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ECOLOGICAL AND EVOLUTIONARY RESPONSES OF CHINCHILLA RATS (FAMILY
ABROCOMIDAE) TO PAST ENVIRONMENTAL CHANGES IN THE CENTRAL ANDES

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A mi madre, Margarita Amelia

A mi hija, Sofía

A mi hermana Fanny y mis hermanos Daniel y Jorge Andrés

A mis sobrinas y sobrinos



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ACTA DEFENSA FINAL DE TESIS

Don Francisco Javier González Pinilla, estudiante del Programa de Doctorado en Ciencias Biológicas Mención Ecología, ha presentado la Defensa Pública de Tesis.

En consideración a los conocimientos generales sobre Ecología, y la defensa de la Tesis Doctoral, titulada **"Ecological and evolutionary responses of chinchilla rats (family abrocomidae) to past environmental changes in the central Andes"**, el Comité de Tesis a resuelto calificar esta actividad académica como Aprobada y con nota 7.0 (siete coma cero).

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ABBREVIATIONS

ADN	Ácido Desoxirribonucleico
BI	Bayesian Inference
bp	Base Pairs
CAPE	Central Andean Pluvial Event
cytb	Cytochrome b
DNA	Deoxyribonucleic acid
e.g.	exempli gratia (for instance)
ENSO	El Niño Southern Oscillation
et al.	Et alii (and others)
GHR	Growth Hormone Receptor
i.e.	id est (this is)
ka BP	Thousand years Before Present
MAR	Mean Annual Rainfall
masl	Meters Above Sea Level
MAT	Mean Annual Temperature
ML	Maximum Likelihood
Mya	Million years ago
RAG1	Recombination Activating Protein 1

ABSTRACT

The 21st century poses one of the most crucial challenges for ecologists and conservation biologists: to predict and to mitigate future threats to biodiversity resulting from human-induced global changes. Over the last decade, researchers have argued that any elaboration of conservation strategies should also rely on the paleontological record and paleoecological archives for understanding how biota responded to past environmental changes at multiple timescales. This emerging frontier between paleoecology, conservation biology, and Earth sciences, however, is relatively recent and few studies have integrated these disciplines. Chinchilla rats, hystricognath rodents of the family Abrocomidae endemic to South America, offer a potential study model for exploring micro- and macroevolutionary responses of biota to past environmental changes at geological and millennial timescales bridging multiple research areas. Two particular attributes of interest from this group include: first, species of chinchilla rats are mostly distributed over the central Andes, an area where past geologic, climatic, and ecologic changes are well-documented. Second, species inhabiting drylands of this region create organic deposits (fossil middens or paleomiddens) which remain unchanged for millennia and have been widely employed in paleoclimatic and paleoecological studies.

The main objective of this doctoral thesis was to understand how ecological or evolutionary processes impacted chinchilla rat responses to past environmental changes in the central Andes using methods from the Evolutionary Biology and Paleoecology. Central questions to this work were: How did past geological/millennial climate change in the central Andes impact the diversity and distribution of chinchilla rats? How are these responses linked to micro- and macroevolutionary processes? Using DNA sequences from one mitochondrial and two nuclear genes, I start by first addressing the molecular systematics of Abrocomidae. Phylogenetic reconstructions performed by Maximum Likelihood and Bayesian Inference methods recovered three main clades differing markedly habitat, morphology, and

genetics. Additional molecular analyses suggest these might indeed represent different genera. Then, using multispecies coalescent methods and information from the paleontological record, a time-calibrated species phylogeny is shown. Here I estimated that all living Abrocomidae originated during the Middle and Late Miocene (13 – 7 Million years ago). Divergence of the three aforementioned clades was coeval with major Andean uplift episodes and ecological speciation seems to have promoted most diversification through adaptation to contrasting environments. No diversification was found to have occurred during the Quaternary ice ages.

By using *Abrocoma cinerea* fecal pellets obtained from modern and fossil middens collected in the central Atacama Desert, I reconstruct how this species responded to past hydroclimatic variability. Previous studies in other group of rodents have shown that fecal pellet diameters provide an estimate of body size. Owing to limitations in capturing living individuals this could not be tested in *A. cinerea* and I focus on the relation between modern pellet size and rainfall across a latitudinal gradient. The ensuing correlation enabled the reconstruction of rainfall variability in the central Atacama Desert from paleomiddens over the past 16,000 years. Comparison of these pluvial episodes to other regional and extra-regional paleoclimatic records allowed identification of inter-hemispheric forcings of rainfall variability which are crucial for projections of future water availability in this region. This study further suggests a link between phenotypic changes of body size in *A. cinerea* in response to rainfall variability, which can occur even on centennial timescales.

Conservation strategies under ongoing climate change in the 21st century can greatly improve by including a long-term retrospective standpoint. The use of information from paleoarchives, DNA sequences, or computer modeling alone, limits the identification of the range of processes by which species resisted past environmental changes. Despite difficulties in capturing living individuals, chinchilla rats provide a unique study system that facilitates the integration between Evolutionary Biology and Paleoecology across timescales. Based on their historical geography and analyses in

paleomiddens, this group of rodents responds differently to environmental change according to the nature and temporal extension of the events. Middle to late Miocene central Andean uplift would have thus generated divergence by not only explaining the current diversity of chinchