). A second factor is the cold Humboldt Current, which reached its present intensity by the early Pliocene (Zinsmeister, 1978). The South Pacific Anticyclone, a semi-permanent feature of large-scale atmospheric circulation largely responsible for the aridity of the Pacific slope of the Central Andes, has been "anchored" against the westward bend in the South American continent throughout the Neogene (Caviedes, 1973).

While this antiquity has had profound effects on the distribution of modern day Andean floras, these have also experimented profound redistribution during the climate changes that have occurred over the Pleistocene as documented by numerous pollen records in the northern and central Andes (Graf, 1992; Hooghiemstra & Van der Hammen, 1993; Hansen, 1995; Hooghiemstra, 1995). Because the NW/SE precipitation gradient present over the central Andes is so pronounced, any changes in this system would have had a profound effect on the Puna biota. This can be analyzed in more detail during past glacial-interglacial cycles along the hyperarid edge of this system were rainfall peters out. Any movement of this sensitive climatic boundary would produce a concomitant descent of the lower limits of the vegetation as well as reduce the area of the Atacama Desert as demonstrated by recent paleoecological studies (Betancourt *et al.*, 2000; Betancourt & Saavedra, 2002; Latorre *et al.*, 2002a; Latorre *et al.*, 2002b).

MATERIALS AND METHODS

Mean monthly precipitation and temperature values for the sparse network of weather stations in northern Chile were obtained from the Dirección General de Aguas, Ministerio de Obras Públicas, located in Santiago, Chile. Plant distribution data was collected between October 1997 and February 2001. Plants were surveyed with two different objectives: 1) to establish local species richness, total percent cover and relative cover of the dominant life forms, and 2) establish the altitudinal ranges of individual taxa. To this purpose we performed eight altitudinal surveys between 18-25.5° S latitude with plots every 50-100 m in altitude. Surveys began at lower vegetation limit and reached close to the upper vegetation limit along the Andean crest (Fig.1; Table 1).

Survey transects were chosen based on accessibility by major roads that cross mountain passes from Chile to either Bolivia or Argentina. The large majority of the plots were taken on either north or west facing slopes and local run-on situations or dry washes were avoided. Elevations (masl) were measured using a Thommen Altitronic Traveller digital altimeter. A Garmin 12XL Global Positioning System device was used to gather plot co-ordinates with a resolution of ±30 m. Altimeter measurements were checked against 1:50,000 topographic maps of Chile published by the Instituto Geográfico Militar. Local species richness was determined by identifying and collecting all plant species present within the plots which were either pressed in conventional size plant presses (50 cm x 30 cm) or handheld notebooks. Species not identified in the field were identified at the Herbarium of the Departamento de Botánica, Universidad de Concepción, where voucher samples are also deposited. Species nomenclature and life form type are after Marticorena *et al.* (1985; 1998).

Percent cover was measured every 100 m along six of these transects from 19.28°S to 25.5°S. “Ellenberg” plots or point-intercept methods (Mueller-Dombois & Ellenberg, 1974) have traditionally been used to measure vegetation distribution in the Chilean Andes (Arroyo *et al.*, 1982; Villagrán *et al.*, 1981; Villagrán *et al.*, 1999), and 8-16 m^2 “Ellenberg” plots were used in the earlier surveys presented here. In later surveys, we also employed 250 m^2 log-series survey plots recently developed and specifically designed for arid regions were total plant cover is less than 25% (McAuliffe, 1990). In two cases, both methods were used to ensure that the plant cover data obtained was consistent (Table 1.1). Though both methods yielded similar trends, the smaller “Ellenberg” plots tended to overestimate total cover with increased variance when compared to the larger plots using the log-series survey method.

We also established altitudinal ranges for each species of vascular plant along four surveys. Three of these surveys were along the Pacific Andean slope and an additional “range” transect was performed along the coastal region, from the Agua Verde Station (1500 m) to the port of Chañaral (Table 1.1, Fig. 1.1). Altitudinal surveys were accomplished by placing stations every 50 or 100 m in altitude and then determining the number of species within a 250-m radius. Floristic compositions were plotted using Tilia 2.0 and Tiliagraph (Grimm, 1991-1993) and analysed through the use of a Constrained Incremental Sum of Squares (CONISS) cluster analysis (Grimm, 1987).

RESULTS

We collected and inventoried a total of 120 species belonging to 22 different plant families along the eight transects located along the Andean front (Fig. 1.3a). This represents 23% of the 521 species reported by Arroyo *et al.* (1988) for northernmost Chile (18°-24° S). The families Asteraceae, Poaceae, Papilionaceae and Cactaceae account for 56% of the total flora along the transects (Fig. 1.3a). Total species richness for each transect drops off quickly after 18° S, levels off between 21-24° S, and drops again to 10 species by 25.5° S (Fig. 1.3b).

The analyses of floristic dissimilarity along these gradients together with their respective turnover in lifeform cover values were also used to improve delineation of the classic vegetation belts described for northern Chile by previous authors (Arroyo *et al.*, 1988; Squeo *et al.*, 1994; Villagrán *et al.*, 1981; Villagrán *et al.*, 1983). These are the Prepuna and Puna shrub belts, the high Andean Steppe and the Subnival (characterized by cushion and rosette plants) as shown for the transect located at 19.28° S latitude (Fig. 1.4). The use of floristic compositions along these gradients, as well as physiognomic factors, allows for a less arbitrary and better description and quantification of the extension of vegetation belts (Cavieres *et al.*, 2000). Our study suggests the addition of a vegetation belt transitional between the puna shrub belt and the Andean steppe, here termed *high puna*.

The overall physiognomy of the study area is given by measurements of total percent cover, for dominant life forms characteristic of each vegetation belt (Fig. 1.5). In general, the lower limits for vegetation zones decrease as the eastward margin of the absolute desert penetrates inland. At 19.28° S this margin occurs at ca. 2500 m, whereas it is above 3500 m at 25.5° S. An anomalous pattern was identified at 21.83° S within the Río Loa watershed (Fig. 1.5b), where vegetation began at 3500 m; almost 1000 m higher than nearby transects, and had almost no development of a prepuna or puna shrub-belt.

Percent cover values

Maximum cover values, which occur within the puna shrub belt along the northernmost transect (Fig. 1.5a), are displaced upwards in the southern transects where maximum cover occurs at higher altitudes within the ecotone between the puna and the Andean steppe. A secondary peak in cover observed at 2750 m at 19.28° S completely disappears in the transects further south. This peak was caused by the presence of a well-developed prepuna belt in this area, dominated by columnar cacti and the shrubs *Ambrosia artemisioides* Meyen et Walp. and *Atriplex imbricata* (Moq.) D. Dietr. Although not included in the measurements of cover, we also observed numerous dried summer annuals (*Plantago hispidula* Ruiz et Pavón, *Bouteloua simplex* Lag., and *Tagetes multiflora* Kunth among others) forming almost continuous cover within the prepuna belt, a feature that disappeared further south. Total cover values decrease by almost an order of magnitude between the northernmost and southernmost transects which peak at ca. 28% and 3.3 % respectively.

Maximum cover values for the high Andean steppe occur at ca. 4300 m at 19.28° S, at 4100 m for 22.72° S and at 4000 m for 25.5° S. The lower limit of the steppe also decreases by ca. 100 m in altitude with increasing latitude. Finally, the puna and prepuna belts disappear completely at 25.5° S where the only measurable cover is basically due to a single species of tussock grass, *Stipa frigida* Phil.

Species richness patterns

For six of the eight transects analysed the number of species correlated positively with altitude. Two types of patterns emerged, either a clear unimodal curve with peak richness at intermediate elevations or a more "linear" pattern due maximum richness at higher altitudes (Fig. 1.6). The unimodal pattern was predominant in transects north of 23° S, whereas the "linear" pattern was present in transects south of 23°S. The slope of the "linear" pattern tends to become less pronounced with increasing latitude for those transects south of 23° S. Despite a lack of statistically significant correlations, the transects located at 19.28° S and at 22.72° S evidence a closer affinity to the unimodal form as species richness peaks between 3600-4000 m and at 3500 m respectively and then decreases at higher altitudes. Again, the transect at 21.83° S was anomalous in terms of regional context; it exhibited a significant linear relationship between species richness and altitude similar to that observed for the transects south of 23° latitude.

Local species richness correlated positively with total cover only for the transects located at latitudes 21.83° S ($R^2 = 0.4$; $p < 0.1$) and at 23.75° S ($R^2 = 0.47$; $p < 0.05$). This relationship was not significant in the other four transects. Peak cover values, however, tended to occur with maximum species richness in five out of the six transects.

To gain insight into plant structure along these altitudinal gradients, we plotted individual species ranges versus mean range centre for the three transects were species ranges were obtained (Fig. 1.7). A very clear "double bell" shaped pattern emerged for the northernmost transect (18.17° S), which was much less apparent at 22.92° S and then disappeared at 25.50° S. At the northernmost site the highest species richness and concomitant smallest ranges, many of these spanning less than 200 m, centred around 3600 m. Species ranges increased upwards and downwards of this altitude, attaining maximums of 800-900 m at 3100 and 4200 m. Noteworthy among the species with broad ranges were *Atriplex imbricata* (900 m) and *Cryptantha parviflora* (Phil.) Reiche (850 m) along the desert margin and *Azorella compacta* Phil. (900 m) and *Festuca orthophylla* Pilger (900 m) along the upper limit. At the very limits of the vascular plants, however, either along the desert edge or at near the 0°C isotherm, species ranges tended to decrease producing the tail ends of the "double-bell".

This pattern was distinguishable at 22.92° S, although ranges were much less compact and most of the individual species spanned altitudinal ranges greater than 300 m. At 25.50° S, most species were present only at individual plots (i.e. range equal to 0 m) and only two species (*Adesmia spinosissima* Meyen and *Stipa frigida*) had ranges greater than 400 m.

An additional range transect was obtained from the interior desert (Agua Verde Station) at the latitude of Taltal (25.50° S), heading down past the coastal fog zone into the highly endemic Lomas communities (Rundel *et al.*, 1991; Tago-Nakazama & Dillon, 1999). Species richness peaks at 500 m and tails off gradually towards the upper limit and abruptly towards the coast. Although minimum ranges coincided with maximum species richness (Fig. 1.8), maximum ranges occur just above the zone of maximum richness; the few species found above the fog zone (ca. 1000 m) tended to have narrow ranges (< 400 m).

DISCUSSION

We discuss how hyperaridity coupled with low temperatures at high altitudes determine productivity and thus generate the patterns of species richness and cover on altitudinal and latitudinal gradients seen throughout the Andes northern Chile. These environmental factors, however, have experienced notable fluctuations in the recent past and we describe how these past fluctuations have determined the current phytogeography of the Atacama Desert and adjacent Andes. Finally, we discuss the floristic affinities of the southernmost transect (25.5° S) and analyze how these affinities may help understand the manner in which climate fluctuations may have generated corridors of biotic dispersal through the Atacama and over the Andes.

Altitudinal gradients in the Atacama

The central Andes in northern Chile are clearly unique when compared to other Andean regions in terms of the altitudinal patterns in species richness documented here. In both the tropical (Witte, 1994) and mediterranean Andes of central Chile (Arroyo *et al.*, 1988; Villagrán *et al.*, 1998) species richness decreases in linear fashion with altitude. In our study area, local species richness peaks at intermediate altitudes, with maximum richness occurring either in the puna belt (for the two northernmost transects) or in the high puna-steppe interface (Fig. 1.6). Maximum local species richness within the puna belt (ca. 3500 m) produces the "classic" unimodal curve described by previous studies in the Andes of northern Chile (Arroyo *et al.*, 1982; Villagrán *et al.*, 1983; Arroyo *et al.*, 1988; Richter & Schröder, 1998). This maximum is clearly the consequence of reduced environmental stress at intermediate altitudes between maximum aridity and cold (Arroyo *et al.*, 1988). Also, it is almost exactly at the same altitude at which the MAP and MAT curves cross (Fig. 1.2). Hence, it is also the elevation at which maximum productivity is probably reached. This corroborates the explanations put forth by Brown (2001) that use ecosystem properties such as productivity, to explain why mammalian diversity peaks at intermediate elevations in numerous different enviroments.

South of latitude 23° S, local species richness increases in a much more linear fashion and the unimodal distribution becomes much more skewed towards high altitudes. As predicted by the intersection of the MAT and MAP curves (Fig. 1.2), peak local species richness and percent cover are clearly displaced upwards towards the puna-steppe interface (ca. 3900 m) with increasing latitude. The regression slopes of altitude on local richness also decrease with increasing latitude (Fig. 1.6). This may be explained as the result of the decreasing number of species found at high altitudes with increasing latitude.

Interfaces between different vegetation formations seem to be tremendously important for Andean floras in terms of species richness. Similar patterns are observed along the eastern slope of the tropical Andes, where maximum richness occurs along the ecotone between cloud forests and the páramo (Witte, 1994) and between the mediterranean chaparral and the high Andean belts at 38-39°S (Villagrán *et al.*, 1998). In all these cases, maximum richness occurs at the interface between two physiognomically different formations (i.e. woody versus herbaceous perennials) where taxa of both formations co-occur resulting in an increase of local species richness.

Other explanations have been proposed to account for altitudinal plant distributions along the Pacific slope of the Andes. The "Merriam-effect" is cited by Richter and Schröder (1998) to account for the differences seen in plant cover along several transects along the Andean front between 22° to 24.5° S latitude. This effect states that large elevated landmasses such as plateaus serve as focal points for convective activity whereas isolated mountains have much less intense activity. This does not explain the overall regional shift in maximum species richness documented here. We point out that if the "Merriam-effect" were significant then the transect located at 21.83° S should have much higher species richness and cover values as it is located up against the large Altiplano system of southern Bolivia.

More than likely patterns of local species richness are due to decreasing precipitation with increasing latitude, so that as the desert encroaches on the lower limit, plants are forced upslope where precipitation is greater. The drawback is that they encounter colder temperatures and thus overall productivity of the environment is much more limited the further up they go. This is illustrated by the following example: at 19.17° S, percent total cover peaks at close to 25% at 3500 m, and local species richness peaks between 3800-4000m. At 25.5° S, percent total cover (which barely reaches 3%), and local species richness peak at close to 4000 m.

We found only very slight correlation between total cover and species richness along the six transects analyzed here. Data reported by Arroyo *et al.* (1988) showed highly significant correlations between species richness and percent cover along four transects between 18-24° S latitude, although the relationship between the two variables was not strictly parallel. In this study, we found that this correlation was strongest at

21.83° S ($R^2 = 0.4$; $p < 0.1$) and at 23.75° S ($R^2 = 0.47$; $p < 0.05$) but correlations along other transects were statistically non-significant. Differences in sampling methods (especially when the small plots are considered) may account for part of the explanation but other factors that might affect the cover-richness relationship could be due to local dominance by one or two determined shrub species. Peak percent cover values tended to coincide with maximum local species richness along most transects, however, and local dominance by shrubs such as *Atriplex imbricata* (in the prepuna) and *Parastrephia quadrangularis* (Meyen) Cabrera (in the high puna) produce peaks in cover possibly at the expense of other species within a determined plot.

The relationship between species range and altitude was also further quantified by comparing the species range against the center of that range (Fig. 1.7a-c). At 18.28° S, we found that the highest local species richness (around 3600 m) coincides with the smallest altitudinal ranges for those species. Species ranges generally increased at both higher and lower altitudes in the same direction as environmental stress increased (i.e. greater aridity or lower temperatures). This can be viewed as a special case of Rapoport's rule as applied by Stevens (1992) to altitudinal patterns of species richness. The difference in this case is that the presence of two opposing stress gradients produce the double hump shape seen in Fig. 1.7a instead of linear relationship with altitude. This pattern is barely visible in the transect located further south at 22.92° S (Fig. 1.7b) but disappears in the southernmost transect, a consequence of the pronounced species impoverishment of that region (Fig. 1.7c). Surprisingly, and completely contrary to Rapoport's Rule, we also found "extreme specialists" that are highly adapted to the stressful environments found at the tail ends of the double hump for the two northernmost transects. These are species that have small altitudinal ranges and are only found along the absolute desert margin or at the upper vegetation limit. Many species of woody perennials (such as *Tiquilia*) and succulents (*Cistanthe*) of the prepuna as well as rosette (e.g. *Lenzia, Nototriche* and *Chaetanthera*) and cushion plants (e.g. *Pycnophyllum, Urbania*) typical of the subnival fall into this "extreme specialist" category.

Among other Andean floras, Rapoport's rule has also been referred to by Witte (1994) as characteristic of the tropical Andes, where high species richness was related to low range amplitudes. Graf (1986) also found this pattern both in latitude and altitude for two Andean genera typical of the puna belt, *Nototriche* and *Polylepis*. Species of the genus *Nototriche* have narrower amplitudes (ca. 1000 m) in the Andes of Ecuador but these ranges increase to 3000 m at 25° S along the northern Andes of Chile. *Polylepis* evinces a similar pattern, with ranges around 2000 m at 10° N latitude, which then increases to 3000 m between 12-23° S. We demonstrate that this is also the case for those species found at the lowest altitudes, close to hyperarid margin of the Atacama Desert. Species with the broadest altitudinal ranges also tend to have the widest latitudinal ranges, such as *Atriplex imbricata*, which has altitudinal ranges between 950-1200 m and is a species found all over northern Chile, from 18 to 27° S latitude.

The latitudinal gradient in the Atacama

Contrary to most latitudinal gradients described for plant diversity in the literature (e.g., Huston, 1994), the Atacama gradient clearly follows a precipitation gradient, not a temperature gradient. This is characterized by both overall turnover of the dominant life-forms and species richness patterns. The variation along this gradient, however, is not related to temperature but instead is clearly associated with the NW/SE trending summer precipitation gradient, as seen by the overall upslope retreat of the lower vegetation belts from 19.28° S to 25.5° S (Fig. 1.9). This results in a decrease of total cover of almost an order of magnitude and a seven-fold decrease in species richness between the northernmost and southernmost transects. One interesting feature of this study is that the upper limit of the Andean Steppe also decreases in altitude with increasing latitude, despite a relatively constant 0°C isotherm throughout the latitudinal gradient (see Ammann *et al.*, 2001). Mean annual precipitation also decreases as latitude increases at the upper limits of vegetation as well (Fig. 1.2). Precipitation thus seems to play an important role in determining the upper limits of plants across the region of our study area.

Patterns of species composition and percent cover along the latitudinal gradients studied generally agree with previous classifications of vegetation belts in the central Andes as originally described for the semiarid eastern slopes of the Argentine Andes by Ruthsatz (1977) e.g. prepuna, puna, high Andean and subnival. Based on a multivariate analysis of species richness, percent cover and species distribution patterns present along the Pacific Andean slope (see Fig. 1.4), we have felt it neccesary to add an additional vegetation belt to this scheme, the *high puna*, which basically describes the broad ecotone between the puna shrub belt and Andean steppe (Fig. 1.9).

Vegetation belts tend to compact as latitude increases, and in the case of the shrub belts, eventually disappear near the hyperarid core of the Atacama Desert, between 25-26° S. This core, centered inland from the port of Taltal, corresponds to the

Andean area of maximum biotic impoverishment. Further support for this idea is that species richness of vascular plants and Sigmodontine rodents quickly increases south of 26° latitude (Moreno *et al.*, 1994). Figure 1.9 displays a general summary of our findings as well as reinterpreting previous distributions of these vegetation belts in northern Chile based mostly on physiognomic criteria (Villagrán *et al.*, 1981; Villagrán *et al.*, 1983).

Pleistocene climate fluctuations in the central Andes and Atacama Desert

From the altitudinal and latitudinal patterns previously described, the harsh Andean habitats of northern Chile have clearly had a pronounced effect on regional phytogeography. Nevertheless, profound climatic fluctuations during the Pleistocene have been documented for northern Chile and the central Andes, which must have had an additional influence on the source floras of the Puna Province. These impacts affect floras either through the presence of large barriers to dispersal or migration, such as extensive paleolakes on the Altiplano (Simpson, 1979), higher/lower temperatures, or increased precipitation and/or runoff along hyperarid slopes which favors the expansion of vegetation into absolute desert forming biotic corridors (Latorre *et al.*, 2002b).

Pollen records from the Eastern Cordillera of Bolivia (Graf, 1992) and Perú (Hansen *et al.*, 1994) suggest cold and wet full glacial climates as indicated by higher percentages of montane forests (*Podocarpus, Alnus, Hedyosmum,* and *Weinmannia*), ferns and aquatic taxa (*Isoetes, Myriophyllum*). Paleoclimate over the central Andes during the Last Glacial Maximum (LGM, between 21,000 to 17,000 calendar years ago) conflicts as to whether conditions were drier or wetter than today. Evidence for wetter conditions come from an ice core at Nevado Sajama (Thompson *et al.*, 1998) and salt cores obtained from Salar de Uyuni (Baker *et al.*, 2001) and Salar de Atacama (Bobst *et al.*, 2001). Lake levels from the arid Andes south of the Bolivian Altiplano, however, point to arid conditions during the LGM (Grosjean, 1994; Grosjean *et al.*, 2001). This also in agreement with paleofloras from several rodent middens collected along the margin of the Atacama Desert and dated between 35,000 to 22,000 calendar years ago (Latorre *et al.*, 2002b). Summer precipitation is spatially variable and episodic across the central Andes today (Aceituno & Montecinos, 1993; Garreaud, 2000; Garreaud *et al.*, 2002) and it thus clear that further investigation and dating is needed in order to resolve the extent and magnitude of the tropical rainfall belt during the LGM.

A southward shift of the Arid Diagonal during the LGM, may have been even more complex due to the dynamics of the westerly rainfall belt (Messerli *et al.*, 1998; Abraham *et al.*, 2000). The westerlies clearly expanded northward across central Chile during the LGM (Caviedes, 1972; Heusser, 1983, 1984) and at least as far north as 27° S latitude (Lamy *et al.*, 1998) so that winter precipitation and snowfall could have reached more northern latitudes. Increased westerly activity in northern Chile is also indicated by high grass percentages in rodent middens from Quebrada del Chaco (25.40° S) dated between 24,000-16,000 calendar years ago (Betancourt et al., in progress).

Climate was different after the LGM and during the transition between the late Pleistocene and Holocene periods. Pollen records from the high Andes of northern Chile (Laguna Lejía 23°29' S, Tuyajto 23°57' S) indicate wet conditions (high percentages of Poaceae) between 17,000-13,000 calendar years ago (Graf, 1992). An increase of Chenopodiaceae pollen at the beginning of the Holocene is interpreted as an abrupt increase in aridity for the region (Graf, 1992). Grass pollen percentages increased at Laguna Miscanti (23° S) between 11,000 to 9000 calendar years ago as well (Grosjean *et al.*, 2001). Extralocal floras, increased grass percentages and higher ground-water tables indicate a pronounced wet phase along the hyperarid margin of the Atacama Desert between 13,800 to 9500 calendar years ago (Betancourt *et al.*, 2000; Latorre *et al.*, 2002b; Rech *et al.*, 2002). All these records agree on a pronounced phase of increased precipitation that occurred more or less during the late glacial to early Holocene between 18-25° S latitude. As occurs today in northern Chile, past precipitation was clearly of tropical origin, as demonstrated by the descent of summer annuals, C_4 grasses across the hyperarid margin of the Atacama Desert between 22-24° S and the southward expansion of several taxa (Latorre *et al.*, 2002b).

Evidence is yet inconclusive regarding the exact timing and extent of the northward expansion of the westerly rainfall belt during the late glacial to early Holocene. Pollen records and paleosols from north-central Chile (*norte chico*, 30-27° S latitude) point to increased precipitation between 13,000 to 10,000 calendar years ago (Veit, 1993; Villagrán & Varela, 1990). Clay minerals from a marine sediment core obtained further north at 27° S, however, are used to infer arid conditions at the end of the Pleistocene (Lamy *et al.*, 1998).

Biogeographic importance of the arid core region (24-26° S)

The floristic composition of our southernmost Andean transect centered around Quebrada del Chaco-Cerro Los Patitos (25.40° to 25.50° S) allows further insight into the historical biogeography of the Andean flora of northern Chile. The latitudinal distribution of this impoverished flora (36 species total, not including those encountered in "azonal" e.g. riparian and bog habitats) demonstrates that an important component is of Puna origin (16 species) whereas one species (*Stipa frigida*) is of Andean-Patagonian distribution and two species are clearly of mediterranean origin (*Adesmia aegiceras* Phil and *Gilia crassifolia* Benth.) (Fig. 10). A major fraction of this flora (17 species), however, has a distribution clearly restricted to the more arid regions of the Andes between 21° and 26° S latitude, the so called "Desert-Andean" element (Villagrán *et al.*, 1983).

This phytogeographic structure gives us the opportunity to envision the multiple floristic sources and major biogeographical corridors that have been used by plant species to disperse across the barrier posed by the absolute desert. As evinced from the paleoclimate records, for both the maximum and late glacial periods the arid diagonal narrowed and favoured northward (during the full glacial) and southward (during late glacial) plant migrations. Rodent middens illustrate a southward expansion of several puna elements (*Echinopsis atacamensis* (Phil.) Friedrich et G.D. Rowley, *Ambrosia artemisioides, Fabiana* spp.) during the late glacial-Holocene transition (Latorre *et al.*, 2002b).

On the other hand, the northward expansion of the westerlies during the full glacial periods would have allowed the dispersion of several Andean-Patagonian taxa such as *Junellia, Mulinum, Chuquiraga, Azorella,* and *Tetraglochin* (Villagrán, 1995; Villagrán *et al.*, 1998), and the consequent enrichment of the Puna Province. This interchange would explain the high generic affinity between the phytogeographic Provinces of the Puna and Patagonian Steppe as pointed out by Sarmiento (1975) and integrated by Cabrera and Willink (1980) into their Andean-Patagonian Dominion. This was clearly not only limited to plants, however, as migrations associated with wetter climates would also explain the high taxonomic affinity of large mammals (the 'megafauna') between central and northern Chile (Moreno *et al.*, 1994). Azonal formations such as high Andean bogs would have also had a chance to expand and form continuous corridors along the Andes during these humid phases. These formations are characterized by discontinuous distributions and species with broad latitudinal ranges that reach even the temperate latitudes along the Andes (Arroyo *et al.*, 1982). As mentioned by Simpson (1979), high Andean paleolakes and glaciers, while posing formidable barriers to the east-west interchange of zonal floras, actually favored the dispersion of the azonal elements.

An interesting but little explored idea is the role of the coastal fog oases as a possible source of Andean floras. Today these "Lomas" floras are highly endemic and restricted to a few coastal localities along northern Chile between 23-26° S (Johnston, 1929; Rundel *et al.*, 1991; Squeo *et al.*, 1998; Tago-Nakazama & Dillon, 1999). As shown by the species collected along the transect from Agua Verde to Chañaral (Fig. 8) most are desert specialists, as even the species collected at the very limits of their altitudinal distribution tended to have very narrow altitudinal ranges. Just one degree of latitude south from our study area, however, some elements of this flora have continuos ranges with the Andean flora (Fig. 9). The important Desert-Andean component of the Quebrada del Chaco flora suggest that these Lomas floras must have been connected with the Andes during humid phases in the past, especially during full glacial periods which would have allowed dispersal northwards. This process probably produced small pockets of pioneer populations, which were then isolated during arid periods inducing speciation. This would explain the presence of observed species with very restricted latitudinal ranges in the Quebrada del Chaco flora, such as *Opuntia atacamensis*, *Cristaria andicola*, and *Adesmia frigida*. In fact this region also possesses half of the few Andean genera endemic to Chile such as *Cyphocarpus* (3 species), *Dinemandra* (2 species), *Dinemagonum* (3 species), *Phrodus* (3 species), and *Homalocarpus* (6 species). Along the same lines, Arroyo et al. (1982) have also remarked on the pronounced Desert element of the prepuna floras at the northernmost transect (18° S) which include species of *Nolana*, *Cistanthe*, *Tiquilia*, *Atriplex*, *Cryptantha*, and *Hoffmanseggia*, among others.

CONCLUSIONS

Using the relationship between simple climatic parameters such as mean annual rainfall and temperature to infer productivity, in this paper we have documented patterns of local species richness, percent cover and species altitudinal and latitudinal distributions across the Pacific slope of the Andes of northern Chile. The majority of the transects studied exhibited a positive linear relationship between productivity, maximum cover and local species richness. Local species richness peaks at intermediate elevations along the Andes, and the species present at these elevations also tend to have narrow altitudinal ranges. This lends support to the hypothesis that productive environments maintain high local biodiversity through resource partitioning and competetive exclusion (Whittaker, 1975).

As latitude increases, decreasing moisture availability forces species upslope, were they encounter colder temperatures. Theory predicts that when productivity is reduced there should be significantly fewer species and less area should be covered by plants. This is precisely the pattern discerned in the Atacama, were plants are almost completely eviscerated from the landscape at the extreme arid core region at 25.5° S latitude.

Fluctuations in Pleistocene climate have played a major role in producing local endemics and establishing corridors (and barriers) for migrations across the absolute desert barrier. We propose that plants from the Puna Domain have invaded the Atacama repetively during short lived periods of increased summer moisture during glacial to interglacial transitions. During full glacial periods, increased winter moisture brought in from the polar westerlies induced migrations across the Andes from the Andean-Patagonian Domain and possibly may have favored migrations from coastal Lomas communities as well.

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Table 1.1. General information for the eight altitudinal transects discussed in this study. Species number corresponds to the number of taxa present in each plot along the total transect length. Latitude is reported as decimals of a degree. Masl= meters above sea level.

No.	Latitude S (°)	Range (masl)	No. Species	Date	Comments	Reference
1	18.17	2700-4900	72	Sep-00	species ranges (every 50 m)	This study
2	19.28	2600-4280	31	Oct-97	%Cover-16 m^2 plots	Villagrán *et al.*,1999
3	21.83	3500-4300	17	May-99	%Cover- 250 m^2 McAuliffe plots	This study
4	22.72	2700-4250	27	Jan-99	%Cover-16 m^2 plots	Romo *et al.*,1999
5	22.92	2600-4700	31	May-99	species ranges (every 100 m)	This study
6	23.33	2700-4500	34	Jan-98/May-99	% Cover- both methods	Villagrán *et al.*,1998a and this study
7	23.75	2900-4000	23	May-99	%Cover- 250 m^2 McAuliffe plots	This study
8	25.5	3450-4400	10	Feb-01	% Cover- both methods	This study
9	25.5-26	1450-100	31	Feb-01	Species ranges (every 50 m)	This study

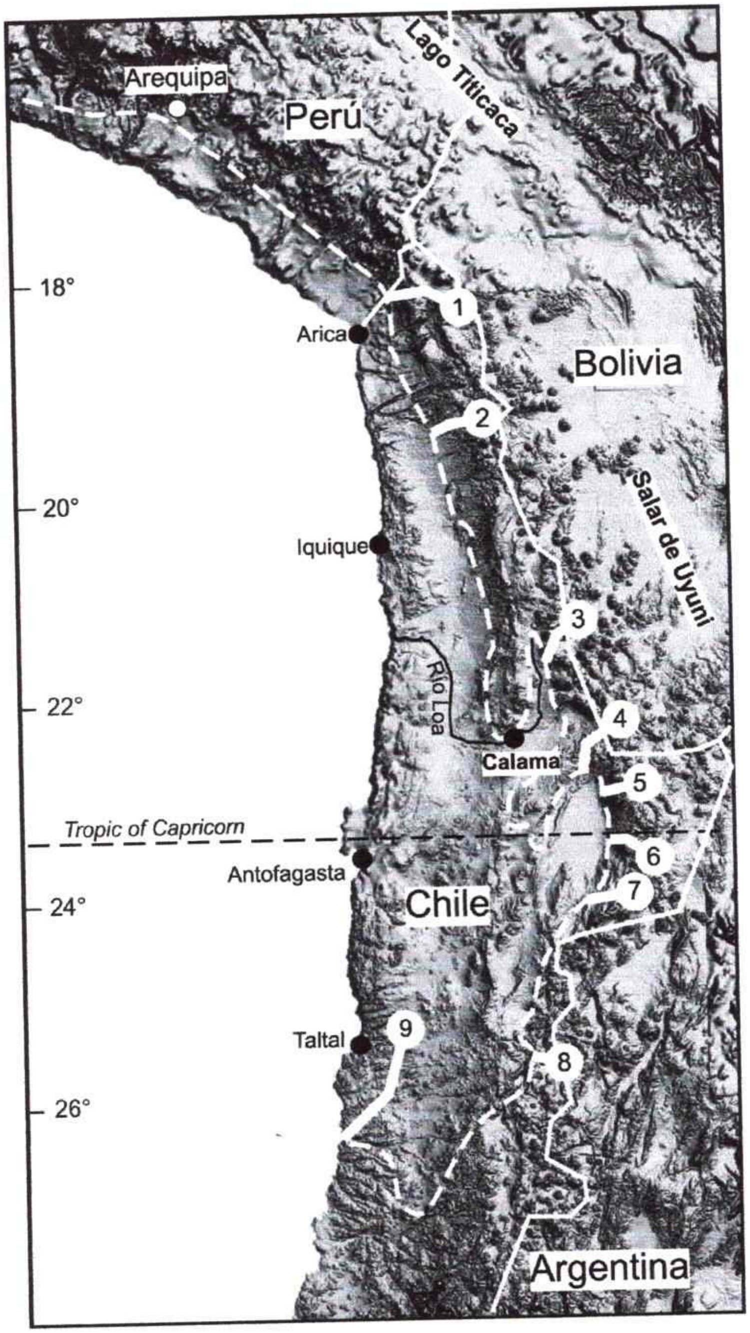

Figure 1.1. Relief map of northern Chile and the central Andes indicating the location of the altitudinal transects utilized in this study. Dashed white line indicates the approximate eastward extent of the absolute desert, defined by the absence of vascular plants save permanent river courses, desert oases and salt-flat (*salar*) margins. Major port cities are also indicated.

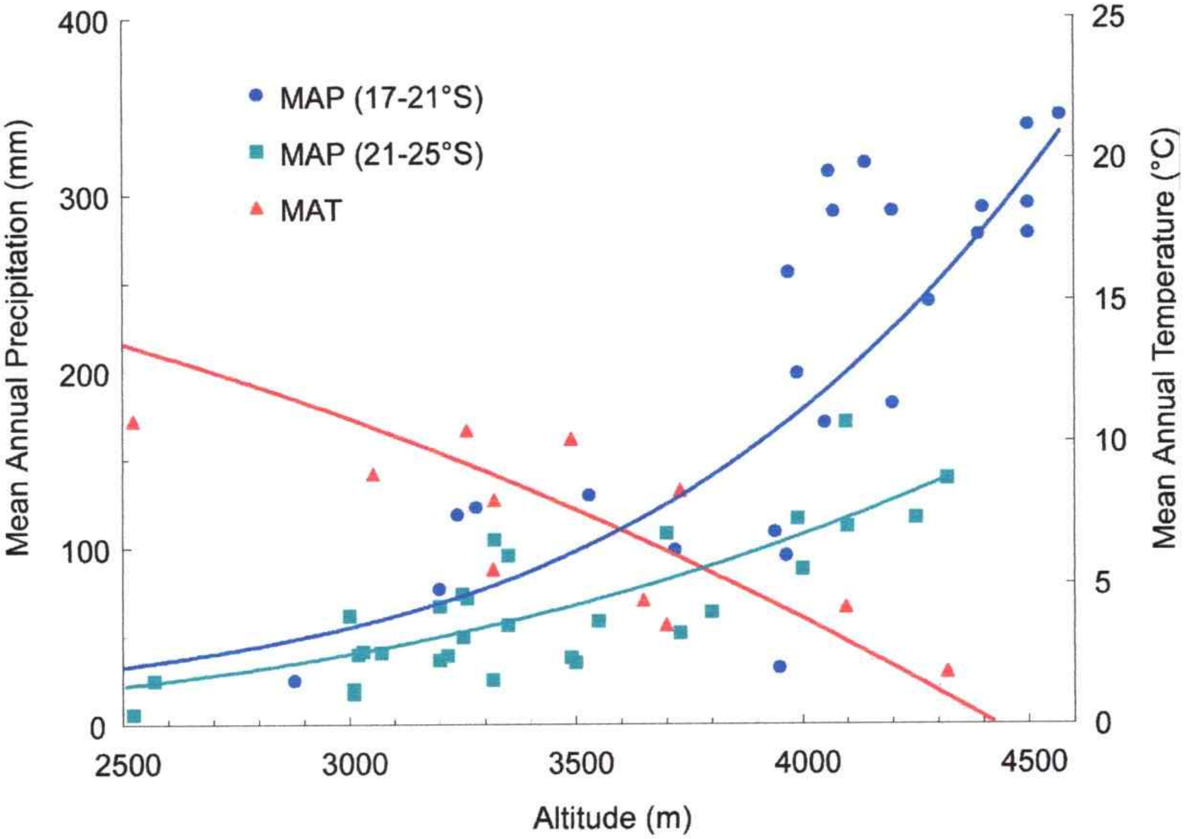

Figure 1.2. Records of mean annual temperature (MAT) and mean annual precipitation (MAP) graphed against altitude along the Pacific slope of the Andes in northern Chile. MAP curves are separated into bands of 4° latitude wide to indicate the relationship between MAP and latitude. MAT records are insufficient for such separation. Fitted curves are second- to third-order polynomials with $R^2 = 0.85$ for MAT; $R^2 = 0.72$ for MAP, 17-21° S; $R^2 = 0.76$ for MAP, 21-25° S.

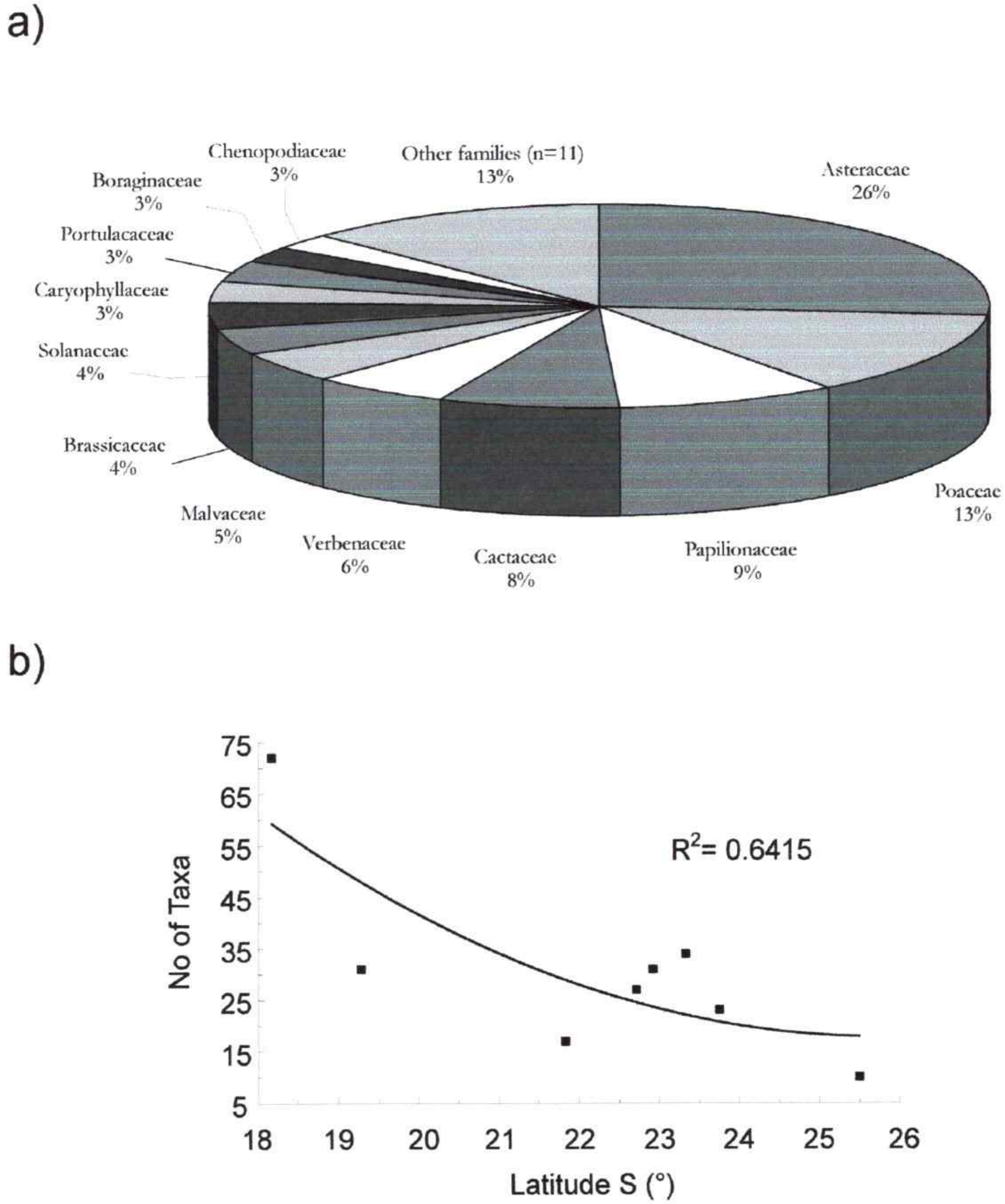

Figure 1.3. **(a)** Floristic composition of the 120 species of vascular plants collected along the eight transects from the Pacific Slope of the Andes. The category "Other families" includes Adiantaceae, Apiaceae, Calyceraceae, Caesalpinaceae, Ephedraceae, Hydrophyllaceae, Krameriaceae, Ledocarpaceae, Plantaginaceae, Polygonaceae, and Rosaceae. **(b)** Total number of species per transect as plotted against latitude. The curve fitted to the data is a quadratic regression.

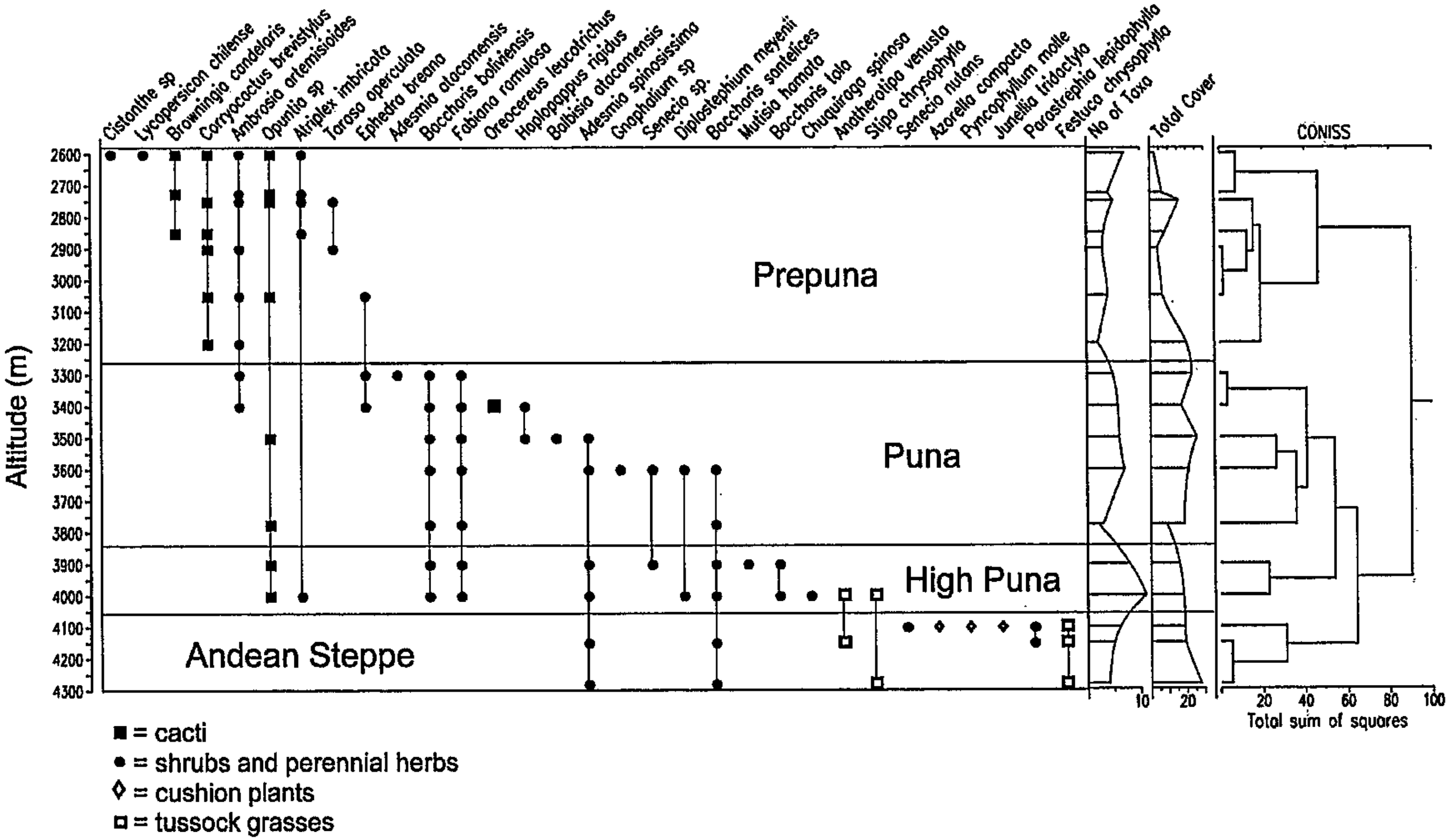

Figure 1.4. Floristic composition, lifeform turnover, and vegetation belts (as delineated by CONISS) of the altitudinal survey located at 19.28° S latitude (Camiña-Cerro Socora). Percent cover was determined using 16 m^2 plots.

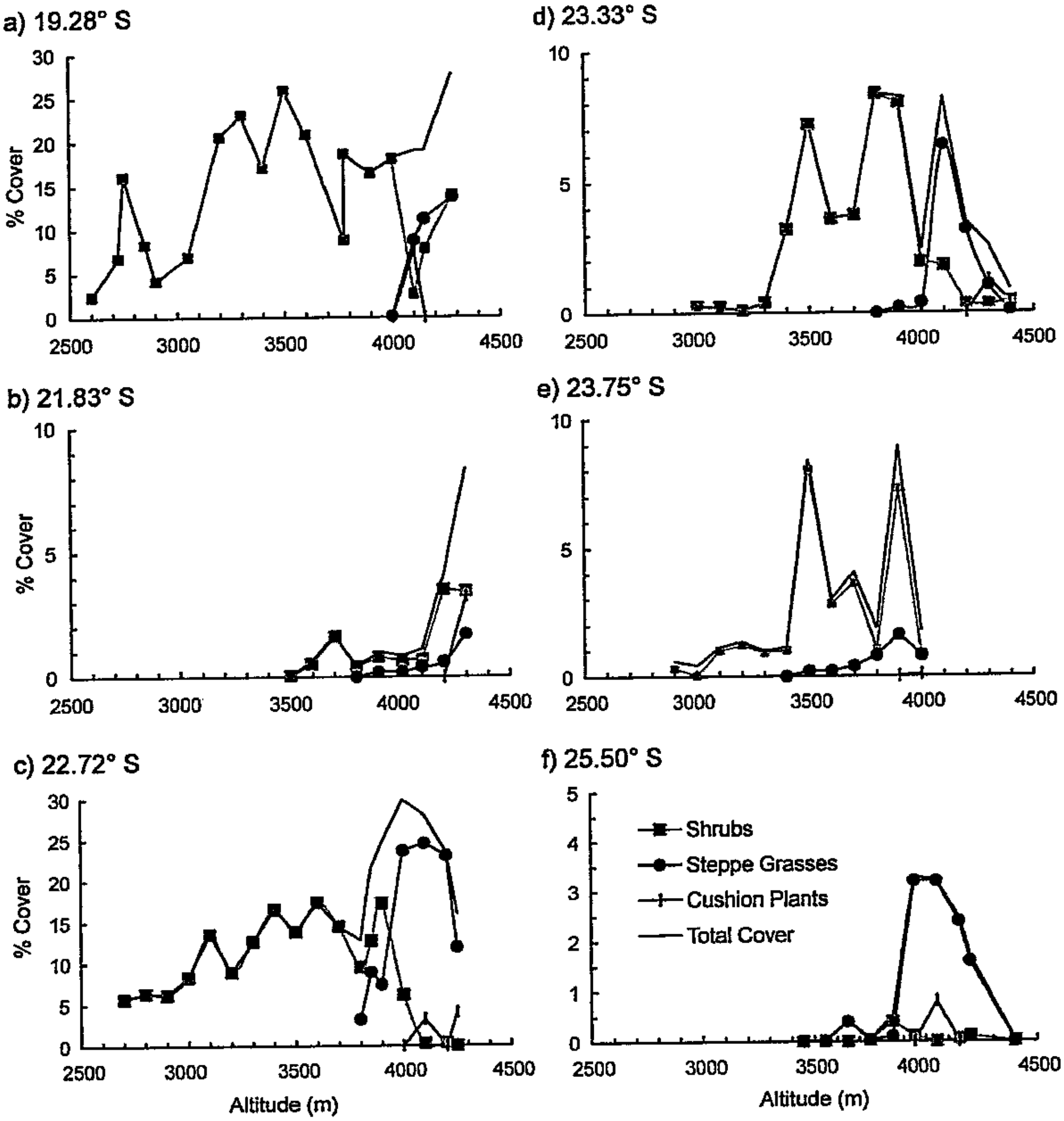

Figure 1.5. Percent total cover for perennial plants and relative cover of dominant life-forms versus altitude for the six altitudinal transects located along the Pacific slope of the Andes of northern Chile. Note changes in *y*-axis scale.

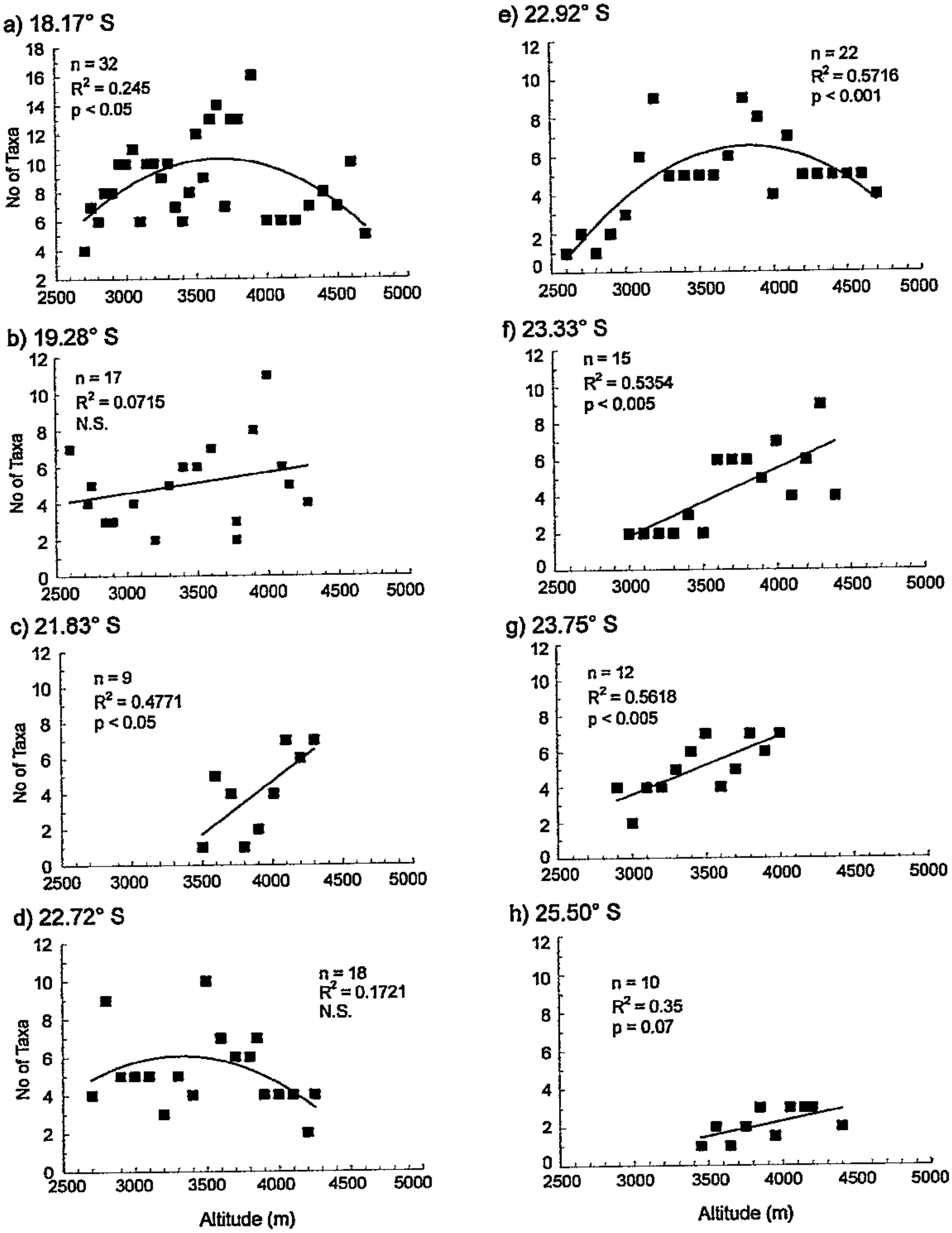

Figure 1.6. Local species richness versus altitude for eight transects along the Andes of northern Chile. Determination coefficients (with level of significance) and total number of plots for each transect (n) are indicated. Note changes in *y*-axis scale.

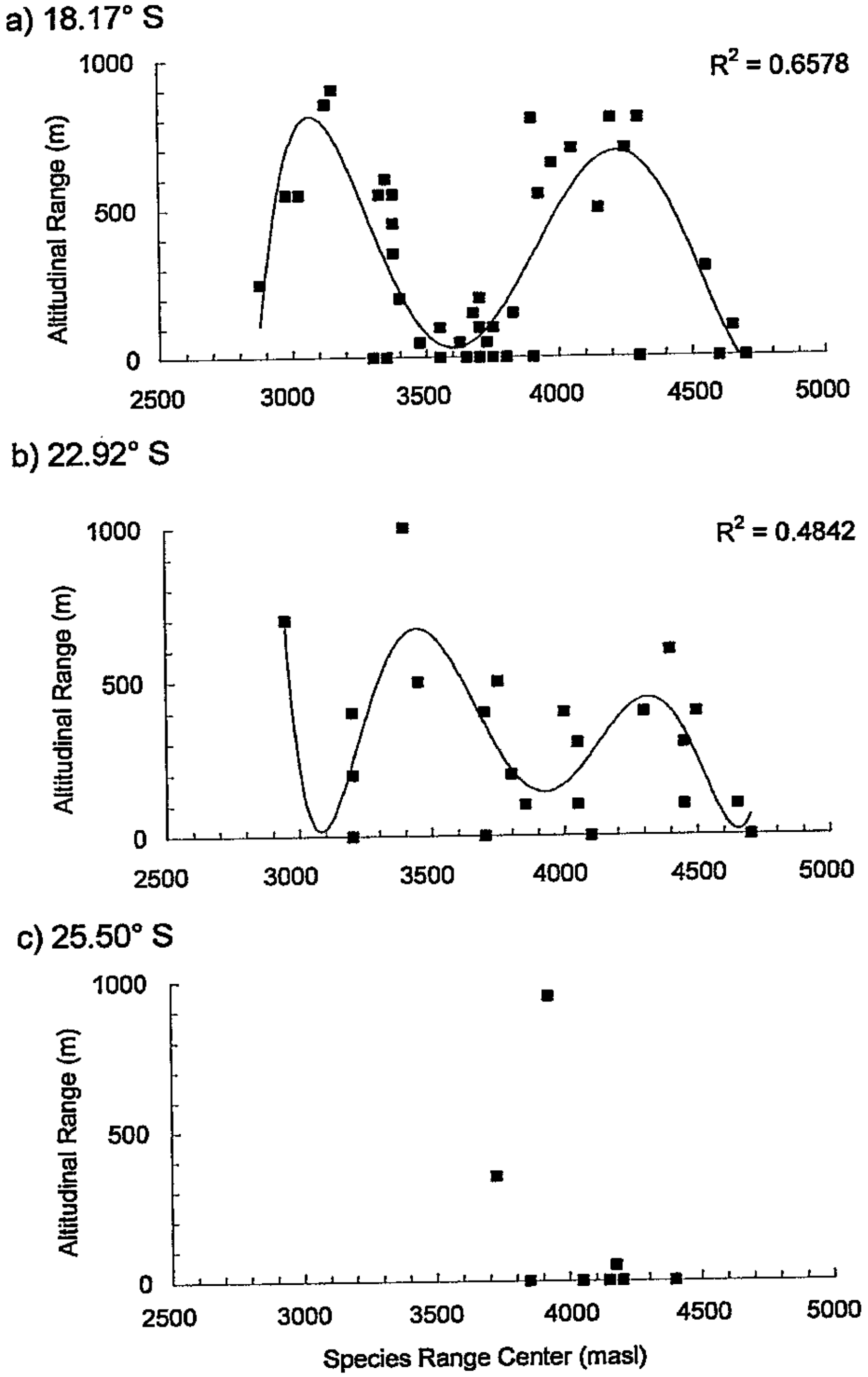

Figure 1.7. Species range center versus species altitudinal ranges for three representative transects along northern Chile. Determination coefficients of the polynomial regressions are indicated for the two northernmost transects. A polynomial regression for the transect located at 25.5° S was not significant.

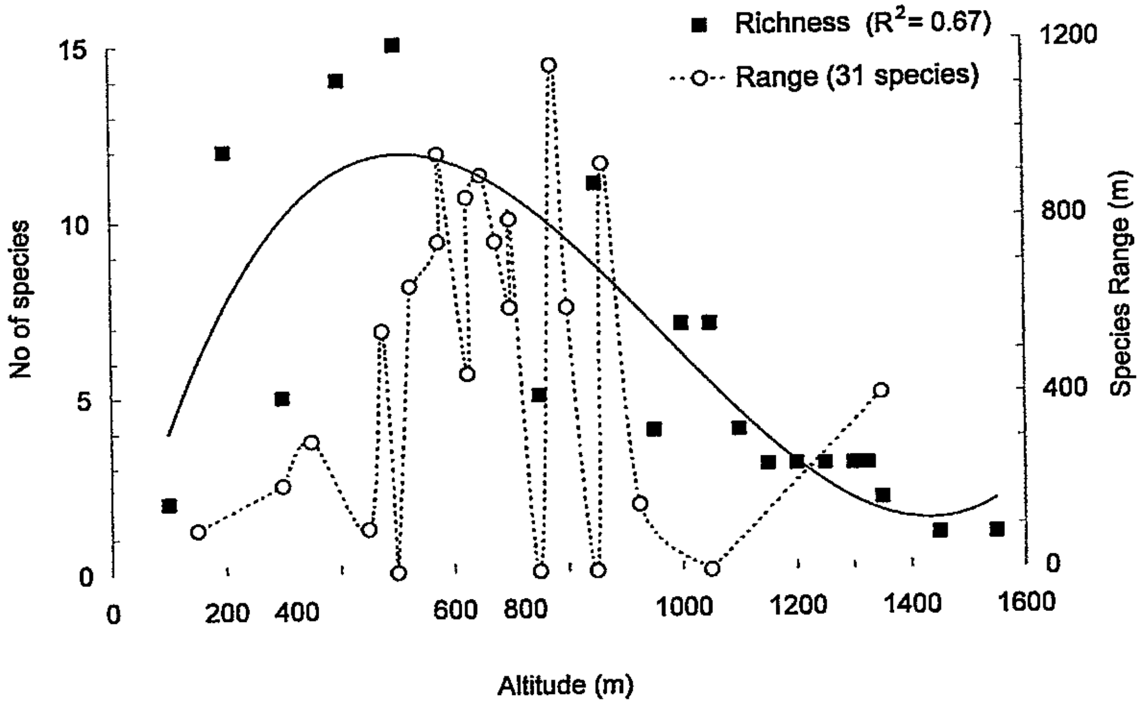

Figure 1.8. Species richness versus altitude for the transect Agua Verde- Chañaral, located at 25.5-26° S and crossing the Coastal Cordillera. The polynomial regression (solid black line, $R^2=0.67$) indicates maximum richness at 400-500 m, within the coastal fog belt. Also shown for comparison are species ranges versus species range centers (dotted line) as in Fig. 7.

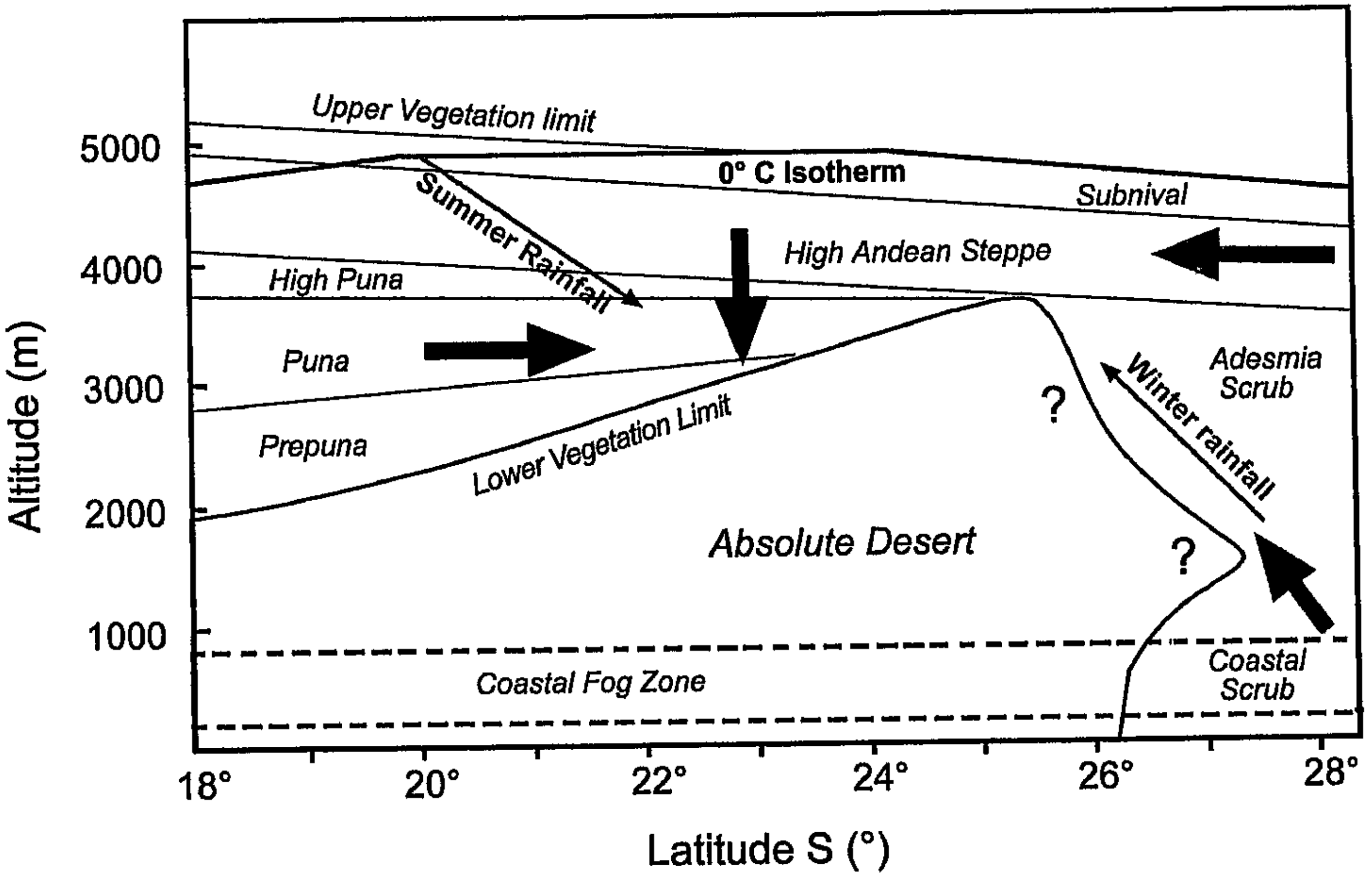

Figure 1.9. Updated summary diagram of the vegetation belts of northern Chile as identified in this paper. High Puna is a new belt used here to designate the transition between Puna and High Andean Steppe. Question marks are shown where the extent of absolute desert is poorly known. The 0° C isotherm is after Ammann *et al.* (2001). Black arrows represent plant migrations during glacial to interglacial transitions (increased summer rainfall) and gray arrows point in the direction of plant migrations during full glacial periods (increased winter rainfall). Heavily modified from Villagrán *et al.* (1983).

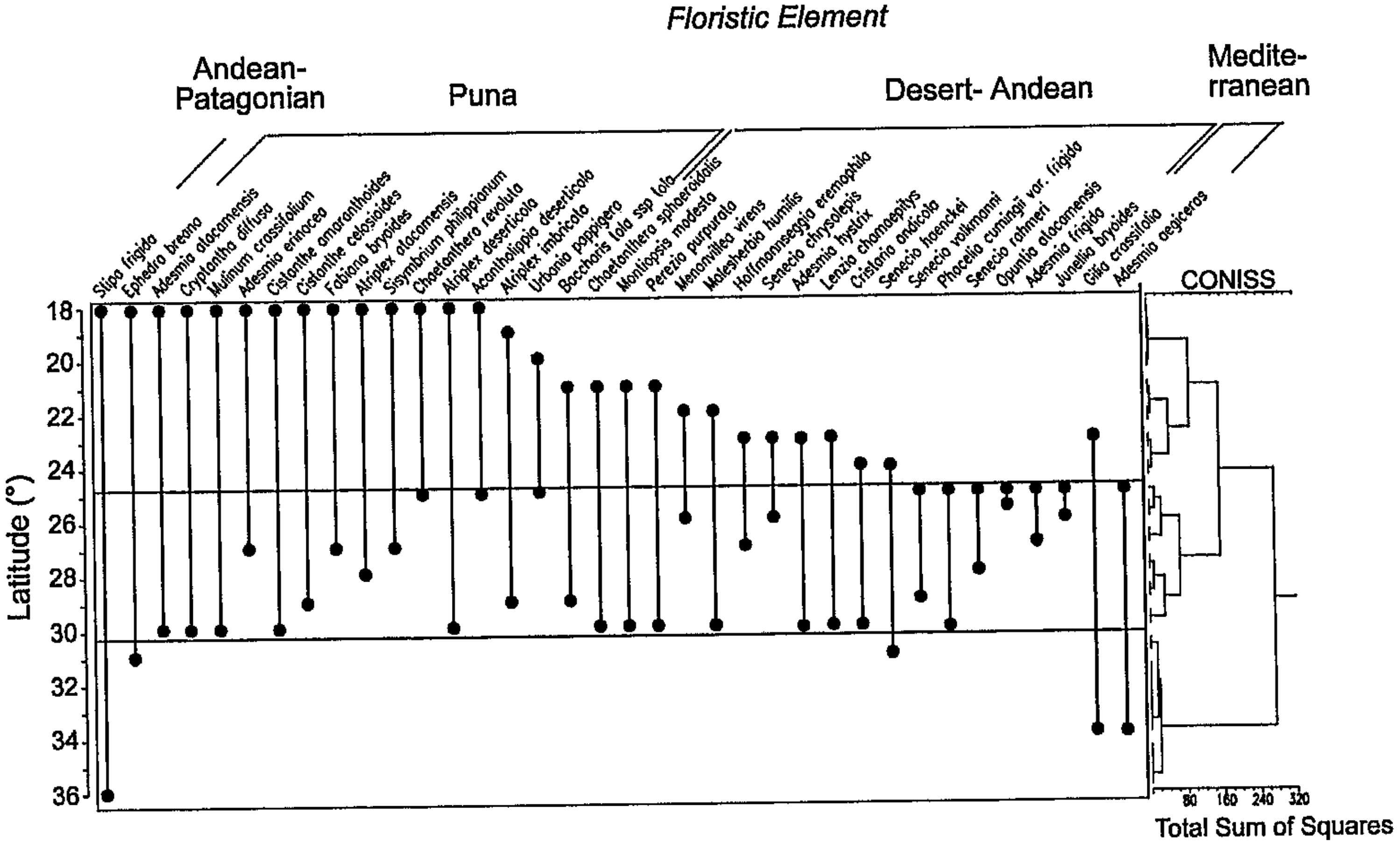

Figure 1.10. Latitudinal range of the flora collected at Quebrada de Chaco-Cordillera Domeyko-Cerro Los Patitos flora (25.4-25.5° S latitude) located at the hyperarid core region of the Atacama Desert. Range data was kindly provided by C. Marticorena from the Herbarium Collection Database located at the Departamento de Botánica, Universidad de Concepción, Concepción, Chile.

Capítulo 2:

"Vegetation Invasions into Absolute Desert: A 45,000-Yr Rodent Midden Record from the Calama-Salar de Atacama Basins, Northern Chile (22-24°S)"

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ABSTRACT

Plant macrofossils, percent grass, fecal pellet $\delta^{13}C$ and plant cuticle content from 49 ^{14}C-dated fossil rodent middens record changes in local vegetation and precipitation for the last 45 cal ka BP in the central Atacama Desert (22-24°S) of northern Chile. The midden sites are along the hyperarid upper margin (2400-3100 m) of Absolute Desert, an extreme environment sparsely vegetated by annual herbs and halophytic shrubs. Conditions between 40-22 ka BP may have been at least intermittently dry, and possibly cooler, as implied by four middens with low species richness. Based on the lowering of steppe grasses by up to 1000 m, prominence of C_4 grasses/summer annuals, high species richness, and displacement of northern species at least 50 km south of their modern ranges, we infer a large increase in summer rainfall between 16.2-10.5 ka BP. Precipitation increase was greatest for a cluster of middens between 11.8-10.5 ka BP. Abrupt drying, evident in a dramatic decrease in grass abundance, occurred after 10.5 ka BP at all four midden localities. Increased percentages of grass, higher species richness and extralocal taxa record slightly wetter conditions between 7.1-3.5 ka BP. Present hyperarid conditions were established after 3 ka BP.

Present-day variability of summer precipitation in the central Atacama Desert and adjacent Altiplano are related to the intensity and position of upper air circulation anomalies, which in turn respond to Pacific sea surface temperature anomalies. Summer insolation over the central Andes (20°S) was at its minimum during the latest glacial-early Holocene transition so regional insolation forcing cannot account for intensified pluvial conditions in the central Atacama. Summer precipitation collapsed abruptly between 11-10 ka BP, indicating either nonlinear relationships with seasonal insolation or a change in intensity of upper air circulation over the Altiplano, effectively blocking moisture transport to the Atacama Desert. Here we suggest that precipitation on millennial timescales in the central Atacama is the result of extraregional forcing of the South American Summer Monsoon through intensified Walker Circulation (stronger easterlies) and La Niña-like conditions operating through insolation anomalies directly over central Asia and the equatorial Pacific.

Keywords: rodent middens, vegetation history, monsoons, late Quaternary, Atacama Desert, northern Chile.

INTRODUCTION

Paleoclimate research has accelerated in the Central Andes with the need for tropical land records to better resolve leads and lags associated with high versus low latitude climate forcing. Ice-age cooling (5-6°C) in the tropics of South America is now evident from multiple records including $\delta^{18}O_{ice}$ in the central Andes (Thompson et al., 1995; Thompson et al., 1998; Thompson, 2000), mixing of temperate and tropical pollen floras in Amazonian sediment records (Colinvaux et al., 2000; Van der Hammen and Hooghiemstra, 2000) and noble gas concentrations in ^{14}C-dated Amazonian groundwaters (Stute et al., 1995). Fluctuations of tropical wetlands, driven by temperature and/or precipitation, are considered important sources of CH_4 recorded in polar ice cores (Chappellaz et al., 1990; Chappellaz et al., 1993; Severinghaus and Brook, 1999; Raynaud et al., 2000). Other notable records in the central Andes include evidence for glacial fluctuations in the Cordillera Real, Bolivia (Seltzer, 1990; Seltzer, 1992), the Andes of Ecuador and Perú (Rodbell, 1993; Rodbell and Seltzer, 2000), and at Salar de Uyuni, Bolivia (Clapperton et al., 1997; Clayton and Clapperton, 1997). Lake level histories are now available for Salar de Uyuni (Servant and Fontes, 1978; Wirrmann and Mourguiart, 1995; Servant et al., 1995; Sylvestre et al., 1999; Baker et al., 2001a), Lake Titicaca (Wirrmann and Mourguiart, 1995; Seltzer et al., 1998; Cross et al., 2000; Baker et al., 2001b), and the Pacific slope of the Andes (Grosjean and Nuñez, 1994; Grosjean et al., 1995; Valero-Garcés et al., 1996; Grosjean et al., 1997b; Geyh et al., 1999; Schwalb et al., 1999; Bobst et al., 2001).

In many of these glacial and lake records, lack of suitable material or hard-water effects may complicate dating, and it may also be difficult to discriminate temperature from precipitation effects in interpreting glacial and lake level histories. These shortcomings can be surpassed in reconstructing a detailed vegetation history for the central Atacama Desert, where summer storms spill over from the Altiplano. The lower limits of plants in this hyperarid environment is governed primarily by seasonal precipitation, with only secondary temperature effects. Hyperaridity also affords excellent preservation of organic vegetal remains that can be dated with ^{14}C-techniques. Although past pluvial phases in the Atacama have been recognized since the 1950's (Brüggen, 1950), there is little indication of how these affected former plant and distributions, specifically whether or not vegetation has ever invaded what is now Absolute Desert. The boundaries of Absolute Desert are assumed to have remained the same throughout the Quaternary, imposing a permanent barrier to the north-south migration of plants and animals (Villagrán et al., 1983; Arroyo et al., 1988; Marquet, 1994).

The Atacama Desert harbors few sites suitable for pollen deposition and preservation. Even where pollen is preserved, taxonomic resolution is poor, as the dominant grasses (Poaceae) and composites (Asteraceae) are seldom distinguishable to species. Prospects for reconstructing Atacama vegetation improved with discovery of fossil rodent deposits similar to North American packrat (*Neotoma,* Sigmodontinae) middens (Betancourt et al., 1990; Betancourt et al. 2000). In the Atacama, middens rich in plant macrofossils are ubiquitous and produced by four different families of rock dwelling rodents (Betancourt et al., 2000). Here, we present a midden record spanning the last 45,000 years from the edge of Absolute Desert in the Calama and Salar de Atacama Basins in northern Chile (Fig. 2.1). We use the resulting vegetation history to infer variations in monsoonal circulation and precipitation over the central Atacama Desert and the central Andes.

The Study Area- Climate

One of the harshest environments on Earth, the Atacama/Peruvian Coastal Deserts extend more than 25° from the Ecuador-Peru border (5°S) to La Serena, Chile (30°S) (Rundel et al., 1991). These deserts encompass vast areas that receive virtually no rain and harbor no vegetation, an Absolute Desert (Fig. 2.1). Arid conditions, which may have begun as early as the Eocene, evolved into hyperarid conditions by the middle Miocene (Mortimer, 1973; Stoertz and Ericksen, 1974; Alpers and Brimhall, 1988). Factors contributing to hyperaridity include: 1) the extreme rainshadow of the high Andes, which blocks the advection of tropical/subtropical moisture from the southern Amazon Basin; 2) the blocking influence of the semi-permanent South Pacific Anticyclone (SPA), which limits winter storm tracks to south of 28°S; and 3) the presence of cold, upwelling waters associated with a subduction zone and the north-flowing Humboldt Current off the northern Chilean coast (Borgel, 1973; Caviedes, 1973; Alpers and Brimhall, 1988).

We focused our midden survey in the Calama and Salar de Atacama basins (Figs. 2.1, 2.2), the midpoint of an ongoing study spanning the entire length of the Atacama Desert. The Calama/Salar de Atacama basins (22-24°S) lie 100-200 km north of the transition from winter rainfall dominance in the southern Atacama (25-30°S) to summer dominance in the central (20-25°S) and northern (16-20°S) Atacama (Fig. 2.1). This abrupt transition in rainfall seasonality makes the central Atacama Desert an ideal region for studying past shifts and intensities of both tropical and extratropical rainfall belts.

Convective summer storms commonly occur north of 25°S on the Pacific slope of the Andes, with the spilling over of moisture from the Amazon Basin. Known locally as *Invierno Boliviano* ("Bolivian winter", in reference to the precipitation that falls as snow on the Altiplano), the magnitude and frequency of these episodic storms reflects the intensity of the South American Summer Monsoon (SASM) (Zhou and Lau, 1998). This seasonal pattern is produced by continental heating over the Altiplano and Gran Chaco during the Austral spring and summer, its intensity linked to upper tropospheric circulation known as the Bolivian High (Lenters and Cook, 1995; Lenters and Cook, 1997; Lenters and Cook, 1999; Zhou and Lau, 1998). South of 25°S, incursions of westerly winds become more frequent and winter precipitation increases in importance (Miller, 1976) (Fig. 2.1). Winter snowfalls can occur as far north as 19°S due to very infrequent cut-off lows (Vuille and Baumgartner, 1998).

The El Niño-Southern Oscillation (ENSO) phenomenon affects interannual precipitation variability on the Altiplano (Aceituno, 1988). The eastern and western Cordilleras, however, exhibit different levels of sensitivity to ENSO (Garreaud, 1999; Vuille et al., 2000). Negative or warm ENSO phases (El Niño) are characterized by high-altitude westerly wind anomalies that inhibit convection over the western edge of the Altiplano. This causes sustained dry conditions by limiting moist air advection from the eastern Cordillera across the Altiplano (Garreaud, 1999). Conversely, positive or cold ENSO phases (La Niña) are characterized by a southward displacement of the

Bolivian High and enhanced easterly circulation that produces greater advection and increased precipitation (Vuille, 1999). These synoptic circumstances seem to explain why precipitation over the entire Altiplano behaves as a coherent, temporal-spatial unit that correlates poorly with adjacent source lowlands to the east (Garreaud, 2000).

In the central and northern Atacama Desert, more than 80% of mean annual precipitation occurs in the summer months (December-March). Absolute precipitation amounts depend on elevation and distance from the crest of the Andes, which controls rainout from spillover storms (Fig. 2.3A). Precipitation data from five weather stations in our study area exhibit only a modest correlation (R^2=0.29) with the Southern Oscillation Index (SOI) for the period between 1980-1993 (Fig. 2.3B). Whereas precipitation increased at all stations during the strong La Niña episodes of 1984 and 1989, precipitation peaks can also happen during El Niño years (e.g., 1987). Spatial and temporal coverage (few records longer than 25 years) is inadequate, yet records from different altitudes (and latitudes) show good agreement after 1980 (Fig. 2.3B). Less agreement before 1980 may reflect problems in the original Dirección General de Aguas (DGA) monthly precipitation data, which underestimate winter snowfall (Vuille and Ammain, 1997; Vuille and Baumgartner, 1998). The extreme aridity of the region accelerates sublimation of light snowpack, however, rendering runoff, infiltration, and soil moisture negligible in winter (Vuille and Ammain, 1997).

The Study Area- Vegetation

The strong north-south and east-west climatic gradients in the Atacama form pronounced gradients in plant distribution (Fig. 2.4). Five major physiognomic vegetation belts characterize northern Chile (Villagrán et al., 1981; Arroyo et al., 1982; Villagrán et al., 1983; Gajardo, 1993). A low fog zone, extending up to 800-1000 meters above sea level (masl), forms discontinuous Lomas communities along the Coastal Range (Rundel et al., 1991). In the study area, Absolute Desert extends 200 km inland from the Coastal Range to the western flanks of the Domeyko and Andes Cordilleras at 2700-3000 masl, close to its maximum extent in northern Chile. The edge of Absolute Desert is defined by the Prepuna, a transitional zone (<30 mm MAP) between 3000-3300 masl with sparse (<5% cover) shrubs and succulent annuals. Common plants include *Cistanthe celosioides* and *C. salsoloides* (Portulacaceae), *Lycopersicon chilense* and *Exodeconus integrifolius* (Solanaceae), *Cristaria* spp. and *Tarasa operculata* (Malvaceae), and *Cryptantha* spp. (Boraginaceae). Halophytic shrubs (*Atriplex imbricata:* Chenopodiaceae), cushion cacti (*Opuntia camachoi*) and Boraginaceae (*Tiquilia atacamensis*) are the only perennials. The shrubs *Acantholippia deserticola* (Verbenaceae) and *Ephedra breana* (Ephedraceae) are common in dry washes and other run-on situations.

Andean Tolar (or Puna belt, e.g. Ruthsatz, 1977) extends from 3200 to ~4000 m, with MAP averaging between 50-100 mm. This diverse, shrub-dominated zone has the highest species richness and total plant cover values (20-30%) in transects spanning the entire gradient at this latitude (Villagrán et al., 1981; Villagrán et al., 1983). Most extensive is the *Fabiana* Tolar, characterized by *Fabiana denudata* and *F. ramulosa* (Solanaceae) commonly found in associations with *Baccharis boliviensis* (Asteraceae) between 3300 to 3500 masl (Armesto and Villagrán, 1987). At higher elevations (3700-4000 masl) the upper Tolar (or Transition) is dominated by the species *Parastrephia* *quadrangularis* and *P. lepidophylla* (Asteraceae). Many C_4 annual and perennial grasses are found in the Tolar, including *Aristida adscensionis, Bouteloua simplex, Enneapogon desvauxii* and *Munroa decumbens*. Other annuals include *Tagetes multiflora* and *Schkuhria multiflora* (both Asteraceae), and *Hoffmannseggia doelli* (Caesalpinaceae). The *Echinopsis* Tolar is dominated by the columnar cacti *E. atacamensis* and *Oreocereus leucotrichus,* and is geographically restricted to areas north of Salar de Atacama (23° S). Other common shrubs in the Tolar are *Junellia seriphioides* (Verbenaceae) and *Chuquiraga atacamensis* (Asteraceae).

The high Andean Steppe, from 4000-4500 masl, receives between 100-200 mm MAP. Perennial bunch grasses, *Stipa chrysophylla, Festuca chrysophylla, Anatherostipa venusta* and *Deyeuxia cabrerae* and other grasses (*Nasella nardoides*) dominate the Andean steppe. Many of these grasses are constrained to high elevations, but *Stipa chrysophylla* occurs as low as 3500 masl on south-facing slopes and shady canyons. Cushion plants like *Azorella compacta* (Apiaceae) and *Pycnophyllum bryoides* (Caryophyllaceae) are common along rocky outcrops. Above the steppe, between 4500 to ~4800 masl, small perennials and flat cushion plants form a sparsely vegetated Alpine belt.

METHODS

Fossil rodent middens are amalgamations of rodent feces, plant, insect, and vertebrate remains encased in hardened urine (amberat) and commonly preserved in rock shelters, caves and crevices. Middens were extracted using a hammer and chisel, cleaned in the field for weathering rinds and surface contaminants, and split along clear stratigraphic units when recognizable. Possible contamination can occur along cracks in the indurated deposits or by inadvertent mixing of different stratigraphic units. AMS ^{14}C dating of suspect plant remains, though costly, is the only means of detecting temporal mixing. Middens in both North and South America are discontinuous in nature, and represent "snapshots" of flora through time (Betancourt et al., 1990; Betancourt et al., 2000).

Midden fecal pellet size and shape are key in telling midden agents apart. Four rodent families produce fossil middens in the Atacama Desert: vizcachas (*Lagidium viscacia*, Chinchillidae); leaf-eared mice (*Phyllotis* spp., Sigmodontinae); chinchilla rats (*Abrocoma cinerea*, Abrocomidae) and brushy-tailed rats (*Octodontomys gliroides*, Octodontidae). *Phyllotis* (average weight is 50 g— all weights from Redford and Eisenberg, 1989) middens are easy to identify by pellet size/morphology. *Abrocoma* and *Octodontomys* are similar in mass (150-300 g) and segregated based on pellet shape. The larger (1-2 kg) and gregarious *Lagidium* (Pearson, 1948) produces middens of considerable size. *Octodontomys* is uncommon in the central Atacama and is not considered here.

Foraging areas for these rodents are usually <100 m (Pearson, 1948; Pearson and Ralph, 1978), though individual vizcachas may stray farther from the colony in search of food. Peruvian species of *Lagidium* and *Phyllotis* (also found in northern Chile) have been reported as dietary generalists (Pearson, 1948; Pizzimenti and De Salle, 1980), which ensures that midden floras are fairly representative of local vegetation.

Forty-nine rodent middens were collected in the field spanning approximately 800 m of elevation between 2400-3200 masl, along the upper margin between Absolute

Desert and Prepuna. Middens were soaked in 10 L buckets of water for two to three weeks to dissolve urine (amberat), wet-sieved with a No. 20 mesh (0.825 mm) and placed in a drying oven at 50-60° C for three days. Dried middens were weighed, quantified for grass abundance, and sorted for plant macrofossils as described in Betancourt et al. (1990).

Between 3-10 g of feces from 47 middens were submitted for bulk dates at Geochronology Laboratories, Inc., Boston, MA. Accelerator mass spectrometry (AMS) was used in cases where insufficient material was available for bulk dates, or when temporal mixing of macrofloras was a concern. AMS targets were pretreated on a vacuum line at the Desert Laboratory and then measured by a tandem accelerator mass spectrometer at the University of Arizona-NSF Accelerator Facility. Radiocarbon ages were calibrated (applying a 24-yr Southern Hemisphere correction) with Method A (ranges with intercepts) from Calib 4.3 (Stuiver and Reimer, 1993) using the Intcal98 calibration curve. Calib 4.3 was also used in generating a summed probability distribution of midden ages. Calendar thousands of years before 1950 (ka BP) is used here to facilitate comparisons across records. Fecal pellet $\delta^{13}C$ values obtained along with bulk ^{14}C dates indicate the proportion of C_3/CAM/C_4 plants in the rodent's diet based on the isotopic difference between C_3 and C_4 plant end members.

Grass abundance was measured as point occurrence on a 120-cell rectangular grid overlain on a sorting tray. A sediment matrix splitter was used to randomly segregate 100 ml of plant debris from each washed and dried midden. Midden debris was then spread uniformly across a 120-1 x 1 in (~6.45 cm^2) cell rectangular grid.

Percent grass abundance was calculated as the ratio of cells out of 120 where grass blades, florets or seeds were identified (i.e. 'hits' on the grid).

Dried middens were sieved into size classes and hand sorted for 3 hours under a binocular microscope (8-35x) for plant macrofossils, including leaves, seeds, wood, grass blades and florets. Insects, vertebrate bones and teeth were also sorted. Plant macrofossils were identified to the highest taxonomic level possible either by direct comparison with our extensive reference collection of modern flora or by reference to specialists. Each taxon was quantified using a relative abundance index (RAI) where 0=absent, 1=rare, 2=common and 3=dominant. The RAI is a quick method at estimating past variations in vegetation composition (Spaulding et al., 1990). Alternate methods, such as absolute counts or pooled weights of individual species, are time-consuming and ultimately biased by midden size and dietary preferences. This is compounded in the Atacama, where several families of rodents produce middens. We used Tilia 2.0 and Tiliagraph (Grimm, 1991-1993) to plot macrofossil abundance and a Constrained Incremental Sum of Squares (CONISS) cluster analysis (Grimm, 1987) to group these assemblages into midden local floras.

Additional fecal pellets were sorted from 41 middens for cuticle analyses (5-6 pellets for *Lagidium* and 10-20 for *Phyllotis*). These were ground using a mortar and pestle, treated with 5% sodium hypochlorite (NaOCl) and wet-sieved using mounted 200 and 100 μm meshes. A small fraction from the 100 μm mesh was then mounted on a slide with silicone oil and viewed at 200x under an optical microscope. Samples were compared with our reference collection of more than 100 taxa. Cuticle identifications are based mostly on shape and size of stomata guard cells, seed testae patterns, and the presence and shape of glandular hairs and trichomes (Metcalfe and Chalk, 1950; Dilcher, 1974). Several genera (i.e. *Cryptantha*, *Cistanthe* and *Atriplex*) and families (Brassicaceae, Poaceae) could not be resolved to species. Quantification was performed using line transects of 2 slides from each midden with a total of 50 fields of view counted. The total number of counts for each taxon is expressed as a percentage of the total fields counted.

RESULTS

Interpretations of midden assemblages are based on modern vegetation transects (Villagrán et al., 1981; Villagrán et al., 1983). We obtained two middens from one locality along the eastern edge of the Calama Basin (Site 1, Figs. 2.1, 2.5) and 47 middens from three localities south of Salar de Atacama (Sites 2-4, Figs. 2.2, 2.5). The age probability distribution obtained from the total sum of 45 calibrated ^{14}C midden dates shows that the largest cluster occurs between 14.0-8.6 ka BP (Fig. 2.6). Three other clusters occur between 8.2-6.5, 6.0-4.4 and 3.0-0.5 ka BP. Discernible gaps in the distribution are apparent between 20-16.8, 8.6-8.2, 6.5-6.0, 4.4-3.8 and from 0.5 ka BP to the present. Limitations in calibration do not allow for conversion of middens older than 22 ka BP. Of the four middens that dated >35 ka BP, two should be treated as minimum ages (LdQ 396: >45,000 ^{14}C yrs BP and VdT 419B: >36,060 ^{14}C yrs BP—Table 2.1). None dated between 35-22 ka BP and only one dated to the Last Glacial Maximum (LGM) (LdT 465, 22 ka BP).

Fecal pellet $\delta^{13}C$ values from forty-seven middens (Fig. 2.7A) show a large spread in values ranging from -24.0‰ (VdT 416, 10.46 ka BP; LdT 472A, 11.54 ka BP) to -16.4‰ (LdT 462B, 0.66 ka BP). Samples >14 kyr average -20.5‰, excluding the oldest midden LdQ 396 (> 44.5 ka BP) which has a $\delta^{13}C$ of -23.2‰. The most striking feature of the $\delta^{13}C$ record is the midden cluster between 13.8-10.2 ka BP, with values that average -22.3‰. From 9.7 to 6.9 ka BP, $\delta^{13}C$ values increase to an average of -20.0‰. Fecal pellet $\delta^{13}C$ averages -20.5‰ between 5.9-3.5 ka BP. A prominent decrease in $\delta^{13}C$ occurred at 4.4 ka BP (LdT 434C2), reflected by a $\delta^{13}C$ of -23.2‰. The greatest increase in $\delta^{13}C$ values occurred between 2.7-0.7 ka BP, with a range between -19.6 to -16.4‰.

Grass abundance (Fig. 2.7B) shows a similar pattern with low percentages before 16.2 ka BP. The midden LdQ 396 (> 44.5 ka BP) has high grass abundance (88%) and is one exception to this pattern. Three middens between 45-22 ka BP have <10% grass. Grass abundance increases to 66% starting at 16.2 ka BP. A cluster of 14 middens between 11.8-10.5 ka BP have grass values that average >50 %. Sharp reductions in grass abundance occurred between 11.9-10.2 ka BP at Quebrada Aiquina, after 10.5 ka BP at Vegas de Tilocalar, after 11.7 ka BP at Lomas de Quilvar and between 10.7-9.5 ka BP at Lomas de Tilocalar (Table 2.1). Values remain <5% until 7 ka BP when they increase to ~10%, although these entail modest increases in summer grasses (see below). Grass abundance drops after 4 ka BP and remains ~0% until 0.9 ka BP, with values >5% at 2 kyr and 0.7 kyr.

Forty-seven middens from sites 2-4 were analyzed for plant macrofossils. In total, 49 taxa were identified, the majority to the species level (Table 2.2). The number of taxa identified per midden ranges from a minimum of seven (VdT 419B, >36 ka BP) to a maximum of 29 (LdT 436, 11.7 ka BP) (Fig. 2.8, Table 2.1). A CONISS cluster analysis on midden macrofloras from sites 2-4 generated six distinct vegetation zones based on species richness similarities sorted by physiognomic affinity and lifeform (*Ti* or Tilocalar zones, Fig. 2.8). A similar pattern was obtained from a CONISS analysis of the species' RAI obtained from these same localities (Fig. 2.9). These patterns of similarity were divided into Midden Local Flora (MLF) Zones and are summarized in Table 2.3.

Fecal pellets from 41 middens (from sites 2-4) were processed for cuticles to characterize rodent diets (Fig. 2.10). The proportion of *Phyllotis* to *Lagidium* middens remained the same throughout the entire record (Table 2.1). Dietary changes likely reflect habitat changes rather than selective preference by particular rodents. Results from the cuticle analysis are summarized in Table 2.4. Twenty-eight taxa were identified, the majority to genus, although in some cases, highly digested cuticles permitted identification only to family (e.g., Poaceae). This analysis added paleoenvironmental information that was otherwise unavailable (e.g. taxa evident in rodent diets were not found as plant macrofossils in the same middens, such as *Fabiana* and *Baccharis* cf. *boliviensis*).

DISCUSSION

Sum probability distributions of ^{14}C dates, along with fecal pellet $\delta^{13}C$ data, grass abundance, plant species richness, and composition of midden macrofloras and rodent diet constitute several independent climate proxies obtained from a single midden record. Agreement between these paleoenvironmental proxies implies common causes, as discussed below.

The largest cluster of ^{14}C dates occurs between 14-8.6 ka BP (Fig. 2.6). Because the probability of midden occurrence decreases exponentially with age, this clustering is either due to sampling biases ('the lure of the Pleistocene') or temporal variability in rodent activity and midden formation as they track ecosystem productivity (Webb and Betancourt 1990). We collected middens in the Atacama more or less randomly without bias for age or appearance, so we attribute the late glacial-early Holocene cluster to heightened productivity.

Most of the late glacial/early Holocene middens (16.2-10.5 ka BP) contained large quantities of annual and perennial grasses (Fig. 2.7B). Because grasses do not occur today at any of our midden sites and are usually found at higher elevations (in the Tolar or Andean Steppe) or in valleys with perennial rivers and wetlands, we interpret grass abundance as a proxy for precipitation and productivity (Betancourt et al., 2000). The average fecal pellet $\delta^{13}C$, -22.0‰ for late glacial/early Holocene reflects an almost pure C_3 diet, though occasionally enriched values in this period may reflect feeding on heavy annual blooms of C_4 grasses.

Midden macrofloras and cuticles reveal several prominent patterns (Figs. 2.8-2.10). Prepuna and summer annuals are scarce (2-3 taxa) in the few middens >22 ka, in contrast with dominance of these taxa (6-8 taxa) during the late glacial and Holocene (Fig. 2.8). Few middens, few annuals particularly sensitive to low temperatures (Arroyo et al., 1988), and the dominance of Prepuna shrubs such as *Ephedra* suggest cold and hyperarid conditions.

A mixed plant community of Steppe grasses, many summer annuals and Tolar taxa expanded across the margin of what is now presently Absolute Desert in the southern Salar de Atacama Basin starting at 16.2 ka BP and most notably, between 13.8 -10.5 ka BP (Figs. 2.8, 2.9). Species richness and macrofossil assemblages indicate that this unique period of plant invasions into what is now Absolute Desert peaked between 11.8-10.5 ka BP and ended abruptly after 10.5 ka BP. The presence of steppe grasses, particularly *Anatherostipa venusta* and *Nasella nardoides* (found today >3900 masl), implies a displacement of at least 800 m. Based on precipitation data from the region (Fig. 2.3A), this must have entailed more than a threefold increase in MAP from 30-50 mm to ~150 mm.

Other steppe grasses in the late glacial-early Holocene middens include *Stipa chrysophylla* and *Nasella arcuata*, a common species in the Altiplano of Arica and Bolivia but now rare in the central Atacama (Matthei, 1965; Marticorena et al., 1998). The numerous C_4 grasses, including *Munroa decumbens*, *Aristida adscensionis*, *Bouteloua simplex*, *Enneapogon desvauxii* and *Pappophorum caespitosum* indicate that the precipitation increase occurred in summer. *P. caespitosum* has never been collected in Chile despite 30 years of intensive collecting efforts (O. Matthei, personal communication), but is common in southern Peru and northwestern Argentina (Nicora and Rúgolo de Agrasar, 1987; Tovar, 1993). Tolar shrubs and cacti such as *Junellia seriphioides* and *Echinopsis atacamensis* are well represented in the macrofloras, as well as *Fabiana* in most cuticle samples (Fig. 2.10). Taken together, these data indicate that 11.8-10.5 ka BP was the wettest period in the central Atacama Desert for possibly the last 45,000 years.

The onset of hyperaridity is recorded by abrupt extirpation of vegetation. Hyperaridity is evidenced by enriched $\delta^{13}C$ values and low grass percentages between 11.8-10.2 ka BP at the northern midden site and between 10.5-9.5 ka BP at the southern sites (2-4). The discontinuity typical of midden series prevents better resolution of this desiccation event, but must have been complete by 9.5 ka BP, when grass abundance dropped to ≤ 3% at all sites. Starting at 9.5 ka BP, the midden record has diminished species richness and lacks Steppe and Tolar elements. Prepuna elements, such as *Atriplex imbricata* and *Opuntia camachoi* are dominant until 7.1 ka BP. *Cistanthe* and *Exodeconus integrifolius*, both Prepuna annuals, are also common. Cuticle samples indicate prevalence of *Atriplex*, *Hoffmannseggia* and *Cistanthe* in rodent diets, although the latter increases in importance throughout the Holocene, while *Hoffmannseggia* percentages decrease dramatically during the early Holocene.

Moisture increased slightly during the middle Holocene (7.1-3.5 ka BP), with a modest increase in grass abundance and a decrease in fecal pellet $\delta^{13}C$ values. A prominent increase in C_3 plant content occurred at 4.4 ka BP as indicated by a $\delta^{13}C$ of -23.2‰. This coincides with a large increase of *Fabiana* cuticles in fecal pellets, a C_3

shrub. Grass percentages hovered at ≥ 10% during much of this period and decreased after 4.4 ka BP. Tolar shrubs *Junellia, Krameria* and the cactus *Echinopsis* reappear briefly during the middle Holocene, starting at 7.1 ka BP. This was accompanied by the presence of wetlands near the Salar de Atacama, as indicated by seeds of *Scirpus* cf. *californicus* at Vegas de Tilocalar (VdT 417, 6.9 ka BP). A few C_4 grasses and summer annuals (*Munroa decumbens, Aristida adscensionis* and *Euphorbia amandi*) in middens between 7.1-3.5 ka BP point to increases in summer rainfall. Although cuticle samples are dominated by high percentages of *Atriplex* and *Cistanthe*, they also indicate the presence of Poaceae and *Fabiana*. The latter could not have become established or survived at such low elevations without some rainfall every year, arguing against a disproportionate influence of the occasional storm and so-called annual bloom once every few decades.

In contrast, late Holocene grass percentages are <2% throughout except for two middens at 2 and 0.7 ka BP with values slightly above 5%. These samples could represent very brief surges in summer rainfall, causing local annual blooms. The late Holocene $\delta^{13}C$ record is remarkably uniform and characterized by higher isotopic values, indicating strong C_4 and CAM plant influences in rodent diets. The highest percentages of *Atriplex* and *Cistanthe* in cuticle samples occur during the late Holocene, however, especially after 3.5 ka BP (Fig. 2.10). Midden macrofloras indicate low species richness and abundance of Prepuna shrubs and annuals (Figs. 2.8, 2.9). Only the youngest midden at 0.5 ka BP shows evidence for a slightly more humid climate, as evinced by the presence of single seeds of *Junellia seriphioides*, *Krameria lappacea* and the annuals *Munroa decumbens* and *Euphorbia amandi.* These taxa represent a more diverse assemblage than indicated by a one-day survey of the modern landscape. This might be explained by accumulation over several decades in a single midden, generating higher diversity than found at the site today.

REGIONAL PALEOCLIMATOLOGY

To facilitate comparisons with other records, we have established a relative paleoproductivity curve (Fig. 2.11) using two independent parameters, plant species richness and grass abundance. This proxy is based on the strong correlation between modern plant cover, plant species richness and precipitation in northern Chile (Meserve and Glanz, 1978). We calculated an anomaly (departure) curve for productivity and precipitation using statistical normalization methods based on the mean from 3 middens spanning the last 1,000 years. Positive departures indicate increased precipitation with respect to the last 1,000 years whereas negative departures indicate increased aridity. We limit our paleoproductivity curve to the last 22 ka BP, when we have adequate coverage.

The Late Glacial Period

Most late Quaternary geological records of climate change in the Atacama are derived from lake sediments on the Chilean Altiplano (Messerli et al., 1993; Grosjean, 1994; Grosjean and Nuñez, 1994; Grosjean et al., 1995; Valero-Garcés et al., 1996; Geyh et al., 1999). Other records include wetland deposits at Quebrada Puripica (Grosjean et al., 1997a) and a 106 ka halite core obtained from the deepest portion of the Salar de Atacama (Bobst et al., 2001). Using ^{14}C dates on terrestrial macrofossils from Laguna Lejía, organic sediments at Laguna Tuyajto, diatomites at Salar de Punta Negra and peat beds in the Salar de Atacama, all sites between 23° and 25°S (see Fig. 2.1), Geyh et al. (1999) identified a wet phase between ~15-9.2 ka BP that agrees with our midden record. Based on a simple hydrologic model, Kull and Grosjean (1998) concluded that precipitation must have doubled to account for increased lake levels at 4300 masl on the Chilean Altiplano. Our vegetation record suggests more than threefold precipitation increases on the margin of Absolute Desert at 2400-3000 masl. A recent 22,000-^{14}C year pollen record from Laguna Miscanti (4140 masl, Grosjean et al., 2001; Fig. 2.1) indicates dry conditions during the LGM with a strong lake transgression during the late glacial, as evidenced by high levels of aquatic pollen. A sharp increase in pollen concentrations of grasses and other taxa at the beginning of pollen zone MIS-3 (ca. 17-14 ka BP with uncorrected ages or ca. 11-9 ka BP with reservoir-corrected ages) may be concomitant with grassland expansion in our midden record. A record of past regional fluctuations of ground-water levels reconstructed from paleowetland deposits in the central Atacama also indicates a major increase in discharge between 16-9 ka BP (Betancourt et al., 2000; Rech et al., 2001).

Paleoclimate records from the Altiplano typically have older dates for the wet phases. Ice cores spanning the last 25,000 years from the summit of Nevado Sajama indicate above-average ice accumulation, temperatures 8-12°C colder than today, and low atmospheric dust concentrations synchronous with Altiplano paleolake highstands between 25-22, 19-15.5, and 14-9.5 ka BP (Thompson, 2000). A recent study using U-series dating and validation of ^{14}C dates on shoreline tufas in the Uyuni-Coipasa Basin (Sylvestre et al., 1999) identified two wet phases: one major event between 18.9-14.0 ka BP (Tauca Phase); and a minor event between 10.8-9.5 ka BP (Coipasa Phase), separated by a dry phase (Ticaña event) between 14.0-10.8 ka BP. These highstands are younger than those inferred from a ^{14}C-dated sediment core in the center of the Salar de Uyuni, which indicates wet phases at >42, 33.4-31.8, 30.8-28.2, and 26.1-14.9 ka BP, followed by a minor lake stand ~12.5 ka BP (Baker et al., 2001a). Possible conflicts can arise from U-Th dating of lakeshore carbonates in the Altiplano, which incorporate a considerable detrital correction (Sylvestre et al., 1999) or large reservoir effects on ^{14}C dates. ^{14}C-dates on terrestrial organic matter and macrofossils preserved in wetland deposits found downslope from the Uyuni and Coipasa Basins, however, show a rise in water table between 15-9 and 8-3 ka BP that concurs with our record (Rech et al., 2000).

Sedimentologic changes in a U-series dated core from the Salar de Atacama (Bobst et al., 2001) indicate wet phases between 75.8-60.7, 54-15.2, 11.2-10.3 and 5.3-3.5 ka BP. Subaqueous halite formed between 26.7-16.5 ka BP is interpreted as the maximum wet phase at Salar de Atacama. Despite good agreement between midden evidence and the late glacial wet phases on the Altiplano (and middle Holocene for the Salar de Atacama core), we found only one midden between 26.7-16 ka BP, which indicates arid conditions at 22 ka BP (low grass abundance and absence of steppe and Tolar taxa). We remain cautious about overinterpreting full glacial aridity from negative evidence or incomplete coverage, but suggest that at the very least it was intermittently dry.

Records from the Andes of Perú and Bolivia indicate older dates for the end of the late glacial humid phase. Glaciers retreated in the Cordillera Blanca of Perú before 12.8 ka BP (Rodbell and Seltzer, 2000) and were apparently synchronous with glacier retreat and Lake Tauca desiccation at Salar de Uyuni (Clayton and Clapperton, 1997).

The Holocene

Lakes on the Chilean Altiplano disappeared completely after 8.9 ka BP (Grosjean, 1994; Geyh et al., 1999), more than 600 years after our vegetation records indicates abrupt drying (9.5 ka BP). The inference from these lakes is for drier conditions than today persisting throughout the middle Holocene.. The evidence includes gypsum beds at Laguna Miscanti (Valero-Garcés et al., 1996), lower lake levels at Laguna Negro Francisco (Grosjean et al., 1997b), Lago Titicaca (Seltzer et al., 1998; Cross et al., 2000; Baker et al., 2001b) and Lago Taypi Chaka Kkota in the Cordillera Real of Bolivia (Abbott et al., 2000). The onset, duration and persistence of mid-Holocene aridity are poorly documented and vary from site to site. Local hard-water effects confound radiocarbon dating of the Laguna Negro Francisco and Miscanti records (Grosjean et al., 1997b), but low lake levels (85 m below present) inferred from a core drilled in the deepest portion of Lago Titicaca are well dated between 8.0-5.5 ka BP (Baker et al., 2001b).

In contrast, midden macrofloras show modest increases in precipitation (relative to modern) during the mid-Holocene relative to the hyperaridity in the early and late Holocene. Summer annuals, C_4 grasses, *Fabiana* (in rodent diet) and *Echinopsis* in middens between 7.1-3.5 ka BP suggest rainfall increases from tropical, not extratropical sources. Other evidence for a mid-Holocene wet phase comes from wetland records at Tilomonte, Río Salado and Río Loa, which indicate high regional water tables between 7-3 ka BP (Betancourt et al., 2000; Rech et al., in press). Río Desaguadero ^{14}C-dated river terrace deposits, formed by either Lake Titicaca spillover or changes in local precipitation budgets, suggest highstands between 4.5-3.9 and 2.2-2.0 ka BP (Baucom and Rigsby, 1999). A brief increase in moisture between 5.7-4.4 ka BP is also documented at the Laguna Seca pollen site, only 200 km south of Lago Titicaca and northwest of the Salar de Uyuni (Baied and Wheeler, 1993). Lake levels were also higher during the middle Holocene at Lago Aricota (17°S), a moderate-sized lake on the Pacific slope of the Andes in southern Peru (Placzek et al. 2001). An extensive series of rodent middens between 2350-2750 m near Arequipa, Peru (16° S) shows that vegetation was relatively stable during the middle Holocene (Holmgren et al. 2001).

Contrasting interpretations for the mid-Holocene bear directly on interpretation of the region's archaeological record. Sustained hyperaridity has been invoked to explain the paucity of mid-Holocene human occupation in the Atacama Basin, the so-called *Silencio Arqueológico* or Archaeological Hiatus (Grosjean and Nuñez, 1994; Nuñez and Grosjean, 1994). Mid-Holocene human occupation was apparently limited to springs and wetlands. At Quebrada Puripica, a steep canyon northeast of Salar de Atacama, 30-m thick stacks of diatomite are interbedded with alluvium and archaeological materials dating between 6.8 and 3.2 ka BP. The diatomite beds are perched high up above the present streambed and local groundwater table. Grosjean et al. (1997), who studied the site in 1993, interpreted the diatomite beds as lake deposits dammed behind a side-canyon debris flow, which could not be breached by mainstem low flow conditions during a hyperarid middle Holocene. Quebrada Puripica was reexamined by our group in 2000, who came to a different conclusion. The presence of diatomite for several kilometers above and below the suggested side-canyon dam suggests that the diatomite actually formed in springs fed by a higher groundwater table, not a lake. The diatomite at Quebrada Puripica is contemporaneous with other perched wetland deposits indicating higher ground-water levels in the central and northern Atacama (Betancourt et al., 2000; Rech et al., 2001; Quade et al., 2001). Grosjean (2001) suggests that these wetland deposits and locally-elevated water tables result from alluviation in canyons during low-flow conditions. Mid-Holocene wetland deposits indicating higher ground-water levels, however, are not confined to deep, erosive canyons in the central and northern Atacama (18-24°S). They crop out in small channels and interfluves outside of mainstem channels, in open, marshy environments and around spring vents on hillslopes (Betancourt et al., 2000; Rech et al., 2001; Quade et al., 2001). Contrary to Grosjean's (2001) assertions, mid-Holocene and late glacial-early Holocene spring deposits, the latter which he accepts as evidence for wetter conditions, occur in the same geomorphic settings. We believe that wetland deposits in the central and northern Atacama imply wetter conditions, and pose a challenge to the conventional assumption of mid-Holocene aridity on the Pacific slope of the Andes. Finally, we agree with Grosjean et al. (1993b) that Early Archaic (13-9 ka B.P.) occupation of the Atacama was disrupted by the end of the late glacial-early Holocene pluvial. We suggest, however, that the resettlement of the Atacama later in the Holocene might have been complex, involving not just climatic variations but also diffusion of technologies from other areas, such as domestication of camelids ~6-7 ka B.P. in Peru.

What drives the intensity of the South American Summer Monsoon?

Summer and seasonal insolation forcing of Amazon Basin convection has been used to explain millennial timescale variations in central Andes lake records (Martin et al., 1997; Seltzer et al., 2000; Baker et al., 2001a; Baker et al., 2001b). Limited adiabatic heating over the South American tropics during periods of minimal summer and seasonal insolation would lead to reductions in precipitation over the central Andes. An 18,000 ka BP record of $\delta^{18}O_{calcite}$ from Lago Junín, central Peruvian Andes (11° S), implies low lake levels during the late glacial/early Holocene transition that matches the January (summer) insolation minimum at 10° S (Seltzer et al., 2000). Lago Titicaca levels, as reconstructed from several climate proxies (Baker et al., 2001b), fell after 11.5 ka BP. Amazon River discharge records, however, conflict regarding moisture budgets during the late glacial/early Holocene. Evidence from planktic foraminiferal $\delta^{18}O$ (Showers and Bevis, 1988) and clay minerals (Harris and Mix, 1999) point to increased discharge during the Younger Dryas, whereas a recent record using the isotopic difference between foraminiferal $\delta^{18}O$ and global ice volume indicates decreased discharge (Maslin and Burns, 2000). The Atacama pluvial phase between 16.2-10.5 ka BP described here, however, suggests that, at the tail end of the tropical rainfall belt, the wettest episode in the last 45,000 years occurred at a time of minimum summer insolation and insolation seasonality at 20°S (Berger and Loutre, 1991) (Fig. 2.11). This leads us to look elsewhere for explanations of the intensity of the SASM on millennial timescales.

Our record indicates that maximum rainfall in the central Atacama Desert was achieved between 11.8-10.5 ka BP, with a lesser pluvial phase between 7.1-3.5 ka BP. Modern precipitation over the Bolivian Altiplano occurs during the mature phase (mid-summer) of the SASM (Zhou and Lau, 1998). As previously stated, regional variations in precipitation spillover onto the highlands of the Atacama Desert are strongly dependent on upper air conditions favorable for moisture transport across the Altiplano and independent of fluctuations in lowland moisture source areas (Garreaud, 2000; Vuille et al., 1998; Vuille et al., 2000). Thus, any relationship between the past intensity of the SASM and the wet phases that occurred over the central Andes and the Atacama Desert should incorporate forcing other than warming of the continental interior or variations in source areas for moisture.

Strong easterlies during La Niña conditions produce a southward displacement and intensification of the Bolivian High, favoring convection and moisture transport across the Altiplano. The reverse occurs during El Niño, when upper level westerly winds suppress convection (Vuille et al., 2000). Thus, remote forcing by variations in Walker Circulation is capable of modifying SASM intensity. Research with coupled ocean-atmosphere models (Cane and Clement, 1999) suggests that variations in orbital insolation produced nonlinear effects in tropical Pacific sea surface temperature gradients. Recent climate modeling (Liu et al., 1999) also links maximum summer insolation in the northern hemisphere to an intensified Asian Monsoon, strengthened Pacific trades and intensified Walker Circulation, producing La Niña-like conditions during the early Holocene. We propose that this would have also increased precipitation over the central and northern Atacama Desert and the western Altiplano through an intensification of the SASM. Conversely, abrupt drying by 9.5 ka BP may have been caused by strengthened westerlies over the Altiplano, inhibiting convection and precipitation similar to an onset of sustained El Niño-like conditions. A cold tropical Pacific during the middle Holocene, indicated by several marine and terrestrial proxies

(Cole, 2000), would have intensified upper level circulation, enhancing the transport of tropical moisture across the Altiplano and onto the central Atacama.

PALEOBIOGEOGRAPHY IN THE CENTRAL ATACAMA DESERT

Biogeographers have traditionally referred to present and past biotic distributions in the Atacama Desert as the outcome of a "natural experiment" (Arroyo et al., 1988; Marquet, 1994; Villagrán et al., 1983). Low diversity and a high degree of endemism, the result of pronounced climatic and biological barriers, are key features of the modern Atacama (Rundel et al., 1991; Marquet et al., 1998). Climate change plays a pivotal role among the many hypotheses proposed to account for these distributions. The lowering of vegetation into Absolute Desert presumably formed filters or corridors for north-south dispersal from northern into central Chile during the Pleistocene (Moreno et al., 1994), whereas sustained desiccation would have imposed formidable barriers (Villagrán et al., 1983; Arroyo et al., 1988).

Latest Pleistocene plant communities on the margin of Absolute Desert in the Atacama were more diverse and probably occupied a much larger area than today, forming extensive mixed Tolar-Steppe grasslands. Prepuna communities were enriched by an 800 m descent of Andean Steppe species at the peak of the wettest phase, between 11.8-10.5 ka BP. This brief interlude of increased moisture is in strong contrast with sustained hyperaridity, probably during the full glacial and certainly for the early and late Holocene. Although plant invasions into Absolute Desert were likely extensive, lowland biogeographic corridors during the late glacial/early Holocene were probably short lived. Indeed, low affinity between Puna (northern Chile) and Mediterranean (central Chile) Andean floras suggests that isolation predates the Quaternary (Villagrán et al., 1983). Sustained hyperaridity (and very low bioproductivity) would also explain the lack of reliably dated latest Pleistocene extinct "megafauna" sites (Moreno et al., 1994) in the Atacama Desert. For Early Archaic cultures in the Atacama, however, the late glacial/early Holocene pluvial apparently stimulated a population explosion evident in numerous sites dated between 13-10.2 ka BP (Nuñez and Grosjean, 1994) (these sites are actually coeval with Paleoindian cultures elsewhere).

As witnessed in the present study, the sudden loss of steppe grasses at the end of the Pleistocene reveals that plant species in the Atacama are subject to constant "local" extinctions or extirpations. Such extirpations occurred throughout the Holocene, including the northerly retreat of *Echinopsis* and *Ambrosia artemisioides* and the disappearance from northern Chile of the perennial C_4 grass, *Pappophorum caespitosum* ~2,000 years ago.

Finally, we point out that the central Atacama presents a unique natural experiment in which life and water overruns lifeless landscapes at known times in the past, leaving an organic lag and a host of fluvial landforms. There is no other comparable circumstance on Earth, save for the early Holocene expansion of tropical savannas into the hyperarid core of the eastern Sahara Desert (Ritchie et al., 1985; Ritchie and Haynes, 1987).

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TABLE 2.1. GEOCHRONOLOGICAL AND BIOLOGICAL DATA FOR THE 49 MIDDENS USED IN THIS STUDY

Midden Field No.	Radiocarbon Lab No.[*]	Radiocarbon Age (^{14}C yrs B.P.)	δ^{13}C (PDB)	Calendar age (yr B.P.)[†]	Intercept or midpoint[§]	Elevation (masl)	No. of Taxa	% Grass	Midden Agent	Slope Aspect
1) Quebrada Alquina A (S 22°17.5'; W 68°21.1')										
1 QA-A 349	GX-23853	9140±130	-22,4	10470 (10240) 10190	10240	2986	--	1	Phyllotis	N
2 QA-A 352	GX-25659	10110±380	-20,9	12610 (11640, 11610, 11580) 11170	11890	2986	--	35	Phyllotis	N
2) Vegas de Tilocalar (S 23°47'; W68°09')										
3 VdT 417	GX-25252	6050±260	-18,9	7250 (6860, 6820, 6810) 6550	6900	2360	10	3	Lagidium	SE
4 VdT 416	GX-25251	9250±250	-24,0	10730 (10400, 10315, 10310, 10300, 10290) 10180	10460	2360	12	20	Phyllotis	E
5 VdT 419C	AA-32648	13500±90	-17,0	16440 (16190) 15950	16190	2400	17	66	Phyllotis	NE
VdT 419C	GX-24916	13330±960	-19,0	17122 (15990) 14307	15990	2400	17	66	Phyllotis	NE
6 VdT 419A	AA-33385	35100±700	-20,0	uncalibrated	uncalibrated	2400	13	2	Lagidium	NE
7 VdT 419B	GX-24832	>36060	-20,8	uncalibrated	uncalibrated	2400	7	1	Lagidium	NE
8 VdT 418	AA-32649	40900±1400	-20,5	uncalibrated	uncalibrated	2400	9	0	Lagidium	NE
3) Lomas de Quilvar (S 23°50.6'; W 68°02.4')										
9 LdQ 395B1	GX-25059	2560±320	-18,6	2950 (2720) 2160	2720	3050	13	1	Phyllotis	NW
10 LdQ 399	AA-32650	4340±65	-15,7	4960 (4860) 4830	4860	3050	9	0	Lagidium	W
11 LdQ 400	GX-24831	10120±150	-23,6	12095 (11690, 11680, 11640, 11605, 11600) 11260	11680	3087	25	100	Lagidium	W
12 LdQ 397A	GX-24877	11270±220	-19,6	13450 (13160) 13000	13160	3110	27	100	Phyllotis	W
13 LdQ 398A	GX-25250	11860±180	-23,9	14080 (13830) 13510	13830	3050	21	14	Abrocoma/Phyllotis	W
14 LdQ 396	GX-25249	>44560	-23,2	uncalibrated	uncalibrated	3100	10	88	Lagidium	W
4) Lomas de Tilocalar (S 23°53' to S 23°58'; W 68°08' to W 68°10')										
15 LdT 470	AA-36773	530±35	-19,9	542 (527) 513	527	2954	14	0	Phyllotis	W
16 LdT 462B	GX-25258	725±70	-16,4	680 (660) 560	660	2875	11	7	Phyllotis	W
17 LdT 464B	GX-24023	990±75	-19,6	950 (920)790	920	2820	10	0	Lagidium	E
18 LdT 425B	GX-25037	1095±70	-19,1	1060 (970) 930	970	2650	9	0	Lagidium	SE
19 LdT 432	GX-25038	1485±175	-18,1	1530 (1350, 1340, 1330) 1190	1360	2840	12	1	Phyllotis	E
20 LdT 464A	GX-25259	1805±75	-19,5	1820 (1710) 1570	1710	2350	9	0	Lagidium	E
21 LdT 439	GX-25040	2035±75	-19,0	2040 (1985, 1980, 1970, 1960, 1950) 1880	1960	2650	16	8	Lagidium	E
22 LdT 444	GX-25253	2330±55	-19,1	2350 (2340) 2210	2340	2600	11	0	Phyllotis	E
23 LdT 437A	GX-24932	2400±125	-19,5	2710 (2350) 2210	2350	2825	10	1	Lagidium	W
24 LdT 437B	GX-24974	3250±95	-20,8	3570 (3460) 3360	3460	2825	14	0	Lagidium	W
25 LdT 434C2	GX-24976	3940±400	-23,2	4860 (4410) 3730	4410	2840	19	11	Phyllotis	W
26 LdT 463	GX-25043	4670±190	-20,2	5590 (5440, 5420, 5320) 5050	5320	2950	9	0	Phyllotis	W
27 LdT 462A	GX-25257	4820±150	-18,8	5660 (5590, 5500, 5490) 5323	5490	2875	15	12	Phyllotis	W
28 LdT 422	GX-25062	4920±160	-20,6	5860 (5610) 5470	5610	2650	12	0	Lagidium	SE
29 LdT 453	GX-25042	5140±160	-21,2	6170 (5910) 5660	5910	2675	14	11	Lagidium	E
30 LdT 446A	GX-25255	6170±280	-18,9	7410 (7140, 7130, 7010) 6670	7020	2640	13	10	Phyllotis	N
31 LdT 461A	GX-24977	6240±120	-20,3	7430 (7180, 7170, 7160, 7110, 7100) 6680	7050	2780	15	7	Phyllotis	E
32 LdT 478	GX-25260	6260±120	-17,5	7270 (7200, 7190, 7180, 7170, 7160, 7110, 7100) 6950	7110	2910	11	0	Phyllotis	W
33 LdT 446B	GX-24933	7060±250	-18,7	8150 (7920, 7900, 7840) 7610	7880	2640	13	0	Phyllotis	N
34 LdT 468	AA-39721	7341±54	-18,3	8177 (8157, 8136, 8131, 8119, 8112, 8078, 8061) 7979	8080	2785	17	--	Phyllotis	W
35 LdT 442	GX-24975	8140±210	-23,2	9400 (9030) 8650	9030	2950	13	3	Lagidium/Phyllotis	W
36 LdT 464C	GX-24024	8460±340	-19,4	9890 (9470) 9010	9470	2820	13	1	Lagidium	E
37 LdT 471	GX-24936	8590±150	-19,3	9690 (9530) 9440	9530	2954	13	5	Lagidium	W
38 LdT 449A	GX-24934	9470±530	-19,2	11340 (10690, 10650, 10640) 9980	10660	2610	19	34	Phyllotis	E
39 LdT 438B	GX-25039	9570±320	-19,8	230 (11055, 11050, 11040, 11020, 11000, 10960, 10760) 103	10760	2825	19	66	Phyllotis	W
40 LdT 433	GX-24931	9600±450	-20,0	11550 (11060, 10940, 10850, 10830, 10790) 10240	10890	2840	26	53	Phyllotis	E
41 LdT 438A	GX-25063	9610±170	-17,8	180 (11070, 10940, 10860, 10820, 10810, 10800, 10790) 106	10870	2825	19	49	Lagidium	W
42 LdT 434A	AA-39272	9610±59	-18,9	116 (11067, 10940, 10857, 10825, 10807, 10798, 10792) 106	10900	2825	11	--	Phyllotis	W
43 LdT 472C	GX-24879	9710±140	-23,1	11200 (11160) 10760	11160	3030	22	50	Lagidium	W
44 LdT 472A	GX-24876	10000±150	-24,0	11880 (11340, 11320, 11300, 11260) 11200	11540	3030	14	30	Lagidium	W
45 LdT 436	GX-25026-PRI	10150±150	-23,1	12270 (11690) 11260	11690	2825	29	98	Lagidium	W
46 LdT 441	GX-25041	10160±150	-23,4	12280 (11730, 11720, 11700) 11300	11790	2950	18	61	Lagidium	W
47 LdT 460	AA-29273	10183±70	-16,5	099 (11900, 11856, 11839, 11823, 11750, 11707, 11703) 115	11840	2850	17	--	Phyllotis	NE
48 LdT 447	GX-25256	10730±440	-21,8	13150 (12840) 11960	12840	2610	16	11	Phyllotis	N
49 LdT 465	GX-24978	18550±680	-19,0	22860 (22000) 21150	22000	2825	9	11	Phyllotis	W

[*] GX = Geochron Labs; AA= Arizona-NSF Accelerator Facility. Geochron dates were performed on bulk (3-10 g) fecal pellet samples; Arizona dates were performed on plant macrofossils or fecal pellets. All standard deviations are at 1 sigma.

[†] Calibrated ages are in Calendar years before 1950 at 1 sigma, and where obtained using Method A of the Calib 4.1.3 (intcal98 dataset) software. A southern hemisphere deduction of 24 years was applied to all calibrated dates.

[§] In case of more than one intercept, a range midpoint (at 1 sigma) was calculated.

TABLE 2.2. LIST OF PLANT SPECIES IDENTIFIED FROM RODENT MIDDEN MACROFOSSILS

Taxa	Family	Life form	Phytogeography	Plant part identified
Gymnospermae				
Ephedra breana Phil.	Ephedraceae	shrub	Prepuna and Tolar	seeds, bark
Angiospermae-Dicotyledoneae				
Ambrosia artemisioides Meyen et Walp.	Asteraceae	shrub	Prepuna	fruits
Helogyne macrogyne (Phil.) B.L.Rob.	Asteraceae	shrub	Tolar	achenes
Schkuhria multiflora Hook. Et Arn.	Asteraceae	summer annual	Tolar	achenes
Tagetes multiflora Kunth	Asteraceae	summer annual	Tolar	achenes
Cryptantha diffusa (Phil.) I.M. Johnst.	Boraginaceae	annual	Prepuna	nutlets
Cryptantha hispida (Phil.) Reiche	Boraginaceae	annual	Prepuna	nutlets
Cryptantha limensis (A.DC.) Reiche	Boraginaceae	annual	Prepuna	nutlets
Cryptantha phaceloides (Clos) Reiche	Boraginaceae	annual	Prepuna	nutlets
Cryptantha spp.	Boraginaceae	annuals	Prepuna	leaves, fruits
Pectocarya linearis (Ruiz et Pavón) DC.	Boraginaceae	perennial herb		nutlets, leaves
Tiquilia atacamensis (Phil.) A.T. Richardson	Boraginaceae	subshrub	Prepuna	nutlets, leaves
Sysimbrium spp.	Brassicaceae	subshrub to annual	Prepuna and Tolar	siliques, pedicels, leaves
Opuntia camachoi Espinosa	Cactaceae	perennial herb	Prepuna and Tolar	seeds
Opuntia cf. *ignescens* Vaupel	Cactaceae	perennial herb	Tolar	seeds
Opuntia cf. *sphaerica* C.F. Först.	Cactaceae	perennial herb	Prepuna	seeds
Echinopsis cf. *atacamensis* (Phil.) Friedrich et G.D. Rowley	Cactaceae	tree	Tolar	seeds
Hoffmannseggia sp.	Caesalpiniaceae	perennial herb	Prepuna and Tolar	seeds, leaves
Atriplex imbricata (Moq.)D.Dietr.	Chenopodiaceae	shrub	Prepuna and Tolar	leaves, fruits
cf. *Chenopodium quinoa* Willd.	Chenopodiaceae	annual	culitvated	seeds
Euphorbia amandi Oudejans	Euphorbiaceae	annual	Tolar	seeds, fruits
Phacelia sp.	Hydrophyllaceae	perennial herb to annual	Prepuna and Tolar	seeds
Krameria lappacea (Dombey) Burdet et B.B. Simpson	Krameriaceae	shrub	Tolar	leaves, fruits
Huidobria fruticosa Phil.	Loasaceae	shrub	Prepuna	seeds, bark
Dinemandra ericoides A.Juss.	Malpighiaceae	shrub	Prepuna	fruits
Cristaria sp1	Malvaceae	annual	Prepuna and Tolar	seeds
Cristaria sp2	Malvaceae	annual	Prepuna and Tolar	seeds
Tarasa cf. *operculata* (Cav.) Krapov.	Malvaceae	subshrub	Prepuna	leaves, seeds
Nolana cf. *tarapacana* (Phil.) I.M. Johnst.	Nolanaceae	perennial herb	Prepuna	mericarps, leaves
Alliona incarnata L.	Nyctaginaceae	perennial herb		seeds
Adesmia cf. *erinacea* Phil.	Papilionaceae	shrub	Tolar	spines
Adesmia cf. *spinosissima* Meyen	Papilionaceae	shrub	Tolar	spines
Chorizanthe commisuralis J. Remy	Polygonaceae	annual	Prepuna and Tolar	fruits, stems
Cistanthe spp.	Portulaceae	CAM annuals	Prepuna	seeds, leaves
Exodeconus integrifolius (Phil.) Axelius	Solanaceae	annual	Prepuna	seeds
Lycopersicon chilense Dunal	Solanaceae	shrub	Prepuna	seeds, leaves
Acantholippia deserticola (Phil. ex F.Phil.) Moldenke	Verbenaceae	shrub	Prepuna and Tolar	seeds, wood
Junellia seriphioides (Gillies et Hook.) Moldenke	Verbenaceae	shrub	Puna	seeds
Angiospermae-Monocotyledoneae				
Scirpus cf. *californicus* (C.A.Mey.) Steud.	Cyperaceae	perennial herb	Wetlands	seeds
Anatherostipa venusta (Phil.) Peñail.*	Poaceae	C_3 perennial herb	Steppe	florets
Aristida adscensionis L.	Poaceae	C_4 summer annual	Tolar	florets
Bouteloua simplex Lag.	Poaceae	C_4 summer annual	Tolar	florets
Enneapogon desvauxii P. Beauv.	Poaceae	C_4 perennial herb	Tolar	florets
Munroa decumbens Phil.	Poaceae	C_4 summer annual	Tolar	florets
Munroa sp2	Poaceae	C_4 summer annual	Tolar	florets
Nasella arcuata (R.E. Fries) Torres*	Poaceae	C_3 perennial herb	Steppe	florets
Nasella cf. *nardoides* (Phil.) Barkworth	Poaceae	C_3 perennial herb	Steppe	florets
Pappophorum caespitosum R.E. Fries	Poaceae	C_4 perennial herb	Tolar	florets
Stipa chrysophylla E.Desv.*	Poaceae	C_3 perennial herb	Steppe	florets, awns

* Identified by O. Matthei, Dept. Botánica, Universidad de Concepción.

TABLE 2.3. MACROFLORAS OF47 MIDDENS FROM THE CENTRAL ATACAMA DESERT

Midden Local Flora Zone	Age (ka BP)	Number of Middens Analyzed	Description	Inferred Paleoclimate
Ti-2C	0.5 - 2.7	10	Modern floras. Species richness averages 12 taxa. Prepuna shrubs and annuals are dominant. Last appearance of *Pappophorum caespitosum* at 2.0 ka BP. Youngest midden indicates rare occurence of two summer annuals (*Aristida* and *Euphorbia amandi*).	Modern hyperarid climate. Slight increase in precipitation may have occured at 0.5 ka BP.
Ti-2B	3.5 - 7.1	10	Average species richness increases to 14 taxa. Tolar cacti and shrubs (*Echinopsis* and *Junellia*), C_4 annuals and perennials, as well as *Scirpus* cf. *californicus*, appear in several middens.	Moderate increase in summer rainfall. Proximity of wetlands at Vegas de Tilocalar.
Ti-2A	7.1 - 9.5	6	Dramatic drop in species richness and absence of Steppe and Tolar taxa. Cactaceae (*Opuntia camachoi*), *Atriplex imbricata* and *Ephedra* are common shrubs. Prepuna annuals abundant as well.	Conditions arid to hyperarid with floras resembling those of present-day middens.
Ti-1C	10.5 - 16.2	16	Highly distinctive macrofloras and elevated species richness. *Scirpus* cf. *californicus* present at Vegas de Tilocalar. First appearance of *Pappophorum caespitosum*. Average species richness between 13.8-10.5 ka BP is 21 species, the highest in the record. Four species of Andean steppe grasses present in most middens. Several Tolar species present as well as abundant C_4 grasses and summer annuals. Prepuna shrubs and annuals rare to common.	Wettest period in the record. Descent of *Anatherostipa venusta* and *Nassella nardoides* (both steppe grasses) imply rainfall 3-5 times greater than today. Precipitation from tropical sources is indicated by C_4 grasses and southward migration of several species
Ti-1B	22 - 40.9	4	Low species richness in all four samples (7-13 species). *Atriplex*, *Cistanthe* and *Nolana* abundant. *Ambrosia artemisioides* (absent from the rest of the record) and *Echinopsis atacamensis* present at Vegas de Tilocalar (~50 km south of their current distribution). Very few annuals.	Middens represent conditions that are drier than today, as indicated by abundance of Prepuna vegetation and lack of steppe grasses. Few annuals may indicate possibly colder temperatures.
Ti-1A	>44.5	1	*Atriplex imbricata* and *Sisymbrium* sp are dominant, presence of *Nassella arcuata* and two species of C_4 grasses (*Munroa*)	Wetter than today, summer storms present.

TABLE 2.4. RODENT FECAL PELLET CONTENTS OF 41 MIDDENS FROM THE CENTRAL ATACAMA DESERT

Midden Local Flora Zone	Age (ka BP)	Number of Middens Analyzed	Description	Comments
Ti-2C	0.5 - 2.7	9	*Atriplex* (>60%) and *Cistanthe* (>30%) are present in most samples. *Ephedra* is present in trace amounts at the beginning of this zone, is absent after 1.5 ka BP. A slight increase in *Fabiana* spp (4%) occurs at 0.7 ka BP. A large increase in *Hoffmannseggia* (up to 24%) and Poaceae (18%) occurs at 0.5 ka BP.	Rodent diets are similar in composition to scant vegetation found today at several midden sites. Climate has been hyperarid for the last 2.7 ka although the presence of Poaceae and *Fabiana* implies very slight increases in local precipitation at 0.5 and 0.7 ka BP respectively.
Ti-2B	3.5 - 7.1	9	High percentages of *Atriplex* and *Cistanthe* along with minor increases (>10 %) in Poaceae and *Fabiana* cuticles between 4.9-4.4 ka BP. Very low percentages (<10 %) of *Krameria* and *Hoffmannseggia* are also present in rodent diets.	Generally the same assemblages is present as in zone Ti-2C, but larger increases in *Fabiana* and Poaceae at 4.9-4.4 ka BP could only have been supported by a significant increase in rainfall.
Ti-2A	7.1 - 9.5	5	*Atriplex* cuticles remain at high values (>40%) while *Cistanthe* increases to over 50% at the end of this zone. %*Hoffmannseggia* sharply diminish after 8.5 ka BP.	Diets indicate assemblages similar to modern day vegetation which imply a hyperarid climate.
Ti-1C	10.5 - 16.2	14	Abrupt appearance of unique cuticle assemblages. Up to 50% Poaceae epidermis and a maximum of 80% *Fabiana* (not recorded in macrofossils). *Atriplex* and *Cistanthe* also present, but in lower percentages.	Diets indicate that a diverse and unique plant community was present at the midden sites. High percentage of Tolar shrubs and Poaceae indicate substantial precipitation increases with respect to the present.
Ti-1B	22 - 40.9	3	High percentages of *Ephedra* and *Atriplex*. Tolar elements found only in trace values. *Cistanthe* appears at 40.9 ka BP. Poaceae falls to <10%.	Diets dominated by Prepuna plants and *Ephedra*. Coupled with few trace amounts of grasses, this would imply a hyperarid habitat.
Ti-1A	>44.5	1	Samples contained 80% *Fabiana* and small amounts of Tolar shrubs, *Junellia* and *Baccharis boliviensis*. Also 10% Poaceae and 35% *Hoffmannseggia* were counted.	Diets compatible with the midden macroflora and indicate climate wetter than today.

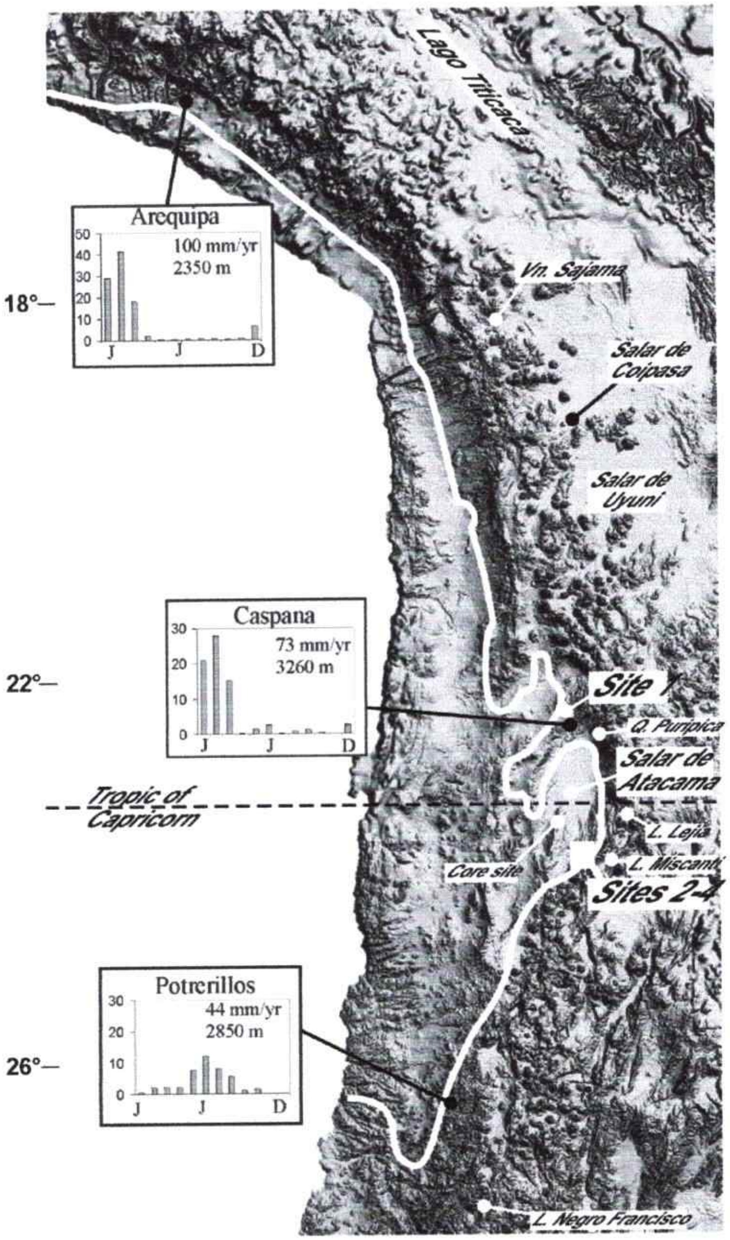

Figure 2.1. Physiography of the Andes Cordillera and Altiplano, with Quaternary records discussed in the text. Precipitation gradients shift from summer- to winter-dominated rainfall within 200 km south of the Salar de Atacama Basin. The white line denotes the approximate extent of Absolute Desert, defined by the absence of vegetation except in a few scattered oases and intermittent and perennial streams. The small white rectangle (sites 2-4) indicates the approximate extent of Figure 2. Insets show rainfall distribution (in mm/yr; J-J-D—January, June, December), mean annual rainfall, and elevation for three locations.

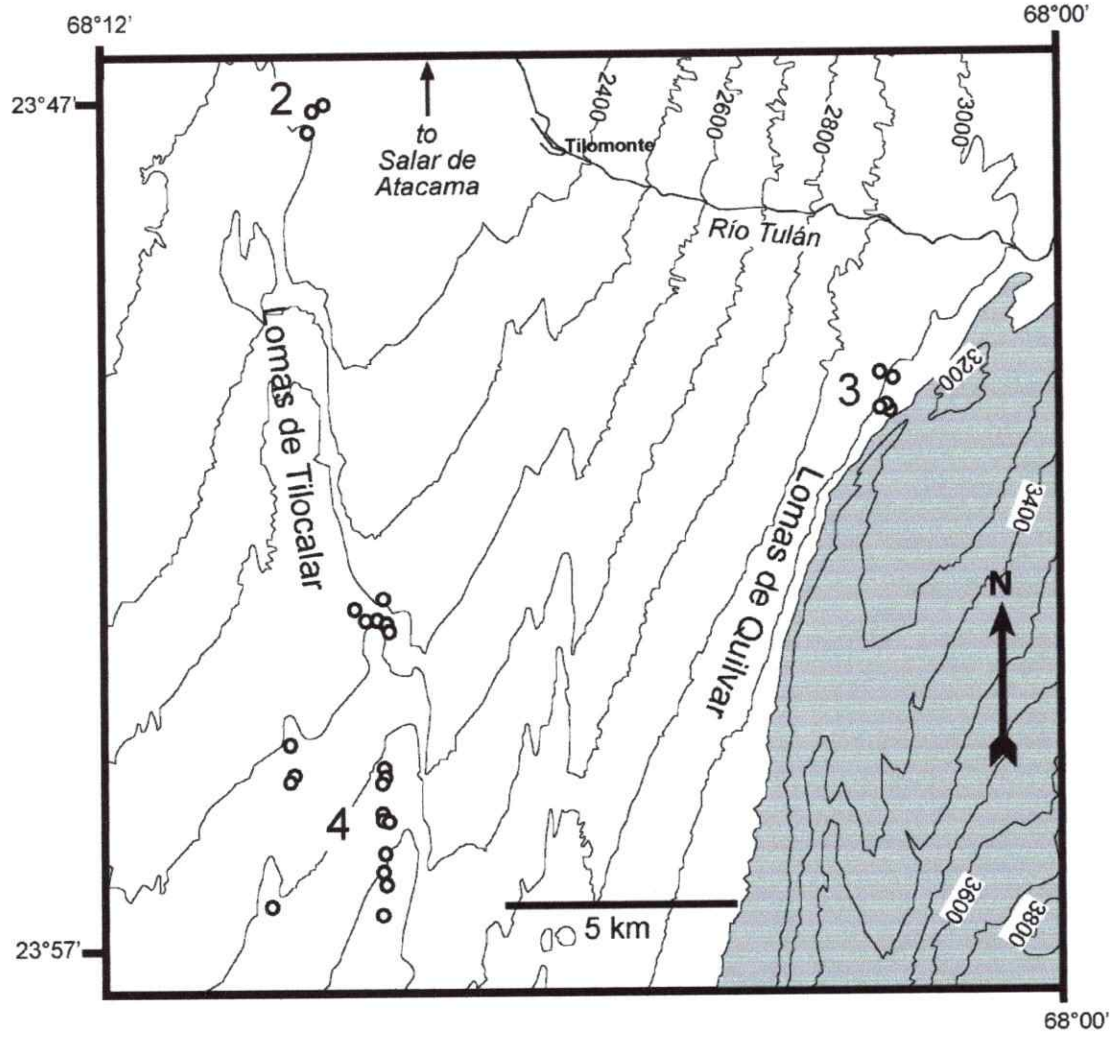

Figure 2.2. Locality map for sites 2-4 indicating distribution of rodent middens (circles). The shaded area shows where vegetation is present today. Plant cover is <1% for the rest of the area. Numbers indicate midden localities 2— Vegas de Tilocalar, 3— Lomas de Quilvar, 4— Lomas de Tilocalar. Elevations are given in meters; contour interval is 100 m.

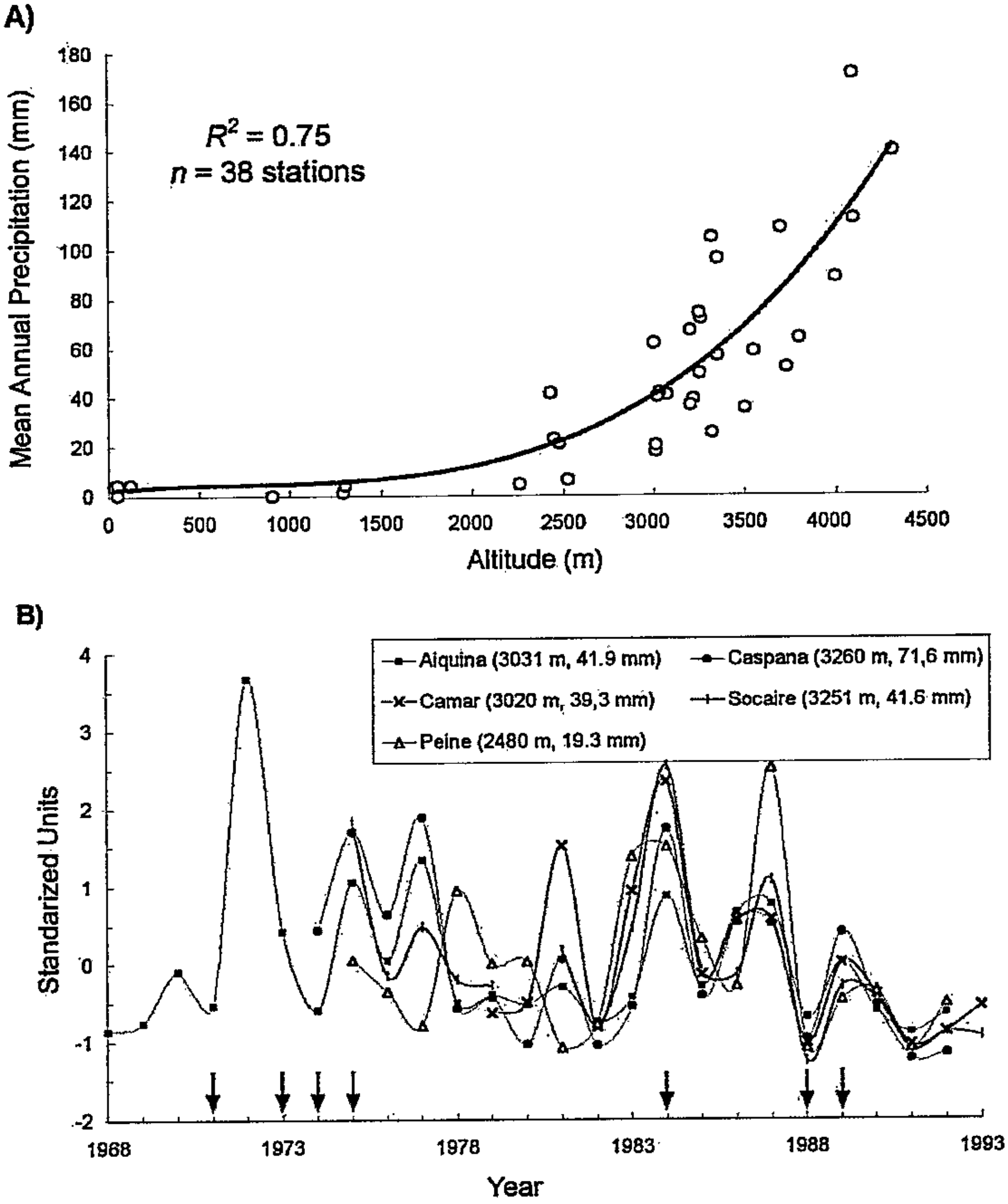

Figure 2.3. **(A)** Relationship between mean annual precipitation (MAP) and altitude for 38 stations in Chile's II Region (21°13'- 25° 24' S) based on monthly DGA measurements. A second-order polynomial was fitted to the data (black line). **(B)** Standardized time series of precipitation records from select stations bordering the Salar de Atacama and Calama basins. Gray arrows along the *x*-axis indicate strong La Niña years. Lack of pre-1980 coherence between records may be due to errors in source data (source: Dirección General de Aguas, Ministerio de Obras Públicas, Santiago, Chile.).

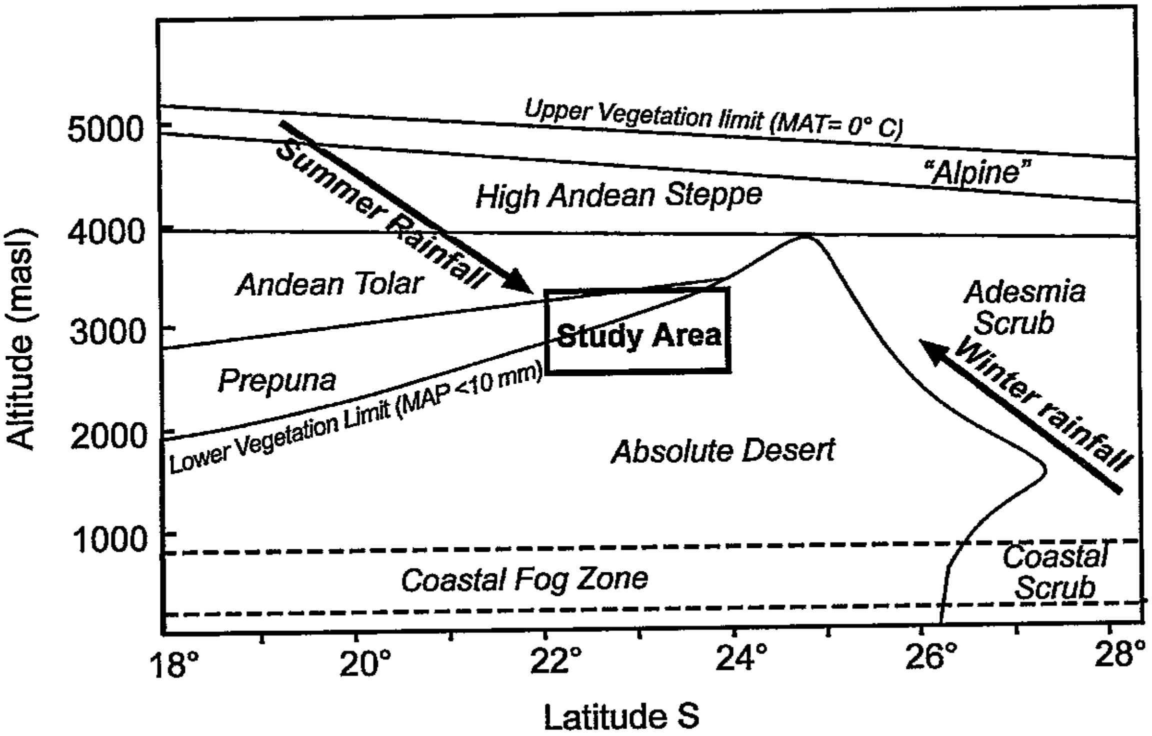

Figure 2.4. Simplified diagram of the major vegetation zones found in northern Chile (modified from Villagrán et al., 1983). The study area (rectangle) is located near the maximum inland penetration of the Absolute Desert. Numerous disjunct Lomas communities inhabit the coastal fog zone (see Rundel et al., 1991).

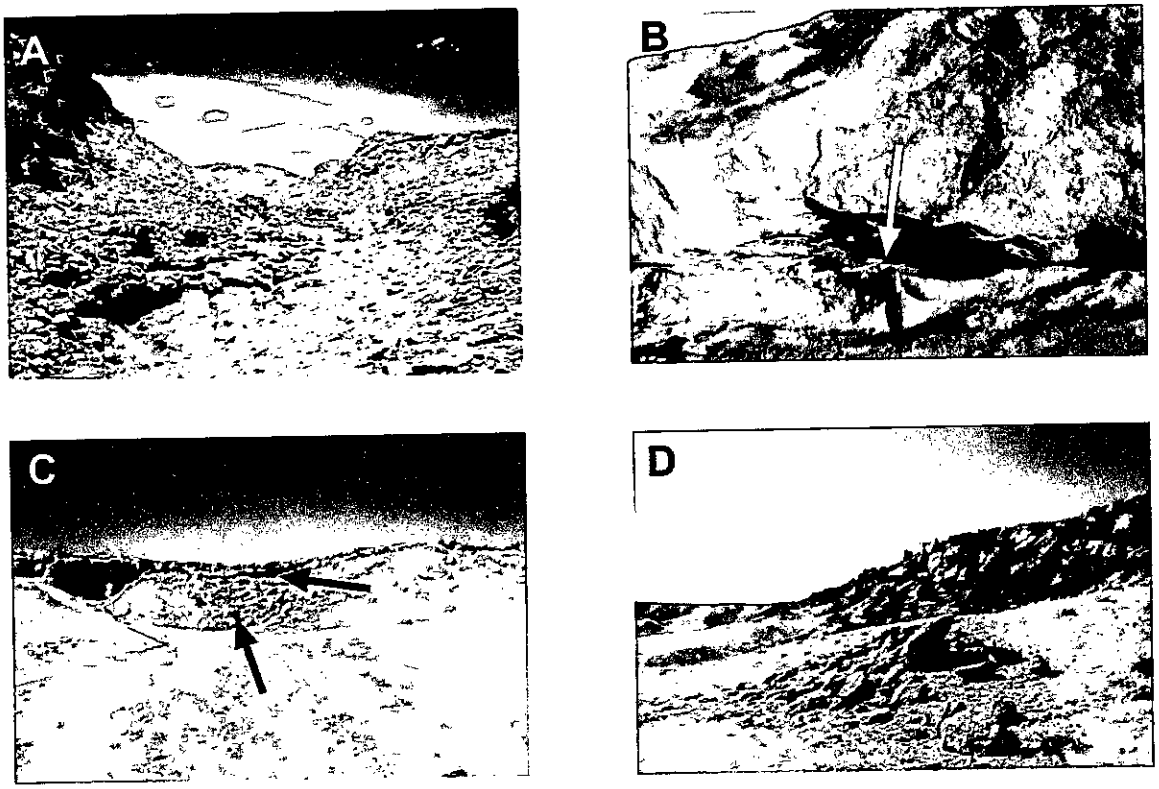

Figure 2.5. Photographs of midden localities sampled on the edge of Absolute Desert. **(A)** View looking upstream (southeast) of Quebrada Aiquina A, a dry, hanging canyon tributary of the perennial Río Salado. Middens come from small cavities and rockshelters along the late Miocene Sifón ignimbrite cliffs. **(B)** A large, exposed 35 ka BP midden (VdT 419A-B, white arrow) found underneath an ignimbrite boulder at Vegas de Tilocalar. VdT 419C was found further back and to the right of 419A-B (note rock hammer for scale). Located at 2400 masl and within a few hundred meters of the edge of the Salar de Atacama, Vegas de Tilocalar sites are mostly east-facing slopes on a low ridge defined by eroded Pliocene Tucúcaro Ignimbrite boulders. **(C)** A view of the Lomas de Tilocalar locality at 2800 masl, showing lack of plants in the foreground or on top of the west-facing Pliocene Tucúcaro ignimbrite scarp. Arrows indicate where middens were found. **(D)** Lomas de Quilvar, 3100 masl, looking northeast, as with Lomas de Tilocalar, plants are almost absent in front of boulders, and are represented by a few dried annuals of *Cryptantha* and *Cristaria*.

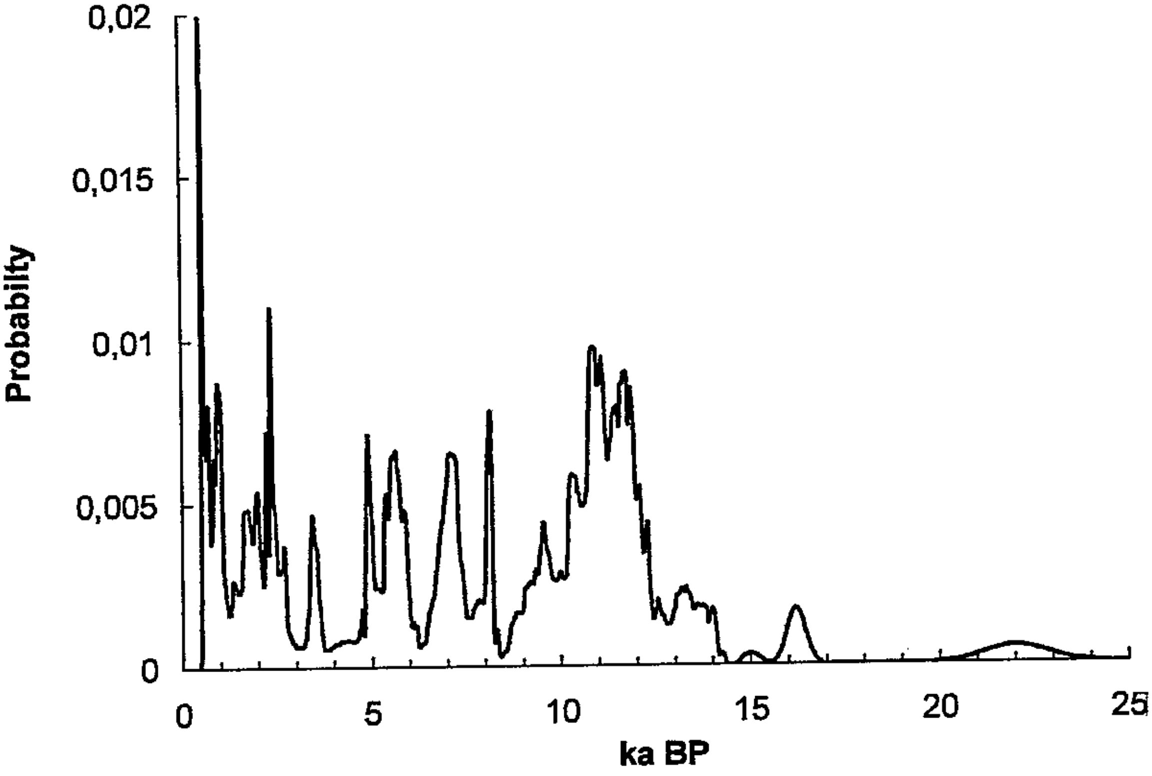

Figure 2.6. Sum probability distribution of 45 calibrated ^{14}C dates on central Atacama Desert middens. Deviations from exponential decay are either due to midden sampling biases or changes in ecosystem productivity. Note large cluster of dates at 14-8.5 ka BP. The sum probability distribution was calculated using CALIB 4.3 (Intcal98) (Stuiver amd Reimer, 1993).

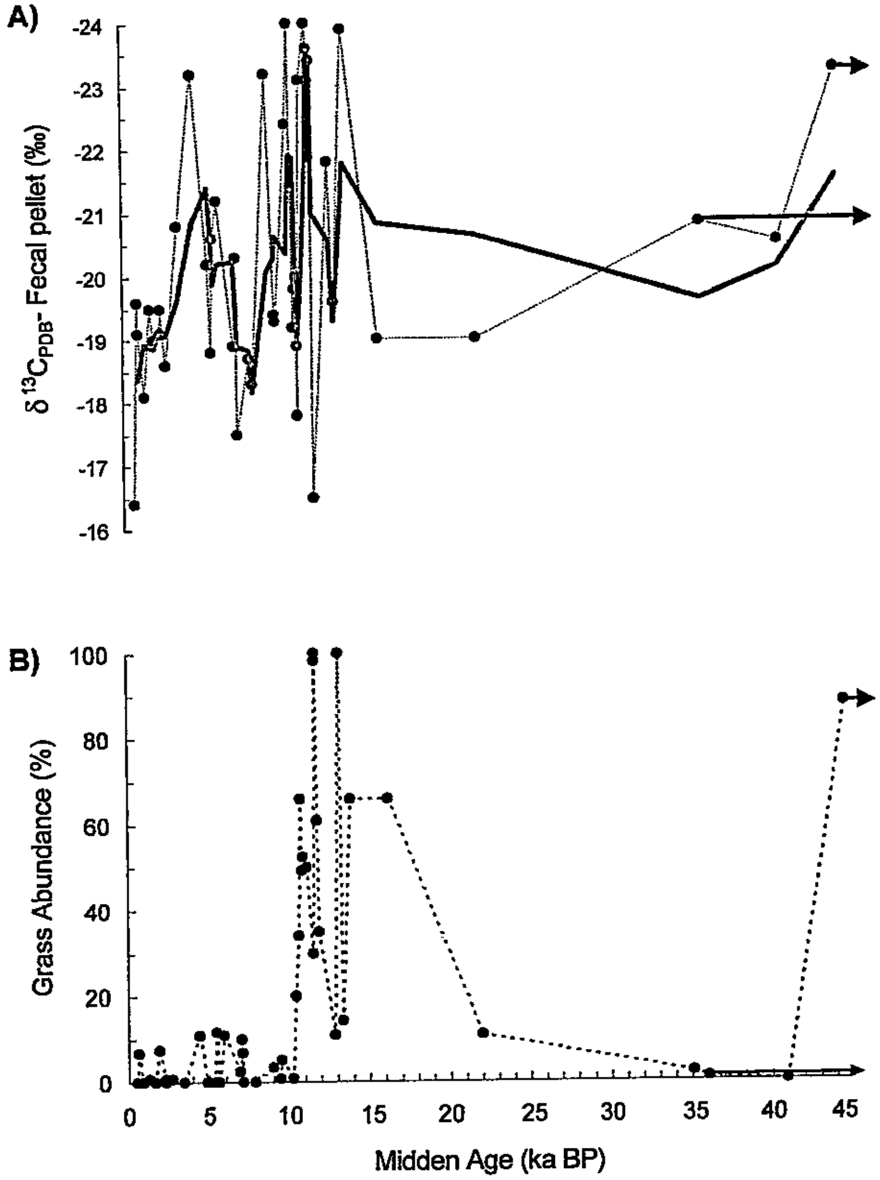

Figure 2.7. A) $\delta^{13}C_{PDB}$ values obtained from bulk fecal pellet ^{14}C dates of 45 middens. The bold line is a smoothing curve generated from a 3-point running average. Note reversed scale on ordinate. In general, rodents consumed more C_3 plants (shrubs and steppe grasses) between 13.8-9 ka BP. More positive values during the Holocene indicate consumption of *Atriplex* and cacti, as well as C_4 grasses. **B)** Total grass abundance (%) calculated from grass point-occurrence obtained from 47 middens. This represents a generalized productivity index for both annual and perennial grasses. Grasses are not found near midden sites at the present. (Note: arrows on samples denote minimum ages).

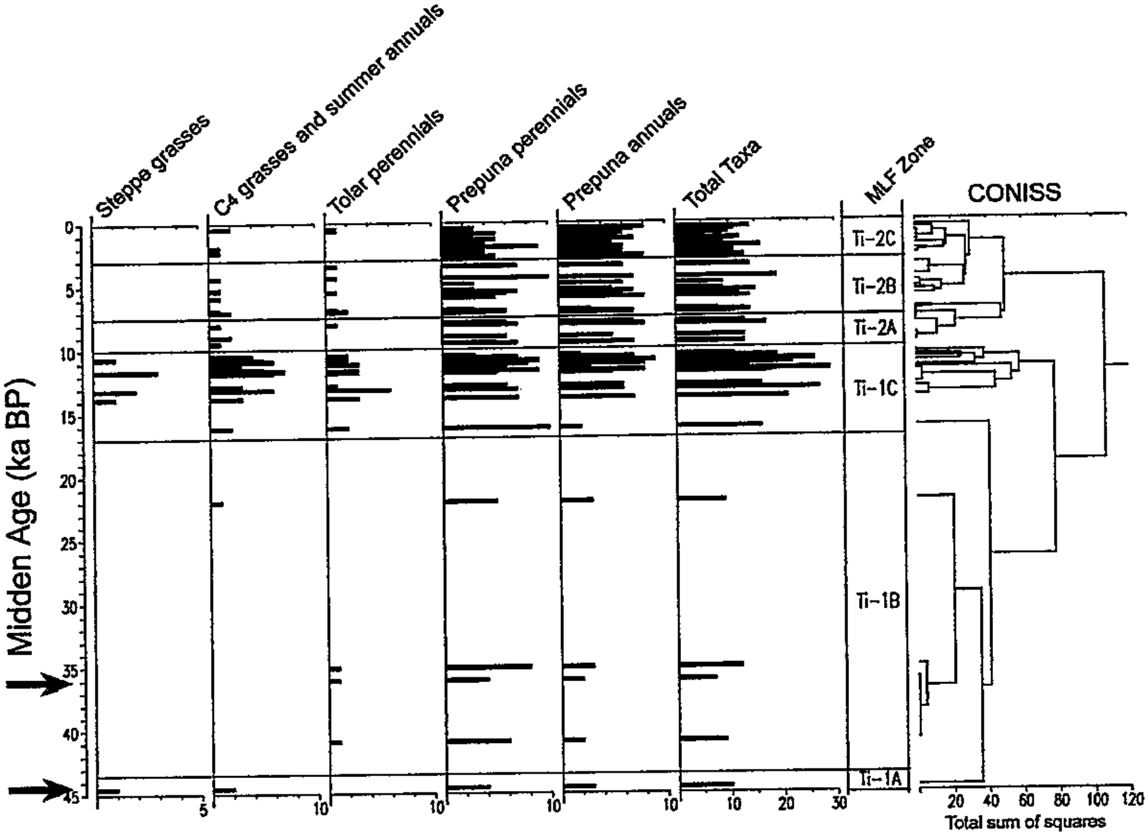

Figure 2.8. Summary diagram indicating the number of taxa obtained from 47 fossil rodent middens from the Tilocalar and Quilvar localities, ordered by lifeform and phytogeographic category (see Table 2). Each dot in the sampling intensity column corresponds to a single ^{14}C dated midden. Midden Local Flora Zones were partly defined using a cluster analysis (CONISS) as well as other floristic similarities. Grey arrows next to age scale indicate middens with minimum ages.

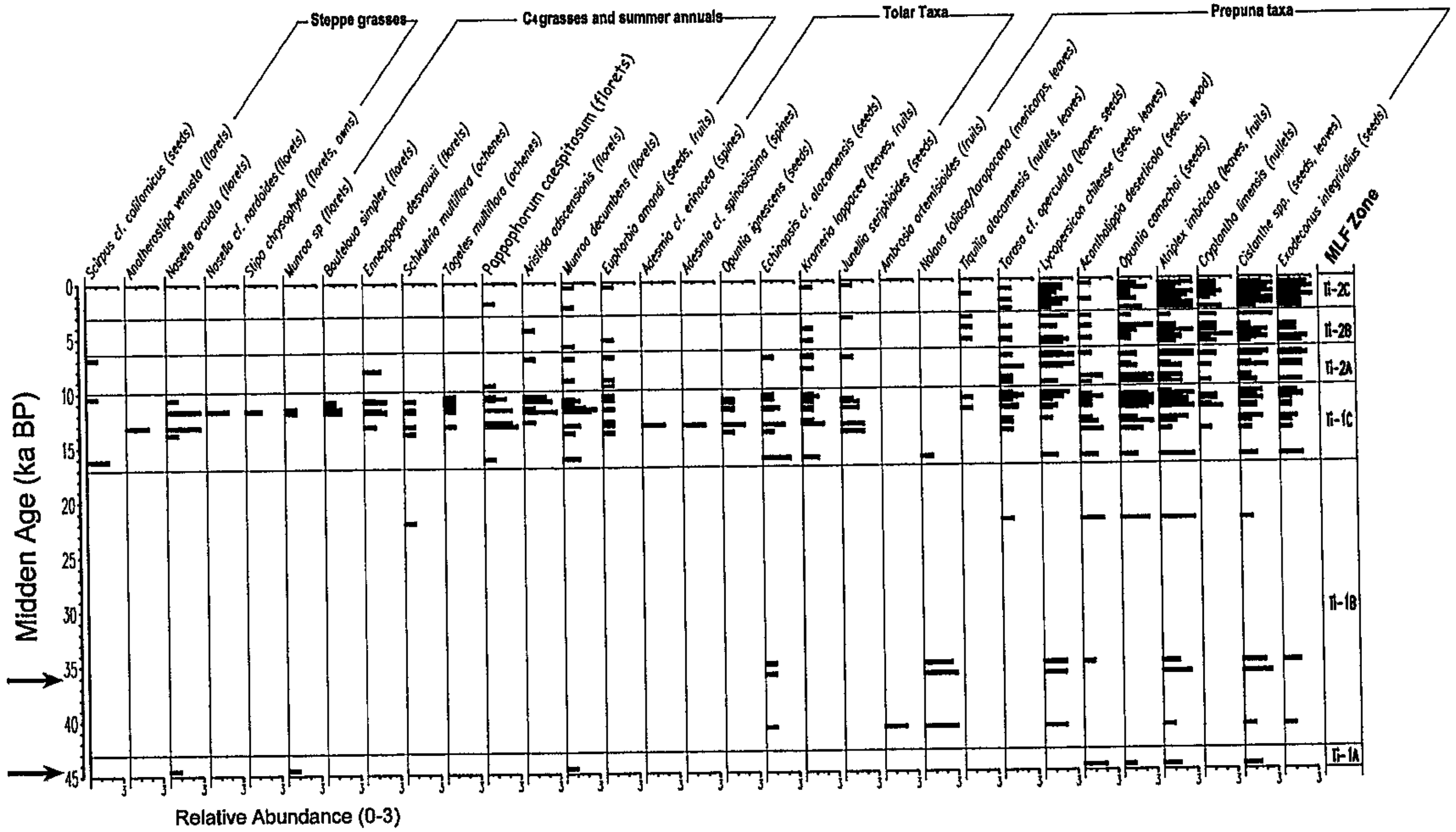

Figure 2.9. Relative abundance diagram for 19 taxa obtained from 47 fossil rodent middens at the Tilocalar and Quilvar localities. Relative abundance scale is: 0=absent; 1=rare; 2=common; 3=dominant. MLF Zones are the same as those in Fig. 8. Grey arrows next to age scale indicate middens with minimum ages. *Pappophorum caespitosum* (in grey) has never been collected in Chile and may be locally extinct.

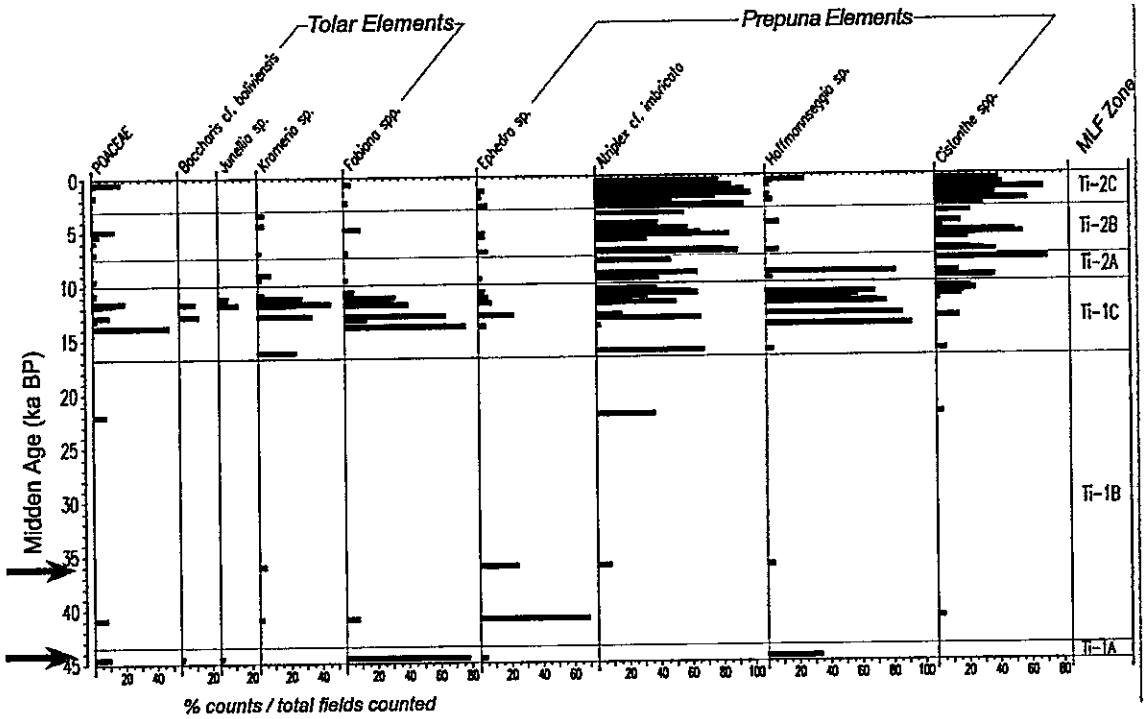

Figure 2.10. Percentage diagram of plant taxa based on rodent diets from 41 middens from the Tilocalar and Quilvar localities. Note presence of the genus *Fabiana*, a Tolar shrub absent from the macrofossil record. MLF Zones are identical to those in Figs. 8 and 9. Grey arrows next to age scale indicate middens with minimum ages.

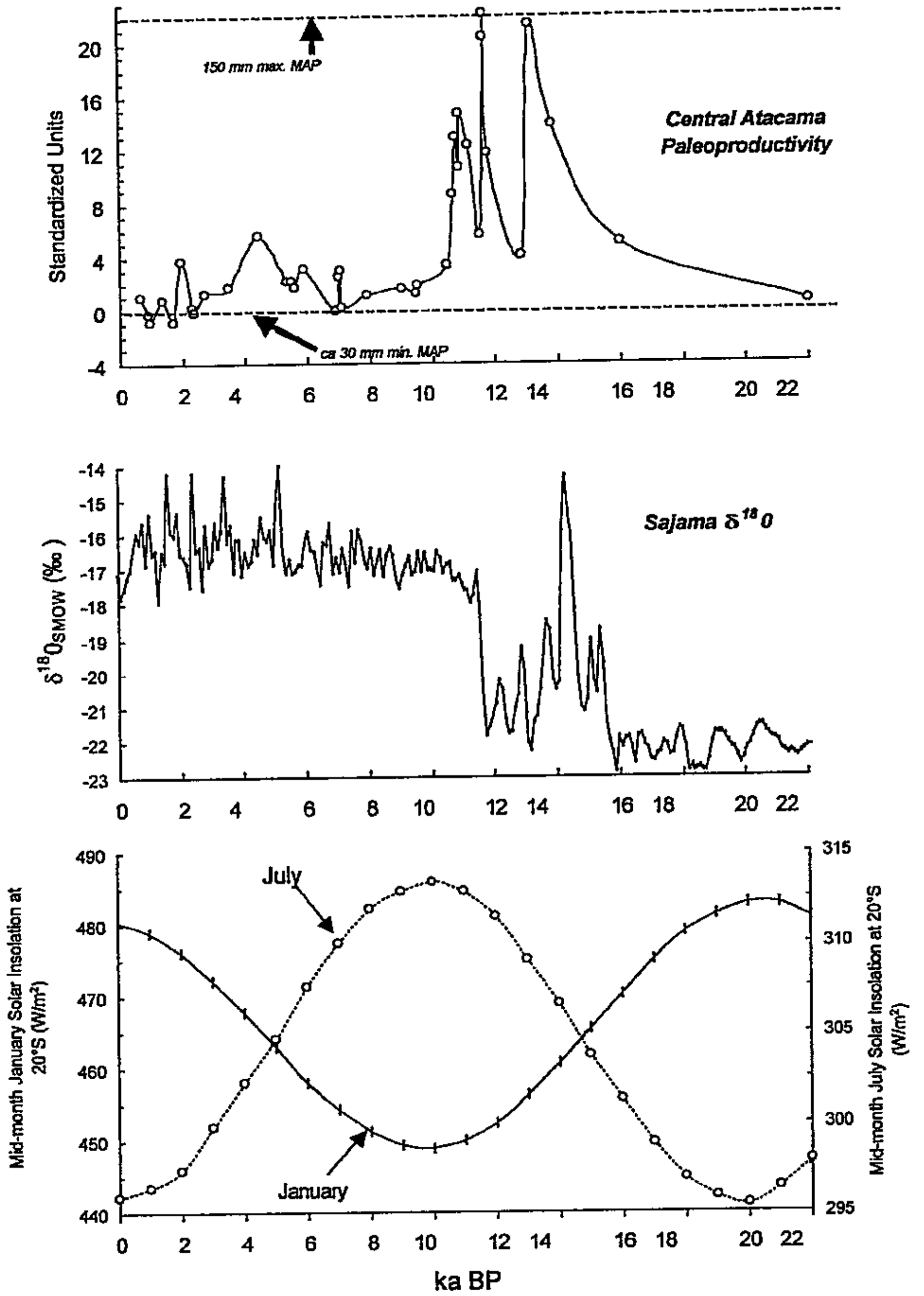

Figure 2.11. Paleoproductivity curve for the last 22,000 years based on grass abundance and species richness departures with respect to the last 1,000 years. Positive departures indicate increased precipitation while negative departures indicate increased aridity. The precipitation minimum is based on mean annual precipitation (MAP) at midden sites today. Steppe grasses today grow in areas with MAP ca. 150 mm and set the past precipitation maximum at the end of the Pleistocene. Solar insolation at 20° S and the Sajama $\delta^{18}O$ ice core record (Thompson et al., 1998) are plotted for comparison to the midden record.

Capítulo 3:

"A vegetation history from the arid prepuna of northern Chile (22-23°S) over the last 13,500 years "

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ABSTRACT

The Quaternary paleoclimate of the central Andes is poorly understood due to numerous discrepancies among the diverse proxy records that span this geographically and climatically complex region. The exact timing, duration and magnitude of wet and dry phases are seldom duplicated from one proxy type to another, and there have been few opportunities to compare climatic records from the same proxy along environmental gradients. Vegetation histories from fossil rodent middens provide one such opportunity on the Pacific slope of the Andes. We previously reported a vegetation history from the upper margin (2400-3000 m) of the absolute desert in the central Atacama Desert of northern Chile. That record identified a distinct wet phase that peaked between 13.8-10.5 ka (thousands of calendar years ago), when steppe grasses and other upland elements expanded as much as 1000 m downslope, and a secondary wet period during the middle to late Holocene (7.1-3.5 ka). The latter wet phase remains controversial and is not as readily apparent in our low-elevation midden record. We thus sought to replicate both phases in a midden record from the mid-elevations (3100-3300 m) of the arid prepuna, where slight precipitation increases would be amplified. Midden records from these elevations identify conditions wetter than today between 13.5-9.6, 7.6-6.3, 4.4-3.2 and possibly between 1.8-1.2 ka. Dry phases occurred between 9.4-8.4 ka and possibly at ca. 5.1 ka. Present floras and modern hyperarid conditions were established after 3.2 ka. The records from the two elevational bands generally match with some important differences. These differences could reflect both the discontinuous aspect of the midden record and the episodic nature of precipitation and plant establishment in this hyperarid desert.

Keywords: rodent middens, vegetation history, Holocene, prepuna, Atacama Desert, northern Chile, central Andes.

1. Introduction

Discrepancies in timing, magnitude and direction of climate change are common among diverse paleoclimate records in the central Andes. These inconsistencies may be due to poor dating, varying temporal resolution, different response times and sensitivities to both temperature and precipitation, disagreements about field evidence and climatic interpretation, or simply the sheer vastness and geographic complexity of the region across which we are trying to find correlation. Because much of the research is recent and many of the proxies are unique, few records have yet to be replicated. Multiple cores can usually be taken and compared from a single site, but there is only one Nevado Sajama (Thompson et al., 1998) and only one Lake Titicaca (Seltzer et al., 1998; Baker et al., 2001b). Syntheses of central Andes paleoclimatology to some extent involve comparing apples and oranges with few chances to duplicate the same kind of record at multiple localities. During the past 3 years, we have been developing vegetation and ground-water histories from fossil rodent middens and wetland deposits, respectively, along a 1500-km transect on the Pacific slope of the central Andes (Betancourt et al., 2000; Holmgren et al., 2001; Placzek et al., 2001; Rech et al., 2001; Latorre et al., 2002; Rech et al., 2002). A strength of this paleoclimate transect is the ability to apply the same methodologies across broad elevational, latitudinal, climatic, vegetation and hydrological gradients.

Here we present a Holocene vegetation history gleaned from plant macrofossil analysis of 44 rodent middens collected in the upper part (3100-3300 m) of the "prepuna" vegetation belt (as defined in Villagrán et al., 1983) of the central Atacama Desert. In a previous study, we focused on rodent middens in the transition from prepuna to absolute desert between 2400 and 3000 m (Betancourt et al., 2000; Latorre et al., 2002). The prepuna is a sparsely vegetated zone, with individual plants every few meters to tens of meters, that grades into absolute desert at lower elevations (<2400 m) and into low (<1m tall) shrublands of the "tolar" zone at higher elevations (>3400 m).

Among the major findings from our earlier study was that, between 16.2 and 10.5 ka (calendar thousands of years ago), indicator species from both tolar (3400-4000 m) and Andean steppe (4000-4800 m) expanded downslope 400-1000 m across the edge of absolute desert, where precipitation is now insufficient to support vascular plants. The period appeared to be wettest between 11.8 and 10.5 ka. We estimated that the vegetation expansions required a three to five-fold increase in summer precipitation (30-50 mm today vs. 100-150 mm during the pluvial period). These late glacial-early Holocene middens contain C_4 annuals and perennials that flower in summer, indicating that precipitation was augmented by greater "spillover" of western Altiplano convective storms onto the Pacific slope of the Andes. In the central Atacama, both lake (Grosjean, 1994; Bobst et al., 2001; Grosjean et al., 2001) and ground-water levels (Betancourt et al., 2000; Rech et al., 2002; Rech et al., this volume) were at their highest during the late glacial-early Holocene (~16-9 ka). We also found rodent midden assemblages slightly wetter than today between 7.1 and 3.5 ka, in agreement with rising ground-water levels inferred from wetland deposits (Rech et al., 2002; Rech et al., this volume). The mid-

Holocene increase in precipitation at these elevations was much less than the increase during the late glacial-early Holocene, and was thus harder to quantify from the rodent midden record.

In an effort to replicate the late glacial-early Holocene pluvial and better evaluate mid-Holocene climate, we developed midden series from multiple localities in the upper part of the prepuna (3100-3300 m), some 100 km north of our low elevations sites in the central Atacama. The slightly higher densities of perennial plants and midden-forming rodents (*Lagidium, Phyllotis, Abrocoma*) at these mid elevations ensure an abundant Holocene midden record. More importantly, precipitation increases of only 10-50% over modern values could have displaced tolar and steppe species downslope into the upper prepuna, amplifying precipitation signals that were barely registered in the prepuna-absolute desert transition. Currently, there is considerable debate over whether the middle Holocene was wet (Quade et al., 2001) or dry (Grosjean, 2001) in the central Atacama. At stake is the precipitation history of the central Atacama Desert, which does not appear to be linked to variations in seasonal insolation over the central Andes, but rather to sea-surface temperature gradients in the tropical Pacific and associated upper air circulation anomalies over the western Altiplano.

2. Physical setting

2.1 Physiography

The hyperarid Atacama Desert extends along the Pacific Andean slope from the southern border of Peru (18°S) to Copiapó, Chile (27° S) (Rundel et al., 1991). This study focuses on the central part of the Atacama (22-24°S) near the Tropic of Capricorn and centered on a conspicuous, structural embayment along the Andean front. Two major mountain ranges, the Cordillera Domeyko and the Cordillera de los Andes run from north to south across our study area, partially enclosing the Calama (or Río Loa) Basin and completely enclosing the Salar de Atacama Basin (Fig. 3.1). The main Andean front consists of late Tertiary and Quaternary ignimbrites and volcanic rocks, with both extinct and active volcanoes forming the highest peaks between 5000 and 6000 m. The Chilean Altiplano above 4000 m is dotted with large salars (salt basins) and a few small lakes (e.g., Laguna Lejia and Miscanti); salars occupy large expanses along the base of the Andes below 2500 m. Branching off the western Andean slope at 22°15' S, the Cordillera Domeyko spans approximately 4° in latitude and runs parallel to the main Andean front. Here, this range includes late Palaeozoic and Cretaceous folded sedimentary rocks partially overlain by Oligo-Miocene alluvial fanglomerates, occasionally capped by erosional remnants of late Miocene ignimbrites (Marinovic and Lahsen, 1984). In this sector, most of the Cordillera Domeyko lies between 3000-3500 m, with a maximum altitude of 4278 m at Cerro Quimal.

The majority of our middens from the northermost outcrops at Cerros de Minta and Cerros de Aiquina (Figs. 3.2A, 3.2E) were collected underneath boulders and outcrops of Cretaceous breccias and conglomerates. Middens from Quebrada Chiquinaputo (Fig. 3.2B) were found within crevices and shelters formed in loosely consolidated Plio/Pleistocene alluvial sediments. Other middens were also found in the upper Paleozoic breccias that commonly outcrop along the Cordón de Tuina (Fig. 3.2C) and are locally abundant along isolated ignimbrite outcrops of El Hotel and Pampa Vizcachilla (Figs. 3.2D, 3.2F).

2.2 Climate

Aridity in the Atacama region may have begun as early as the Eocene and evolved into hyperaridity by the middle Miocene (Alpers and Brimhall, 1988; Mortimer, 1980; Stoertz and Ericksen, 1974). The hyperaridity is due to the extreme rainshadow of the high Andes, which blocks the advection of tropical/subtropical moisture from the southern Amazon Basin; the blocking influence of the semi-permanent South Pacific Anticyclone (SPA), which limits the influence of winter storm tracks from the south; and the generation of a temperature inversion at ~1000 m by the cold and north-flowing Humboldt Current, which limits inland (upslope) penetration of Pacific moisture (Borgel, 1973; Caviedes, 1973).

The scant annual precipitation that falls in the Atacama consists of fog and occasional winter rains in all coastal areas below 1000 m, occasional winter (May-October) rains on Andean slopes south of 25°S, and summertime (November-March) storms that cross the Altiplano, spill over the Andes, and rain out on the Pacific slope north of 25°S. In the monsoonal part of the Atacama (18-25°S), absolute precipitation amounts depend on elevation and distance from the crest of the Andes, which control the rainout from convective storms as air masses descend down the Pacific slope. The hyperarid core of the Atacama, where rainfall is currently insufficient to support vascular plants, spans an elevational range of 3500 to 1000 m in the most arid sector (24-26°S), tapering gradually to the north and abruptly to the south. In the central Atacama, estimated mean annual rainfall averages between 0-20 mm at 1000-2500 m, 20-40 mm at 2500-3000 m, between 40-65 mm at 3000-3500 mm and between 65-200 mm between 3500-4500 m. Mean annual temperature averages 10-15° C between 2000-3000 m (data from Dirección General de Aguas).

Seasonal precipitation in the central Atacama corresponds to the tail end of the South American Summer Monsoon (SASM) (Zhou and Lau, 1998). The SASM is produced by continental heating over the Altiplano and Gran Chaco during the austral spring and summer, modulated by the strength and size of the Bolivian High that forms in the upper troposphere (Lenters and Cook, 1995; Lenters and Cook, 1997; Zhou and Lau, 1998). Modern climatology studies by Aceituno (1988), Garreaud (1999; 2000), Vuille et al. (1999) and Garreaud et al. (this volume) describe El Niño-Southern Oscillation (ENSO) effects on interannual precipitation variability over the Altiplano. Because ENSO regulates the extent of atmospheric transport and convection over this region, different sensitivities should be evident in the eastern vs. western Cordilleras. Negative or warm ENSO phases (El Niño) are characterized by high-altitude westerly wind anomalies that inhibit moist air advection and convection over the western Altiplano. Conversely, positive or cold ENSO phases (La Niña) are characterised by a southward displacement of the Bolivian High and enhanced easterly circulation that produces greater advection and increased precipitation over the western Altiplano (Vuille, 1999). The link between modes of variability for the moisture source (the eastern Cordillera) vs. transport (and convection) to the western Altiplano is poorly understood.

2.3. Vegetation

Pronounced latitudinal and elevational climatic gradients lead to definable vegetation zones on the Pacific slope of the Andes. Five major zones or belts are distinguished: the coastal lomas; prepuna; tolar; Andean steppe; and subnival ("high alpine"). Their physical distribution and association with climate is discussed in several references (Arroyo et al., 1988; Latorre et al., 2002; Rundel et al., 1991; Villagrán et al., 1981; Villagrán et al., 1983). Figure 3.3 indicates the overall altitudinal distribution of vegetation zones along a transect that spans both mountain ranges. Figure 3.4 compares our own floristic transects in the Cordillera Domeyko to those from the Andean slope at the same latitude. Vegetation zones in the Cordillera Domeyko are less distinct, compressed vertically and less biodiverse than the Andean slope. This reflects the greater distance from the Andean crest, hence less precipitation, as well as a "double rainshadow" present on the western slope of the Cordillera Domeyko.

Along the west-facing slopes of Cordón de Tuina, vegetation begins at ca. 2700 m, mostly in dry washes and other concave or level surfaces where water collects (termed "azonal" in the ecological literature). Most perennial species of the Andean prepuna meet their lower limits along washes (Fig. 3.4, grey dots). These include *Lycopersicon chilense, Adesmia atacamensis, Tiquilia atacamensis, Ambrosia artemisiodes* and *Haplopappus rigidus*. Hillslope or "zonal" vegetation begins at ca. 2850 and is dominated by the halophyte *Atriplex imbricata* and the cushion cactus *Opuntia camachoi*.

Columnar cacti, such as *Oreocereus leucotrichus,* appear at ca. 3050 m on hillslopes of the Cordón de Tuina. Although absent from Cordón de Tuina, *Echinopsis* *atacamensis*, another important species of columnar cacti, appears ca. 3150 m on west-facing slopes of Cerros de Aiquina. *Ephedra breana* (Ephedraceae) and *Krameria lappacea* (Krameriaceae) also appear at ca. 3100 m. Several tolar species begin to appear in dry washes and on hillslopes at ca. 3200 m, including *Fabiana ramulosa* (Solanaceae), *Baccharis boliviensis* and *Chuquiraga atacamensis* (both Asteraceae).

Zonal formations are more easily distinguished on east-facing slopes of the Cordillera Domeyko. Despite the dominance of prepuna assemblages along the entire transect up to ca. 3500 m (Fig. 3.4), tolar species show up at low densities at lower altitudes than on west-facing slopes (e.g. 3100 m vs. 3200 for *Fabiana ramulosa*). An isolated patch of *Parastrephia quadrangularis* (Asteraceae), a high tolar species (those that grow >3800 m on Andean slopes) and *Lampaya medicinalis* (Verbenaceae) was also observed at 3300 m growing on a dry lake bed. Finally, a mixed prepuna/steppe community dominated by *Atriplex imbricata*, *Stipa chrysophylla*, *Ephedra breana* and *Opuntia camachoi* grows near the summits (~3500 m) of the Cordillera Domeyko.

3. Methods

Fossil rodent middens are accumulations of organic (faeces, plant, insect, and vertebrate) debris encased in hardened urine (amberat) ubiquitous in rock shelters, caves and crevices. Advantages to rodent midden analyses include the high taxonomic resolution (often to species), the limited origin of plant and animal material (generally within a 100 m of the midden), the abundance of plant and faecal material for radiocarbon and other morphological, geochemical and genetic analyses, and the easy replicability within and across areas. Disadvantages include dietary selectivity of different rodents, occasional temporal mixing of midden assemblages, and discontinuous deposition. In effect, rodent middens represent individual snapshots of vegetation that have to be collated into series or chronologies for any particular site or area (Betancourt et al., 1990).

Middens were soaked in 10 L buckets of water for two to three weeks to dissolve urine (amberat), wet-sieved with a No. 20 mesh (0.825 mm) and placed in a drying oven at 50-60° C for three days. Dried middens were weighed, quantified for grass abundance, and sorted for plant macrofossils as described in Latorre et al. (2002). Most of the middens collected in the Atacama were made either by vizcachas (*Lagidium viscacia*, Chinchillidae) or leaf-eared mice (*Phyllotis* spp., Sigmodontinae). Both species usually have foraging areas <100 m (Pearson, 1948; Pearson and Ralph, 1978). Ecological studies point to a generalized diet for both vizcachas and leaf-eared mice (Pearson, 1948; Pizzimenti and De Salle, 1980), and this is confirmed in our own analyses of modern middens. At midden site Cordón de Tuina-386, we found little difference in the composition of a modern vizcacha midden and an inventory of plants sampled within a 500 m radius on two successive late summers (Table 3.1). We feel that fossil rodent midden assemblages faithfully record local vegetation at the time the midden was formed, and are thus confident in interpreting paleovegetation and paleoclimates in terms of modern vegetation distributions described here and elsewhere (Villagrán et al., 1981; Villagrán et al., 1983; Latorre, unpub. data).

Between 3-10 g of faeces from each midden were submitted for bulk dates at Geochronology Laboratories, Inc., Boston, MA. We used accelerator mass spectrometry (AMS) in cases of insufficient material for bulk dates, or when contamination with younger materials was suspected. AMS targets pre-treated on our vacuum line at the Desert Laboratory in Tucson were then measured by the University of Arizona-NSF Accelerator Facility. All radiocarbon ages were calibrated with the Intcal98 calibration curve, using Method A (ranges with intercepts) from Calib 4.3 (Stuiver and Reimer, 1993). A 24-yr Southern Hemisphere correction was applied to all dates. Radiocarbon ages reported here are in calendar thousands of years before 1950 (ka).

Plant macrofossils were hand sorted and identified to the highest taxonomic level possible and each taxon was quantified using a relative abundance index (RAI) where 0=absent, 1=rare, 2=common and 3=dominant (see Latorre et al., 2002). Macrofossil abundance was plotted with Tilia 2.0 and Tiliagraph software (Grimm, 1991-1993). Grass abundance was measured using a point occurrence method using a 120-cell rectangular grid overlain on a sorting tray. A sediment matrix splitter was used to randomly segregate 100 ml of plant debris from each washed and dried midden. Midden debris was then spread uniformly across a 120-1 x 1 in (~6.45 cm^2) cell rectangular grid. Percent grass abundance was calculated as the ratio of cells out of 120 where grass blades, florets or seeds were identified (i.e. 'hits' on the grid).

4. Results

4.1. Radiocarbon dating

Temporal coverage was quite variable at the six localities studied, where we collected a total of 44 ^{14}C-dated middens (Table 3.2; Fig. 3.5). We managed to find late glacial-early Holocene middens at Cerros de Aiquina, Cordón de Tuina and Pampa

Vizcachilla and El Hotel, but not at Cerros de Minta and Quebrada Chiquinaputo. In general, midden ages clustered in the late glacial- Early Holocene and the late Holocene. The largest cluster of dates occurs between 13.5-9 ka.

4.2. Grass Abundance

Between 13.4-9.4 ka, grass percentages are on average >50% at all localities, despite conspicuous drops at 13.1 and 11.5-11.2 ka (Fig. 3.6A). Percentages remain ≤10% between 9.4-7.6 ka, excluding a brief increase to 47% at 8.4 ka at Cerros de Aiquina. An abrupt increase in percentages occurs at 7.6 k, with values remaining above 40% until 3.2 ka . This middle Holocene interval was punctuated by a brief drop to 3% grass at 5.1 ka at Cordón de Tuina. Modern grass abundance levels (<10%) were established at 2.8 ka, with a slight increase between 1.8-1.2 ka at Cordón de Tuina, Cerros de Minta and Pampa Vizcachilla. By far the most surprising patterns are the sustained, pronounced drops in grass abundance that begin at 10.2 and at 3.4 ka.

4.3. Plant macrofossil assemblages

A total of 59 taxa were identified to genera or species from seeds, achenes, florets, fruits, leaves or stems (Table 3.3; Figs. 3.7-3.10). A summary of the paleoclimate implications are in Table 3.4. The overall trend in species richness at all the localities except Pampa Vizcachilla and Cerros de Minta is a general decrease from the early Holocene towards the present. Although all of these taxa are found in northern Chile, many are currently absent from the midden sites (i.e. extralocal taxa).

The combined macrofossils from Cerros de Aiquina- Quebrada Chiquinaputo (Fig. 3.7) clearly demonstrate this overall trend. Maximum species richness was reached at 9.5 and between 7.6-6.7 ka. The oldest midden in this series, dated at 11.4 ka, has low species richness, low grass abundance, and common plants are the cacti *Opuntia camachoi* and *O. sphaerica* and *Atriplex imbricata.* Macrofloras for middens dated between 9.7-9.5 ka were much more diverse and characterized by steppe, tolar and numerous summer annuals. Prominent among these are *Nassella arcuata, Nassella pubiflora* and *Junellia seriphioides.* Except for *N. pubiflora,* these taxa disappear from the record between 9.2-8.4 ka although many summer annuals and cacti persist in the record. Steppe and tolar taxa reappear in middens dated between 7.6-6.7 ka and species richness reaches a maximum of 30 taxa at 6.7 ka. One curious pattern is the disappearance of "other" taxa (including species with coastal affinities) from the record after 6.7 ka. Macrofloras from a midden dated at 2.8 ka are considerably less diverse and contain mostly cacti and a few summer annuals. These species were present to a lesser extent in the Quebrada Chiquinaputo middens, 10 km from the Cerros de Aiquina localities. Dated between 0.48-0.3 ka, these middens have modern floras with the dominance of prepuna perennials and annuals.

A similar pattern exists at Cordón de Tuina (Fig. 3.8). Macrofossil species were richest between 11.6-10.0 ka. These assemblages included numerous steppe and tolar species and summer annuals. Among these are high tolar species such as *Baccharis boliviensis* and *Baccharis tola* ssp *tola.* The steppe grass *Anatherostipa venusta* is currently found today above 3800 m on the western Andean slope and is not present anywhere in the Cordillera Domeyko. In comparison, the oldest midden dated at 12.0 ka has a reduced species richness with no steppe grasses and only one tolar species, *B. tola* ssp *tola.* Macrofloras change abruptly at 9.6 ka and steppe, tolar and "other" taxa disappear along with most summer annuals. Assemblages were dominated by the columnar cacti *Echinopsis atacamensis* (presently absent from this area) and the common prepuna shrub *Ambrosia artemisioides.* Cacti become less prominent and summer annuals increase in a 5.1 ka midden dominated by *Atriplex imbricata.* These assemblages are similar to those present in the late Holocene middens between 1.1-0.0 ka and in the modern vegetation (see Table 3.1).

Macrofossils assemblages from Pampa Vizcachilla (Fig. 3.9) exhibit a slightly different trend through time than the previous two records. Overall, macrofloras were more stable throughout this record. Most prominent was the presence of the high tolar species *Parastrephia quadrangularis* and *Baccharis tola* ssp *tola* and the coastal Lomas species *Nassella pungens* in only the oldest two middens at 13.0-12.9 ka. Today, these species occur locally some 300 m higher in the Cordillera Domeyko. These late glacial middens also have limited representatives of the more arid floras from the prepuna belt. Species richness reaches a maximum of 26 taxa during the middle Holocene at 6.2 ka and of 22 species between 3.4-3.3 ka. The 6.3 ka midden has two species of Steppe grasses, numerous cacti and summer annuals. Prepuna species such as *Atriplex imbricata* and *Ephedra* become very common and/or abundant for the remainder of this series. *Nassella arcuata* disappears from the record after 3.4 ka although *Stipa chrysophylla* (which was found growing along a small river valley nearby) remains present until recently. Both mid and late Holocene middens (between 2.1-0.17 ka) indicate that numerous summer annuals have been dominant since at least 6.3 ka. The tolar shrubs

Fabiana spp and *Chuquiraga atacamensis* were found growing near the middens today. In fact, late Holocene middens indicate that *Fabiana* may be a recent arrival and that *Chuquiraga* has become dominant in the area only recently. The dominant perennials at present, *Opuntia camachoi* and *Acantholippia deserticola* only became locally important starting at 3.2 ka.

The last two midden series are from west and east-facing slopes along the higher elevations of the Cordillera Domeyko (Fig. 3.10). Although sparse, these records represent the late glacial-early Holocene transition at El Hotel and the middle to late Holocene transition at Cerros de Minta. A diverse assemblage consisting of the steppe grass *Nassella arcuata* and several tolar species occurred at the west-facing site El Hotel between 13.4-13.1 ka. This assemblage contrasts with that present in a midden dated at 9.4 ka, in which all these taxa disappear, including the grass *Nassella pungens*. This younger midden presents mostly modern assemblages, as well as abundant summer annuals.

At the east-facing site Cerros de Minta, a midden from 4.5 ka records the presence of *Nassella arcuata*, numerous summer annuals and maximum species richness (20 taxa). *N. arcuata* is not recorded in any of the younger middens collected here and several of the summer annuals disappear as well. Younger middens reflect the dominance of *Opuntia camachoi* and *Echinopsis atacamensis*, as well as *Stipa chrysophylla*, a steppe grass presently found near Cerros de Minta today. The Lomas grass *Nassella pungens* occurs here at 1.8 ka, the youngest occurrence for any of the middens described in this paper.

5. Discussion

Grass abundance values, which in the Atacama reflect overall productivity and thus track seasonal precipitation amounts (Latorre et al., 2002; Meserve and Glanz, 1978), are highest between 13.5-9.4 ka, 7.6-6.3 ka, 4.3-3.0 ka and from 1.8-1.2 ka. Wet phases are also inferred from high species richness and presence of extralocal taxa, particularly those from higher elevations, specifically between 13.5-9.6 ka, 7.6-6.3 ka, 5.1-3.2 ka and between 2.8-1.2 ka. The chronology of wet and dry phases as inferred from the macrofloras (Figs. 3.5-3.8, Table 3.4) is generally in good agreement with that inferred from midden grass abundance for the last 13.5 ka (Fig. 3.4), despite local site differences in terms of aspect, elevation and microclimate.

5.1. Late glacial to early Holocene plant communities

Overall, late glacial communities present at Cordón de Tuina, Cerros de Aiquina, Pampa Vizcachilla and El Hotel were diverse and dominated by the steppe grasses *Nassella arcuata* and *N. pubiflora,* as well as numerous summer annuals and cacti. *N. arcuata* and *N. pubiflora* are now very rare in the central Atacama, but more common in northernmost Chile (lat. 18° S) and the Bolivian Altiplano (Matthei, 1965; Rojas, 1994). The tolar shrubs *Fabiana* spp and *Junellia seriphioides* were also common during the late glacial at most sites. The high tolar species (that presently grow >3500 m on the Andean slope) *Parastrephia quadrangularis* and *Baccharis tola* ssp *tola* were common at higher (El Hotel) and east-facing (Pampa Vizcachilla) sites. Several other extralocal taxa were also present, such as *Nassella pungens*, cf. *Galium*, *Bidens* spp., and *Bromus catharticus.* Notably, the perennial grass *N. pungens* is found today only at coastal

Lomas localities (Marticorena et al., 1998; Rundel et al., 1996). The presence of steppe and high tolar taxa imply a minimum altitudinal descent of 300 m either from the summits of the Cordillera Domeyko (ca. 3500 m) or the western Andean slope. These descents in turn imply a precipitation increase of at least double the amount that falls today (from 40-50 mm to 80-100 mm).

Among the most prominent changes in the midden macrofloras was the sudden and abrupt disappearance of all tolar and steppe taxa between 10.0-9.6 ka at Cordón de Tuina, and between 9.5-9.2 ka at Cerros de Aiquina, the two most complete series. These taxa had also disappeared from the El Hotel site (which is 100 m higher in elevation) by 9.4 ka. These species departures were accompanied by a large drop in grass abundance that occurred starting at 10.2 ka and culminated at 9.4 ka. Abrupt onset of a sustained drought is the most likely cause for reduced midden species richness and grass abundance that had occurred by at least 9.4 ka at all sites.

By 9.6 ka, a Cordón de Tuina midden reveals an extremely arid flora, as represented by the large decrease in species richness and the dominance of *Ambrosia artemisioides*. Midden macrofloras remained impoverished between 9.2-8.4 ka at Cerros de Aiquina, the only site with a sequence of early Holocene middens (Figs. 3.5 and 3.8). Plant communities during this interval lacked steppe (save for the rare presence of *Nassella pubiflora* at 8.4 ka), tolar taxa, and many summer annuals, characterized instead by the dominance of prepuna shrubs, especially *Ambrosia artemisioides*, *Atriplex imbricata* and *Opuntia camachoi*.

5.2. Middle to late Holocene plant communities

Early Holocene drought conditions did not persist into the middle Holocene, as steppe and tolar taxa returned to the Cerros de Aiquina midden sites by 7.6 ka. This was accompanied by a large increase in grass abundance similar to late Pleistocene percentages (Fig. 3.4). These taxa remained at Cerros de Aiquina until at least 6.7 ka. At Pampa Vizcachilla, both *Nassella arcuata* and *Stipa chrysophylla* were present in a 6.3 ka midden. The large number of cacti and summer annuals present here and at Cerros de Aiquina are responsible for the maximum species richness observed between 7-6 ka in both records.

Younger middens show somewhat drier floras, especially for a 5.1 ka midden from Cordón de Tuina, with diminished grass abundance and dominance by *Atriplex imbricata* and other prepuna taxa. Slightly wetter conditions may have been present at Cerros de Minta by 4.4 ka, as evinced by high grass abundance, high species richness and the presence of *Nassella arcuata* as well as numerous summer annuals. High species richness (22 taxa), *Nassella arcuata* and high grass abundance were also present between 3.4-3.3 ka at Pampa Vizcachilla. Species richness dropped to 12 taxa and grass abundance to 23% by 3.2 ka at Pampa Vizcachilla. These drier conditions are also reflected in a 3.2 ka midden from Cerros de Minta, which also has reduced species richness and summer annuals despite local dominance by *Stipa chrysophylla.*

Modern hyperarid floras were established at most sites by 3.0 ka, concomitant with the large sustained drop in grass abundance by 2.8 ka (Fig. 3.4). Species richness at the higher sites of Cerros de Minta increased between 2.5-1.8 ka. This increase preceded a slight rise in grass abundance (to 20-40%) between 1.8-1.2 ka at this site as well as at

Cordón de Tuina and Pampa Vizcachilla. Three recent middens from Quebrada Chiquinaputo (Table 3.2) reflect modern hyperarid conditions present slightly downslope from Cerros de Aiquina. Midden macrofloras indicate a few summer annuals (none occurred at the site today) and several species of prepuna flora, including abundant *Urmenetea atacamensis*, *Cistanthe* spp and *Atriplex imbricata.* A modern unindurated (still in use or recently abandoned) vizcacha midden collected at Tuina Cave (a few meters from Cordon de Tuina 386) reveals midden macrofloras almost identical with the list of plants collected within a 500 m radius by C.L. and J.L.B in two late summer field seasons (Fig. 3.6 and Table 3.1).

5.3. Comparison with the low elevation midden record in the central Atacama

Our midden record from the arid prepuna of the Cordillera Domeyko provides well-dated chronologies of vegetation displacements caused solely by increases in precipitation. As summarized in Table 3.4, climate wetter than today occurred between 13.5-9.6 ka (9.5 ka at Cerros de Aiquina), and between 7.6-3.2 ka. A short wet interval probably occurred between 1.8-1.2 ka. Increases in summer rainfall were the likely cause for these wet phases due to the abundance of summer annuals and presence of species that today occur further north. Abrupt onset of dry phases (as pronounced as the present hyperarid climate) occurred between 9.6 (9.2)-8.4 ka and from 3.2 ka to the present. A brief arid event may have occurred at 5.1 ka as evinced in one midden from Cordón de Tuina.

Among the key issues to address here is whether the timing and extent of the wet and dry phases from our previous midden record along the edge of absolute desert

(Latorre et al., 2002) are replicated in the record presented here. Overall agreement between the two records is readily visible when grass abundance values from both records are compared (Fig. 3.6). Our previous midden record indicated a major wet phase between 13.8-10.5 ka with minor precipitation increases between 7.1-3.5 ka. The wet phase during the late glacial-early Holocene is similar in timing in both records, despite an apparent lag of one thousand years in the higher elevation record. This lag, however, may be due to the discontinuous nature of the record itself; the lower elevation record lacked middens dated between 10.2-9.5 ka. The higher elevation record, however, provides much more precise timing for the early Holocene arid phase (see Figs. 3.7-3.8), which had clearly begun between 9.6-9.2 ka (within the 2σ errors of the ^{14}C dates).

A major difference between records during the late glacial was the presence of high tolar shrubs between 13.5-12 ka in the higher elevation record. These taxa were completely absent from coeval lower elevation middens. The absence of these important taxa could enable us to place upper limits on our precipitation estimates (which in both records are minimums) but other factors must be considered. Two reasons could explain this absence: 1) precipitation increases were not sufficient or were too brief to cause these species to migrate far enough downslope; 2) current plant distributions preclude the presence of these taxa in middens from the southern end of the Salar de Atacama. The first explanation is unlikely as taxa found even further up the gradient, such as the steppe grasses *Anatherostipa venusta* and *Nassella nardioides* were found in the low elevation record (Latorre et al., 2002). The second explanation seems more likely in this case, as no high tolar species were present on a recent transect run by one of us (C.L.)

across Lomas de Quilvar up to the vicinity of Laguna Miñiques (Fig. 3.1) (Latorre, unpub. data).

An important issue is that mid-Holocene increases in precipitation barely recorded at lower elevations are clearly visible in the record presented here, particularly between 7.6-6.3 ka and between 4.5-3.2 ka. Middens at higher elevations are thus recording vegetation displacements between 100-300 m in altitude caused by lesser increases in precipitation. One reason why these increases produce only faint traces in the midden floras of lower elevations is that productivity would still have been very low along the absolute desert margin, generating few possibilities for midden formation. For the same reason, the records also differ for the last 3 ka. Whereas lower elevation middens indicate that the last 3 ka were probably the most arid for the last 22 ka, upper elevation middens point to a minor wet phase between 1.8-1.2 ka. Yet overall, the higher elevation record not only replicates the major patterns seen in our previous, low-elevation record, but also "amplifies" precipitation signals that were barely recorded at lower elevations.

5.4. Comparison with other records from the central Atacama

A diverse array of paleoclimate records have recently been developed in the central Atacama region. These include lake and pollen histories from the Chilean Altiplano (Geyh et al., 1999; Grosjean et al., 1995; Grosjean and Nuñez, 1994; Grosjean et al., 2001; Messerli et al., 1993; Valero-Garcés et al., 1996); archaeological records (Nuñez et al., 2001); wetland and ground watertable fluctuations at the base of the Andes (Rech et al., 2001; Rech et al., 2002) and a 100 ka salt core obtained from the deepest portion of the Salar de Atacama (Bobst et al., 2001) (see Fig. 3.1 for all locations).

Based on a series of different reservoir corrections on radiocarbon dates from lake sediments, Geyh et al. (1999) identified a general wet phase across the Chilean Altiplano between ~15- 9 ka. Through the use of a simple hydrologic model, Kull and Grosjean (1998) concluded that precipitation must have doubled to account for lake levels some 25 m higher at Laguna Lejía. Increases in lake levels were accompanied by increases in grass pollen between 11-9 ka at Laguna Miscanti (Grosjean et al., 2001) implying expansion of grasslands on the Pacific slope of the Andes. Other evidence for a late glacial wet phase comes from a U-series dated wet phase between 11.4-10.2 ka (Bobst et al., 2001), high ground water tables between 16-9 ka (Rech et al., 2002) and numerous early Archaic sites throughout the central Atacama (Nuñez and Grosjean, 1994; Nuñez et al., 2001). Both our midden records are in agreement with the dating for these wet phases, between 13.8-10.5 ka at lower elevations and between 13.5-9.4 ka at higher elevations; the abundance of summer-flowering annuals and perennials indicate the seasonality of the precipitation. Using the dates reported here for the onset of aridity at 9.6-9.4 ka, lake histories would have lagged 500-600 years behind the rodent middens whereas groundwater fluctuations lagged by approximately 500 years (see also Rech et al., this volume).

There is less agreement about the middle Holocene, which we argue was wetter than today in the central Atacama from both rodent midden and wetland deposits. A case for mid-Holocene aridity has been made on the presence of gypsum and reduced aquatic pollen in Laguna Miscanti sediments between 9-3.9 ka (Grosjean et al., 2001), lower lake levels at Laguna del Negro Francisco (Grosjean et al., 1997b); persistence between 6.8-3.2 ka of debris-flow dammed lakes along Quebrada Puripica, a steep canyon that drains the Andean front (Grosjean et al., 1997a); and a hiatus of human occupations between 9-3.4 ka known as the *Silencio Arqueológico* ("archaeological silence") (Grosjean et al., 1997a; Nuñez et al., 2001).

We feel that most of these indications of mid-Holocene aridity, however, are ambiguous. Although the onset of a dry period at the end of the early Holocene wet phase is well documented at Laguna Miscanti, its duration cannot be determined due to large unsystematic carbon reservoir effects on radiocarbon dates. Furthermore, at ~27°30'S latitude, Laguna del Negro Francisco is more influenced by the southern westerlies and winter precipitation and lies well beyond the reach of spillover, summertime storms from the Altiplano. There is no reason why the climate history at Laguna del Negro Francisco should correlate with that of Laguna Miscanti. At Quebrada Puripica, the purported lake sediments have been reinterpreted as spring deposits by Rech et al (this volume), and correlated with other paleowetland evidence to instead indicate higher ground-water levels in the central and northern Atacama. There is corroborating evidence for a short wet phase dated between 6.2-3.5 ka present in the Salar de Atacama core (Bobst et al., 2001). Finally, the beginning of the *Silencio Arqueológico* surely reflects the onset of hyperaridity in the region, as vegetation retreated upslope and game was restricted to springs and other wetlands. But we feel that the end of the *Silencio Arqueológico* was determined, not by aridity, but by the slow diffusion of critical technologies from Peru, such as domestication of camelids, and the associated increase in human population.

5.5. Comparison with other records from the central Andes

Even larger discrepancies in relative effective moisture arise among records across the central Andes in general. These include cores and shoreline features from Lago Titicaca (Mourguiart et al., 1998; Cross et al., 2000; Baker et al., 2001b) and Salar de Uyuni (Sylvestre et al., 1999; Baker et al., 2001a; Fornari et al., 2001), covered by large and successive paleolakes during the Pleistocene. The late glacial wet phase in the Bolivian Altiplano generally has older dates for the maximum highstands and wet phases. U-series and ^{14}C dating of shoreline tufas in the Uyuni-Coipasa Basin identified two wet phases: one major event between 18.9-14.0 ka (Tauca); and a minor event between 10.8-9.5 ka (Coipasa), separated by a dry phase (Ticaña) between 14.0-10.8 ka (Sylvestre et al., 1999). These highstands are younger than those inferred from a ^{14}C-dated sediment core in the center of the Salar de Uyuni, which indicates successive wet phases throughout the latest Pleistocene, followed by a minor lake stand ~12.5 ka with no wet phase during the Holocene (Baker et al., 2001a). Lago Titicaca was above present day levels before 11.5 ka and plummeted to 85 m below present between 8.0-5.5 ka as inferred from a core drilled in the deepest portion of the basin (Baker et al., 2001b). Sustained aridity between 6.2-2.3 ka has also been inferred from a multiproxy record of hydrologic change at Laguna Taypi Chaka Kkota, located ~75 km east of Lago Titicaca in the Cordillera Real (Abbott et al., 2000). Onset of aridity occurred here some 3,000 years later than at Lago Titicaca and implies that even within the northern Altiplano, sub-regional hydrologic responses at different sites during the late Holocene were complex.

6. Conclusions

This study highlights the value of replicating climatic histories using the same proxy along well-defined environmental gradients. This approach has allowed verification and refinement of paleoclimatic inferences in the central Atacama, though we suspect that disagreements remain over the nature of mid-Holocene climate among the various researchers working in the Atacama. Some of the discrepancies between paleoclimate records in the central and northern Atacama, the southern Altiplano and the Titicaca Basin may be explained by regional circulation, which is considerably more complex today, and probably in the past, than portrayed by paleoclimatologists. There may be at least two general sources of moisture that contribute to summertime precipitation in the central Andes- air masses over the southern Amazon and the Gran Chaco. These sources may have different forcing and modes of variability, and are not clearly segregated over the region, though the southern Amazon source is dominant in the Lago Titicaca basin while the Gran Chaco has a greater influence over the southern Altiplano. This could explain why the large paleolakes (e.g., Tauca and Minchin) that probably developed from Lake Titicaca overflow might be decoupled from precipitation in the southern Altiplano and the central and northern Atacama. Furthermore, variability in the moisture sources may or may not be coupled to atmospheric transport from the eastern to western parts of the Altiplano. This transport seems to be modulated by Pacific SST gradients, with increased advection of tropical moisture and more summer rainy days during La Niña than El Niño episodes (Garreaud et al. this volume). This could explain why the Pacific slope of the Andes might be out of phase with Lake Titicaca and other records from the eastern Cordillera. Finally, the effects of regional seasonal insolation variations on these different moisture sources and transport mechanisms are apt to be either weak or very complex. Discrepancies between paleoclimate records suggest that any simple model of climatic change and forcing in the central Andes is probably premature.

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Table 3.1.
Comparison between vegetation collected by the authors and that present in an active *Lagidium* midden at the Cordón de Tuina 386 site

Taxa	**Collected March, 1998**	**CdT 386-modern**
Ambrosia artemisioides	X	X
Atriplex imbricata	X	X
Cistanthe spp	X	X
Chorizanthe commisuralis		X
Cryptantha spp	X	X
Diplostephium meyenii	X	X
Ephedra breana	X	X
Lycopersicon chilense	X	
Tagetes multiflora		X
Opuntia camachoi	X	X
Oreocereus leucotrichus	X	
Total	9	9

Table 3.2.
Site location and radiocarbon dates for the 44 middens used in this study

Midden Field No.	Radiocarbon Lab No.	Radiocarbon Date (^{14}C yrs	δ^{13}C (PDB)	Calendar age (yr B.P.) 1 sigma	Midpoint	% Grass	No. of taxa	Elevation (masl)	Midden Agent	Slope Aspect
1) Quebrada Chiquinaputo										
1 QC 377A	GX-27818	250±70	-20,6	312 (290) 3	290	20	18	3043	Phyllotis	NW
2 QC 377C	GX-27819	340±50	-21,2	463 (422, 398, 318) 304	398	0	12	3043	Phyllotis	NW
3 QC 376	GX-27817	420±60	-20,5	511 (478) 326	478	0	17	3046	Phyllotis	NW
2) Cerros de Minta										
4 CdM 485	GX-27823	1860±60	-24,2	1863 (1815, 1797, 1775, 1757, 1739) 1706	1775	40	19	3300	Lagidium	S
5 CdM 484	GX-27822	2490±70	-24,2	2728 (2705, 2647, 2489, 2474) 2357	2489	0	13	3300	Lagidium	SW
6 CdM 482A	GX-27821	3060±70	-22,8	3348 (3314, 3313, 3246, 3220, 3214) 3082	3246	37	8	3250	Lagidium	S
7 CdM 481B	GX-25658	4070±80	-22,5	4788 (4523, 4459, 4452) 4419	4459	49	16	3250	Lagidium	E
3) Cerros de Alquina										
8 CdA 483B	GX-25655	2780±80	-22,9	2949 (2850) 2775	2850	7	19	3150	Lagidium	S
9 CdA 458	GX-26622	5920±90	-23,7	6848 (6723, 6697, 6682) 6575	6697	52	30	3174	Lagidium	ENE
10 CdA 457A	GX-25654	6720±110	-23,5	7664 (7571) 7439	7571	97	26	3120	Lagidium	NW
11 CdA 457B	GX-26624	6780±60	-24,1	7668 (7609, 7598, 7590) 7572	7598	10	12	3120	Lagidium	SSW
12 CdA 483C	GX-25656	7710±210	-22,6	8645 (8424) 8221	8424	47	21	3150	Lagidium	S
13 CdA 456	GX-26621	8230±70	-24,1	9396 (9241, 9219, 9188, 9175, 9131) 9029	9188	9	23	3150	Lagidium	S
14 CdA 483A	GX-26625	8470±120	-23,4	9535 (9485, 9476, 9474) 9305	9476	67	16	3150	Lagidium	S
15 CdA 455B	GX-26623	8720±90	-24,6	888 (9676, 9671, 9660, 9648, 9628, 9608, 9603) 954	9648	29	26	3120	Lagidium	WNW
16 CdA 483D	GX-25657	10030±260	-22,6	12100 (11546, 11510, 11403, 11390, 11341) 11175	11403	15	16	3150	Lagidium	S
4) Cordón de Tuina										
17 CdT 386-	modern	modern	–	0	0	0	9	3190		
18 CdT 391A	GX-25418	1100±80	-22,3	1060 (967) 928	967	0	12	3150	Lagidium	N
19 CdT	GX-25419	1240±100	-22,9	1265 (1170, 1156, 1153) 990	1156	30	15	3150	Lagidium	N
20 CdT 388	GX-24208	4540±100	-18,8	5317 (5282, 5161, 5138, 5103, 5074) 4977	5138	3	19	3173	Lagidium	SW
21 CdT 386F	GX-24878	8710±130	-24	7 (9656, 9652, 9626, 9618, 9601, 9584, 9564, 9564)	9618	0	18	3190	Lagidium	SW
22 CdT 387-2	GX-26748	8940±70	-24,3	10188 (10150, 10044, 9987, 9975) 9915	10044	81	20	3150	Lagidium	S
23 CdT 386B	GX-24204	9025±155	-23,8	10356 (10189) 9914	10189	98	23	3190	Lagidium	SW
CdT 386B	AA-44217	9754±67	-25,0	11199 (11171) 11125	11171	–	–	*--date on individual grass blades*		
24 CdT 389C	GX-24210LS	9630±95	-25,8	11166 (11085, 11081, 11072, 10937, 10869) 10703	11072	60	14	3180	Lagidium	NW
25 CdT 386C	GX-24205	9630±140	-23,8	11176 (11085, 11081, 11072, 10937, 10869) 10692	11072	89	10	3190	Lagidium	SW
26 CdT 389A	GX-24209	9800±160	-23,1	11296 (11192) 10875	11192	10	20	3180	Lagidium	NW
27 CdT 386A	GX-24203	10140±160	-24,4	12266 (11691, 11665, 11662) 11262	11655	98	30	3190	Lagidium	SW
28 CdT	GX-24211	10280±150	-23,2	12573 (12069, 12036, 11957) 11645	12036	88	14	3150	Lagidium	N
5) El Hotel- Paso Barros Arana										
29 EH 383	GX-24200LS	8320±90	-23,9	468 (9397, 9386, 9369, 9360, 9345, 9343, 9296) 913	9360	8	20	3219	Lagidium	SE
30 EH 384B	GX-24202LS	11190±120	-24,4	13190 (13148) 13006	13148	5	16	3219	Lagidium	W
31 EH 384A	GX-24201	11480±170	-23,1	13791 (13438) 13168	13438	74	14	3219	Lagidium	W
6) Pampa Vizcachilla										
32 PV 404	GX-24913	220±65	-24,5	302 (281, 169, 154) 2	169	4	17	3125	Lagidium	E
33 PV 405	GX-24912	435±105	-24,2	533 (498) 314	498	2	11	3125	Lagidium	E
34 PV 428A	GX-24913	660±65	-23,0	661 (647, 582, 567) 549	582	1	12	3125	Lagidium	E
35 PV 434B	GX-24980	895±70	-23,0	911 (785, 783, 763) 694	783	2	9	3125	Lagidium	E
36 PV 428B1	GX-24938	1270±70	-23,5	1266 (1175) 1064	1175	24	13	3125	Lagidium	E
37 PV 429B	GX-24939	2005±75	-23,5	1999 (1925, 1906, 1903) 1832	1906	6	13	3125	Lagidium	E
38 PV 429A	GX-24979	2130±75	-24,0	2295 (2105, 2081, 2066) 1953	2081	3	12	3125	Lagidium	E
39 PV 434A	GX-25044	3040±80	-23,2	3341 (3236, 3232, 3211) 3078	3232	23	12	3125	Lagidium	E
40 PV 427	GX-24830	3100±140	-21,8	3447 (3325, 3285, 3269) 3078	3285	63	22	3125	Phyllotis	E
41 PV 431	GX-24915	3230±270	-22,4	3807 (3441, 3427, 3404) 3078	3427	78	22	3125	Phyllotis	E
42 PV 426	GX-24937	5500±160	-22,8	6409 (6286) 6002	6286	100	26	3125	Phyllotis	E
43 PV 402B	GX-24874	10870±180	-25,9	13108 (12905) 12654	12905	98	9	3125	Lagidium	E
44 PV 402A	GX-24875	10960±180	-24,6	13143 (12974) 12679	12974	26	11	3125	Lagidium	E

Table 3.3.
List of 59 taxa identified from macrofossils present in Cordillera Domeyko middens

Taxa	**Family**	**Plant part identified**	**Physiognomic affinity**
Gnetophyta			
Ephedra sp	Ephedraceae	Seeds, bark	Prepuna perennial
Anthophyta- Dicotyledons			
Ambrosia artemisioides	Asteraceae	pseudoachenes, leaves	Prepuna perennial
Baccharis boliviensis	Asteraceae	leaves	Tolar
Baccharis tola ssp incarum	Asteraceae	leaves	Tolar
Bidens aff *pilosa*	Asteraceae	achenes	
Bidens aff *pseudocosmos*	Asteraceae	achenes	
cf. *Conyza chilensis*	Asteraceae	achenes	Prepuna annual
Chuquiraga atacamensis	Asteraceae	achenes, leaves	Tolar perennial
Diplostephium meyenii	Asteraceae	leaves	Prepuna/Tolar perennial
Helogyne macrogyne	Asteraceae	achenes	Prepuna/Tolar perennial
Parastrephia quadrangularis	Asteraceae	leaves	High Tolar perennial
Schkuhria multiflora	Asteraceae	achenes	Tolar annual
Senecio aff *atacamensis*	Asteraceae	leaves	Tolar perennal
Tagetes multiflora	Asteraceae	achenes	Tolar annual
Urmenetea atacamensis	Asteraceae	achenes	Prepuna annual
Cryptantha diffusa	Boraginaceae	nutlets	Prepuna annual
Cryptantha hispida	Boraginaceae	nutlets	Prepuna annual
Cryptantha limensis	Boraginaceae	nutlets	Prepuna annual
Cryptantha phaceloides	Boraginaceae	nutlets	Prepuna annual
Pectocarya dimorpha	Boraginaceae	nutlets	
Tiquilia atacamensis	Boraginaceae	nutlets, leaves	Prepuna annual
Lepidium sp	Brassicaceae	siliqules	Prepuna/Tolar annual
Sisymbrium phillipianum	Brassicaceae	siliques	Prepuna annual
Echinopsis atacamensis	Cactaceae	seeds	Prepuna/Tolar perennial
Opuntia camachoi	Cactaceae	seeds	Prepuna/Tolar perennial
Opuntia ignescens	Cactaceae	seeds	Tolar perennal
Opuntia sphaerica	Cactaceae	seeds	Prepuna perennial
Oreocereus sp	Cactaceae	seeds	Prepuna/Tolar perennial
Hoffmannseggia sp	Caesalpinaceae	seeds, leaves	Prepuna perennial
Spergularia sp	Caryophyllaceae	seeds	Tolar
Atriplex imbricata	Chenopodiaceae	seeds, leaves, bark	Prepuna perennial
Euphorbia sp	Euphorbiaceae	seeds, flower bracts	Prepuna/Tolar perennial
Adesmia atacamensis	Fabaceae	leaves	Prepuna perennial
Adesmia spp.	Fabaceae	seeds	
Phacelia sp	Hydrophyllaceae	seeds	Prepuna perennial
Krameria lappacea	Krameriaceae	fruits	Prepuna/Tolar perennial
Cristaria spp	Malvaceae	seeds	Annual

Taxa	**Family**	**Plant part identified**	**Physiognomic affinity**
Tarasa operculata	Malvaceae	seeds	Prepuna subshrub
Plantago hispidula	Plantaginaceae	flowers	Prepuna/Tolar annual
Gilia cf *glutinosa*	Polemoniaceae	flower bracts	Prepuna/Tolar annual
Chorizanthe commisuralis	Polygonaceae	fruits	Prepuna/Tolar annual
Cistanthe spp	Portulacaceae	seeds, leaves, stems	Prepuna annual
cf. *Galium* sp	Rubiaceae	seeds	
Exodeconus integrifolius	Solanaceae	seeds	Prepuna annual
Fabiana spp	Solanaceae	stems	Tolar perennal
Lycopersicon chilense	Solanaceae	seeds, leaves	Prepuna perennial
Acantholippia deserticola	Verbenaceae	seeds, leaves	Prepuna perennial
Junellia seriphioides	Verbenaceae	seeds	Tolar perennial
Anthophyta- Monocotyledons			
Anatherostipa venusta	Poaceae	florets	Steppe perennial
Aristida adscensionis	Poaceae	florets	Tolar C_4 annual
Bouteloua simplex	Poaceae	florets	Tolar C_4 annual
Bromus catharticus	Poaceae	florets	
Munroa cf. *andina*	Poaceae	florets	Tolar C_4 annual
Munroa decumbens	Poaceae	florets	Tolar C_4 annual
Nassella arcuata	Poaceae	florets	Steppe perennial
Nassella nardoides	Poaceae	florets	Steppe perennial
Nassella pubiflora	Poaceae	florets	Steppe perennial
Nassella pungens	Poaceae	florets	Lomas perennial
Stipa chrysophylla	Poaceae	florets	Steppe perennial

Table 3.4.

Paleoclimatic implications from macrofloras of 44 middens collected from the Cordillera Domeyko, Central Atacama Desert

Interval (ka)	Number of Middens Analyzed	Description	Inferred Paleoclimate
0.0-1.0	9	Modern assemblages dominated by prepuna taxa. Species richness averages 15 taxa. Summer annuals relatively rare. *Stipa chrysophylla*, a steppe grass and tolar taxa are rare and found on east-facing slopes (e.g. Pampa Vizcachilla).	Present hyperarid climate.
1.2-2.8	7	Average 14 taxa. Cacti (several species), prepuna taxa and annuals are common at most localities. *Stipa chrysophylla* is present ~2.0 ka BP at higher elevations. Last appearance of *Nassella pungens*, a coastal species, at 1.9 ka BP.	Generally hyperarid with slightly wetter climate between 1.2-1.8 ka indicated by increases in grasses and cacti diversity at some localities.
3.2-5.1	6	Average 16 taxa. Abundant summer annuals, cacti and prepuna taxa. Two species of steppe grasses present in minor amounts at two east facing localities. Low species richness and plant assemblages similar to modern at 5.1 ka.	Generally wetter than today. Moisture was probably greatest near the youngest part of the interval. Possibly arid at 5.1 ka at Cordón de Tuina.
6.3-7.6	4	Average 23 taxa, the highest in the record. Characterized by numerous annuals. Three species of steppe grasses are present. A Few tolar taxa are also present. Cacti and prepuna shrubs, notably *Atriplex imbricata*, are abundant. *Nassella pungens* is very abundant.	A wet interval. High diversity implies high plant cover. Presence of steppe grasses indicate rainfall greater than twice the present amount.
8.4-9.6	5	Average 20 taxa. Steppe and tolar taxa are almost completely absent. Cacti and prepuna shrubs are very abundant as well as summer annuals.	Aridity abruptly increased as evidenced by the disappearance of steppa and tolar taxa. The abundance of cacti, however, indicates rainfall greater than today
9.6-11.7	8	Very diverse assemblages at most sites. Average 19 taxa. Steppe grasses include *Anatherostipa venusta, Nassella arcuata* and *Nassella pubiflora*. Abundant summer annuals and tolar shrubs. Prepuna shrubs and annuals present in low numbers.	The wettest interval in the record. Steppe grasses indicate large rainfall increases. Diverse assemblages without present day analogues
12.0-13.5	5	Average 13 taxa. Only appearance of *Parastrephia quadrangularis*, a high tolar species, in the record at two sites. Steppe grasses and other tolar taxa common. Few annuals and prepuna perennials.	Climate much wetter than today and possibly cooler as evidenced by lack of both summer and prepuna annuals

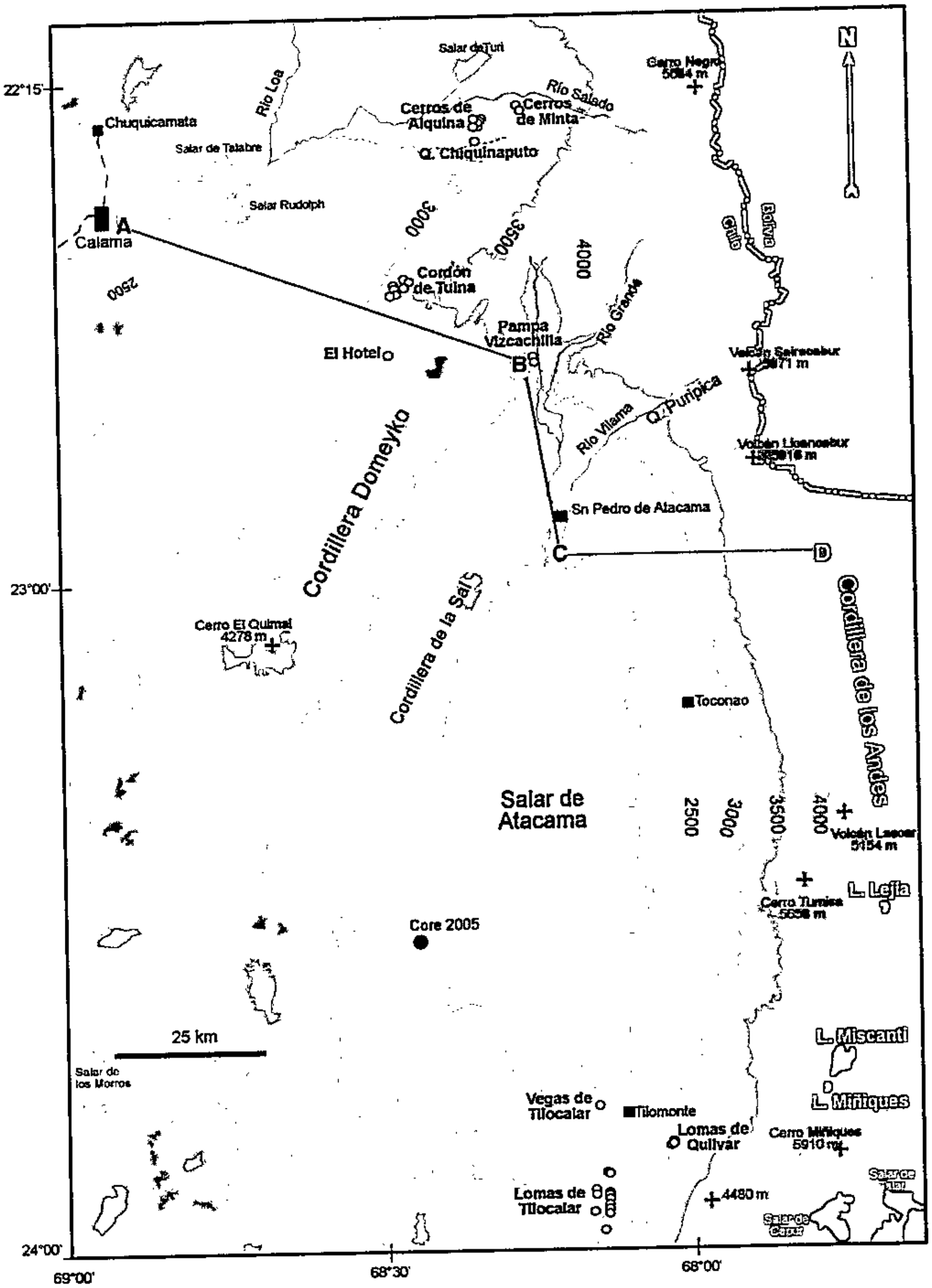


Figure 3.1. Map of the central Atacama Desert indicating location of midden sites discussed in this study and those from the southern tip of the Salar de Atacama published in Latorre et al. (2002). Other key paleoclimate sites also shown include core 2005 (Bobst et al., 2001), Laguna Lejía (Grosjean, 1994), Laguna Miscanti (Grosjean et al., 2001) and Quebrada Puripica (Grosjean et al., 1997a). Letters A-B-C-D denote the altitudinal transect discussed in Figure 3.

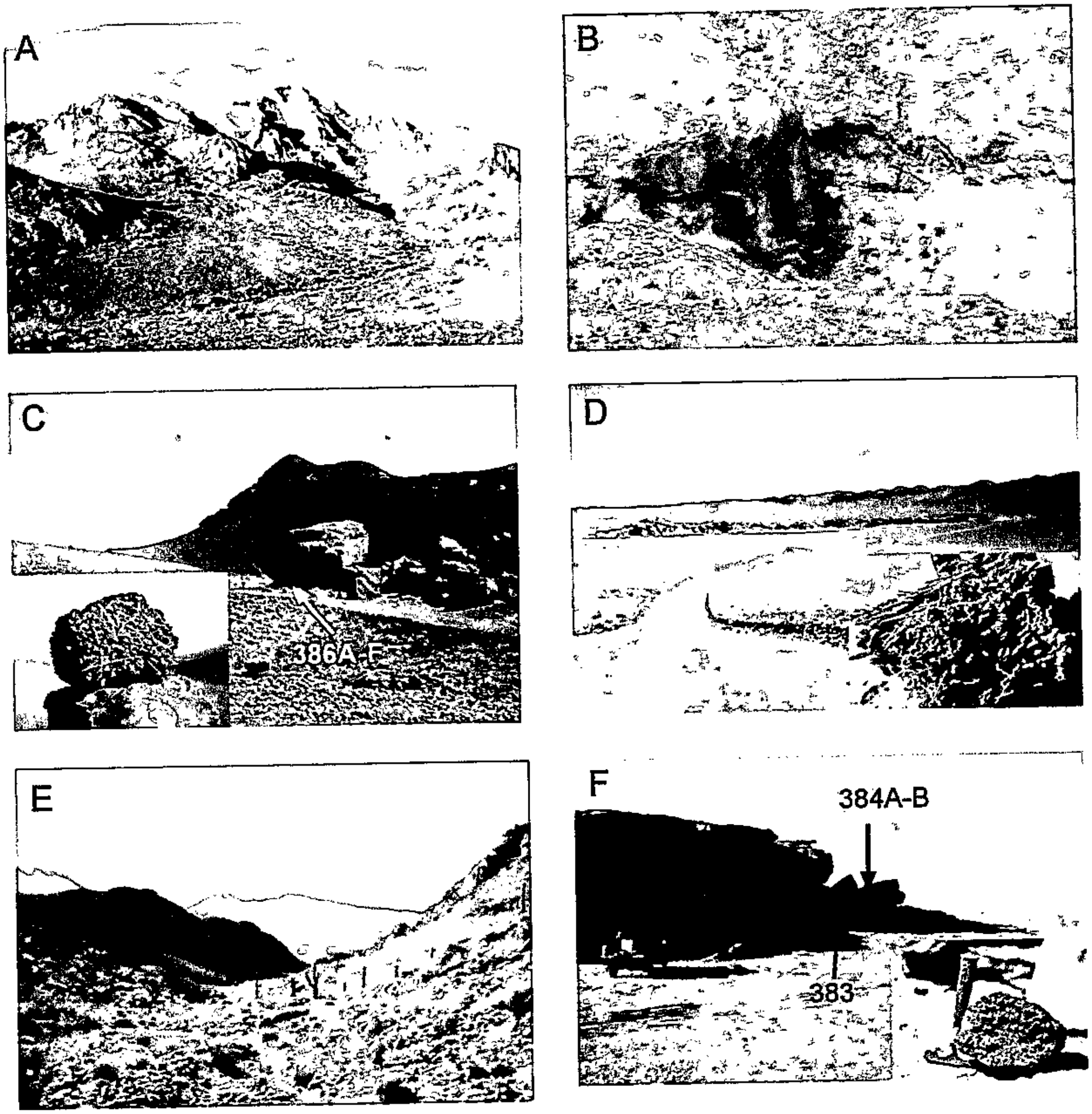


Figure 3.2. Photographs of midden localities. (A) Cerros de Aiquina, viewed from the west. (B) Quebrada Chiquinaputo midden localities within loosely consolidated Plio/Pleistocene conglomerates. (C) Cordón de Tuina looking towards the northwest with arrow indicating large rockshelter with middens 386A-F. Inset: Grassy midden CdT 386B with AMS ^{14}C-dates on grass of 11.2 ka. (D) Pampa Vizcachilla ignimbrite outcrop, view is towards the west. Inset: Grassy midden PV 402A ^{14}C-dated at 13 ka. (E) Cerros de Minta at 3300 m, looking towards the west to the Calama basin. Columnar cacti are specimens of *Echinopsis atacamensis*. (F) El Hotel ignimbrite locality with truck for scale. Arrows indicate were middens EH 383 and 384A-B were found. Inset: Large piece of midden EH 384B dated at 13.2 ka.

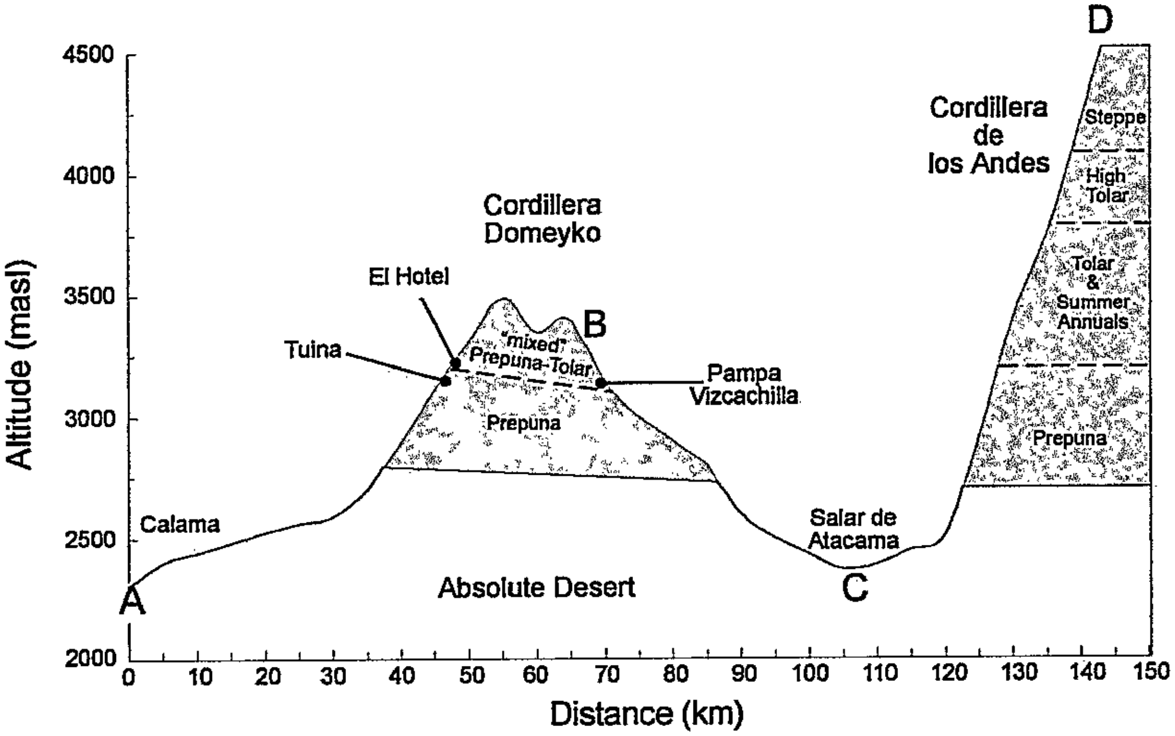


Figure 3.3. Vegetation zones across a generalized east-west transect through the Cordillera Domeyko and the western Andean slope. Letters ABCD are keyed to Fig. 1. Midden sites are shown for comparisons to modern vegetation belts. Unshaded areas correspond to zones devoid of vegetation at present.

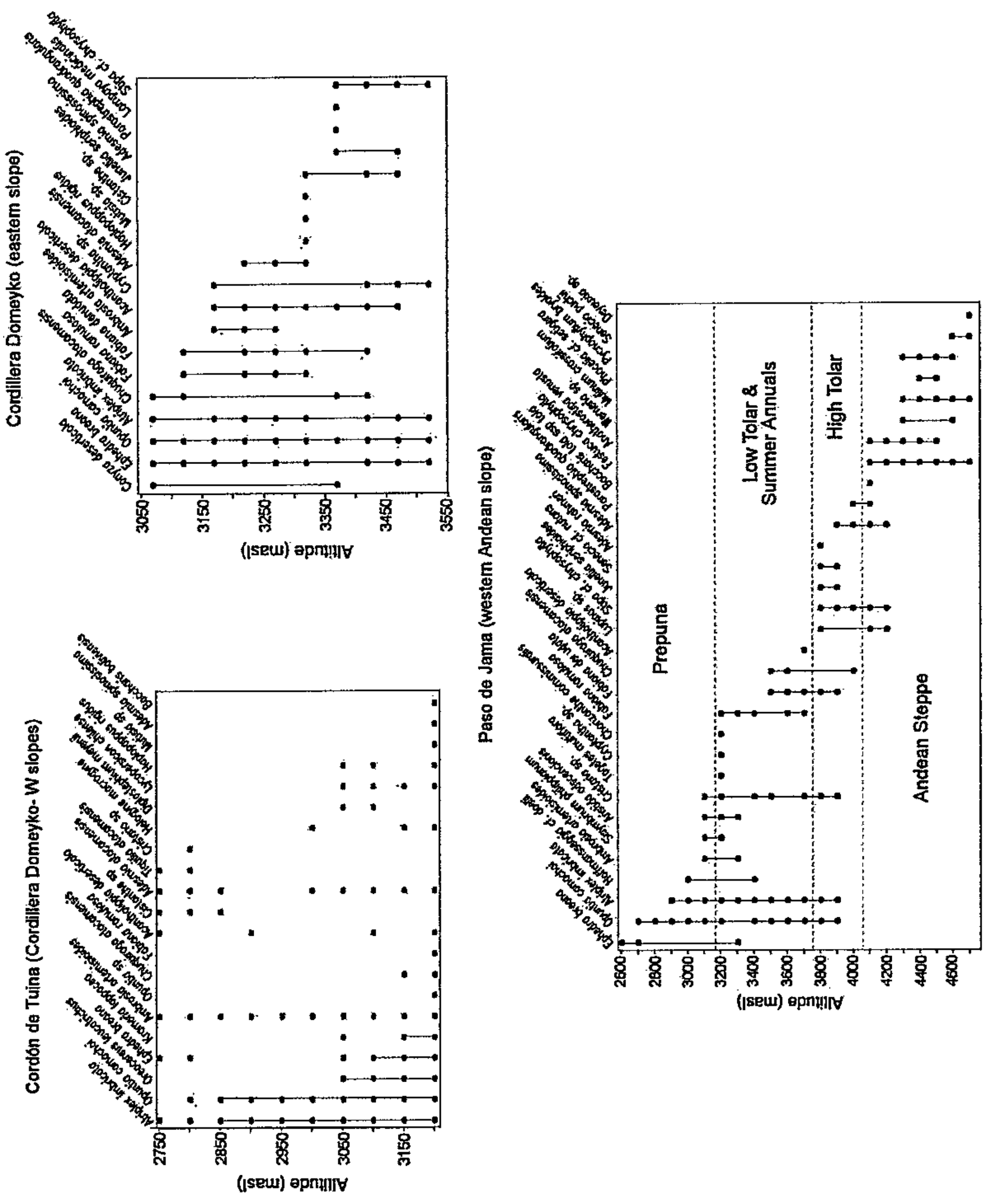


Figure 3.4. Altitudinal plant ranges for three transects in the central Atacama Desert keyed to transect ABCD in Figure 1. Grey dots represent plants occupying azonal habitats (i.e. riparian or other local run-on situations) whereas continuous lines represent a zonal ('hillslope') distribution (see text).

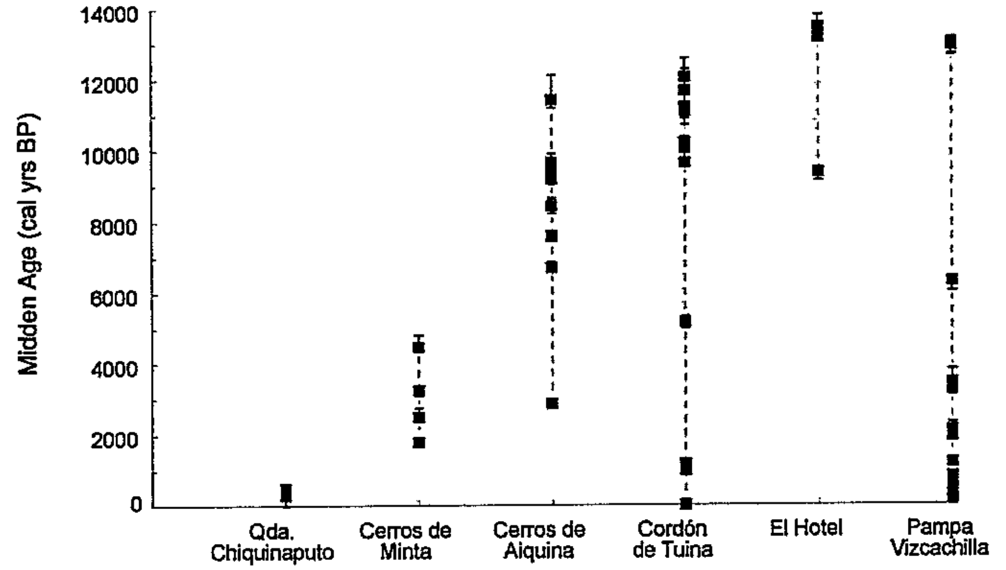


Figure 3.5. Individual time series (in calendar years) for all six midden sites based on midden radiocarbon dates (interval is at 1 σ).

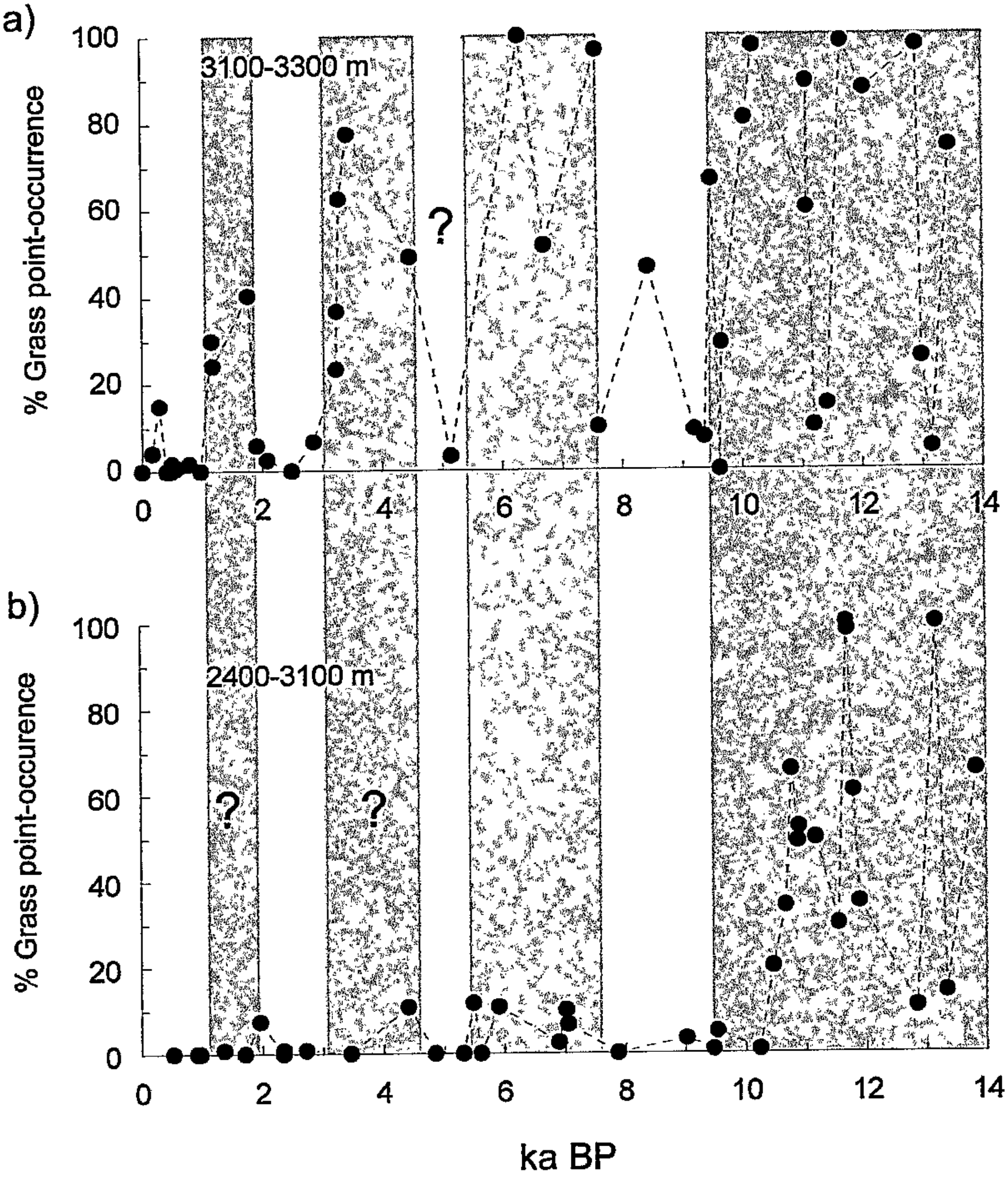


Figure 3.6. Comparison of high (a) and low (b) elevation grass abundance (%) calculated from grass point-occurrence obtained from a total of 100 middens (n=44 in a; n=39 in b). Shading reflects intervals wetter than today whereas white backgrounds are intervals as dry or drier than today (a questions mark signifies lack of replication between records).

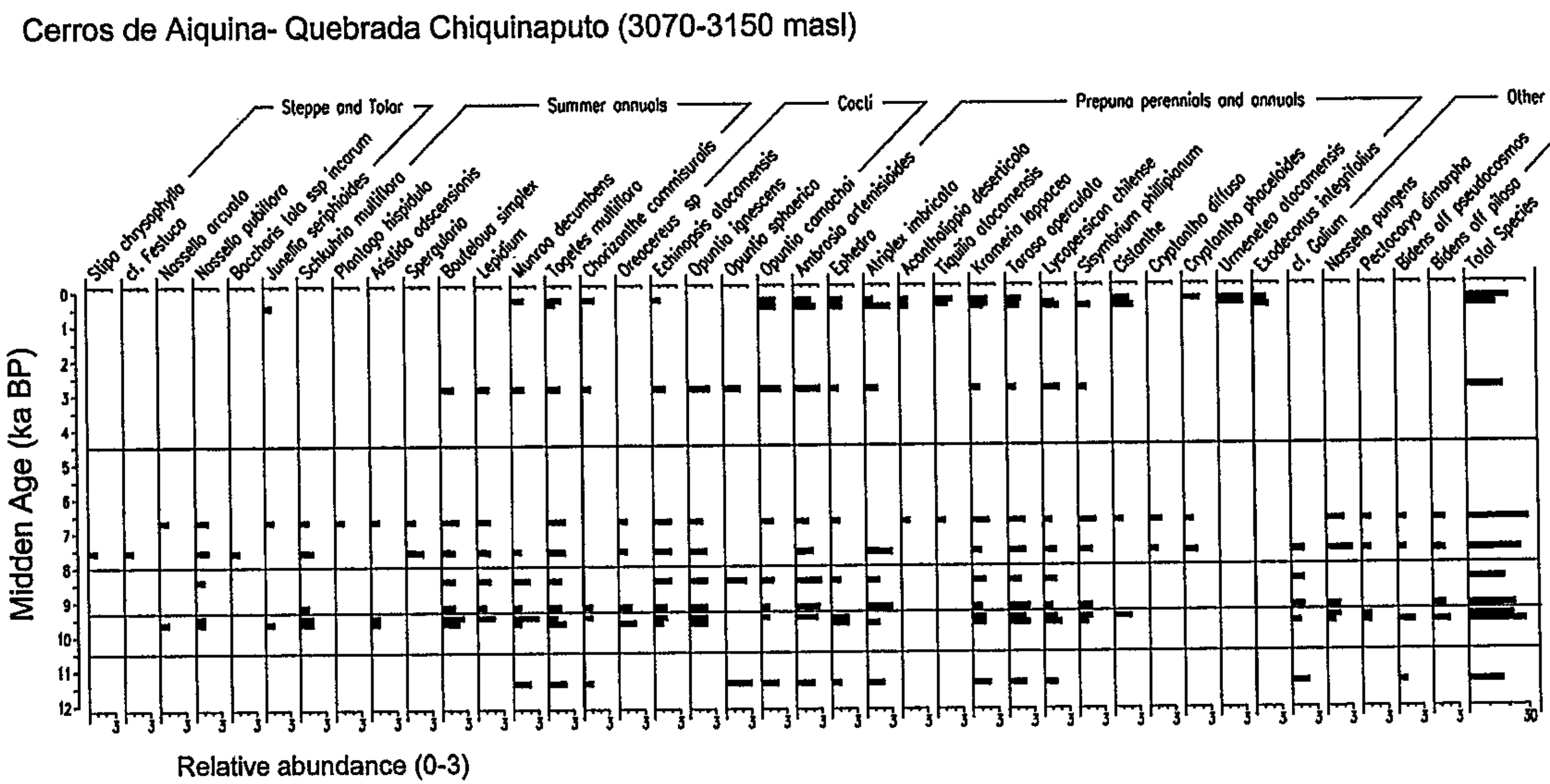


Figure 3.7. Combined macrofossil relative abundance diagram for the Cerros de Aiquina and Quebrada Chiquinaputo localities (12 middens). Major vegetation changes are denoted by horizontal lines. Relative abundance scale is: 0=absent; 1=rare; 2=common; 3=dominant.

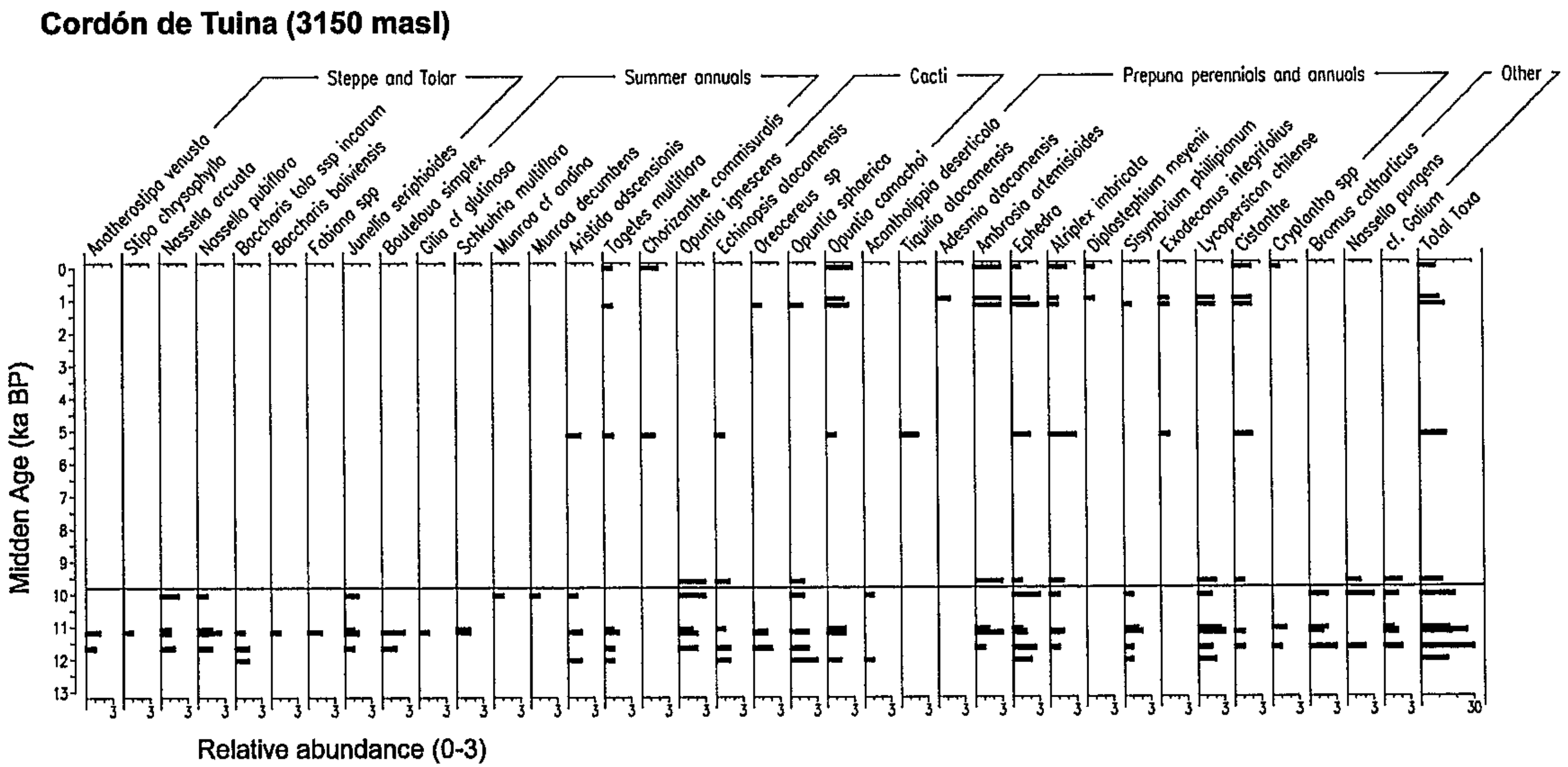
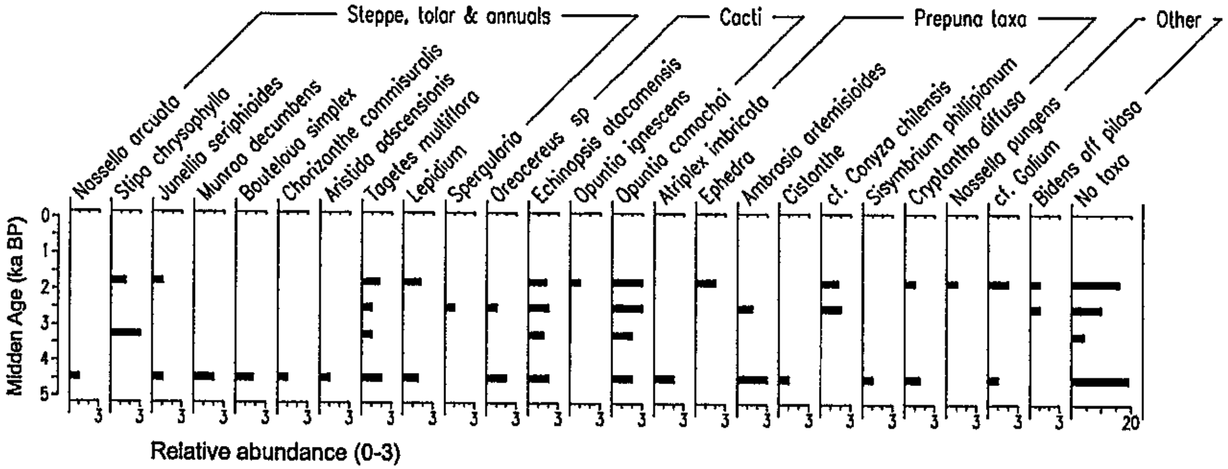


Figure 3.8. Macrofossil relative abundance diagram for the Cordón de Tuina locality (12 middens). Note major vegetation break between 10-9.6 ka. Scale as in Fig. 5.

Figure 3.9. Macrofossil relative abundance diagram for the Pampa Vizcachilla locality (13 middens). Breaks and scale as in previous figures.

Cerros de Minta (3300 masl)



El Hotel (3250 masl)

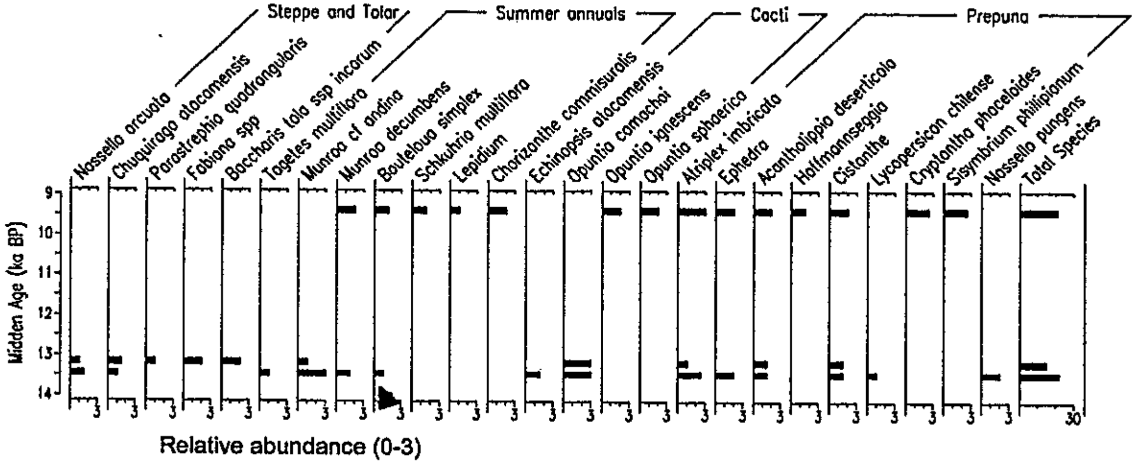


Figure 3.10. Macrofossil relative abundance diagrams for the (a) El Hotel and (b) Cerros de Minta localities (total 7 middens). Scale as in previous figures.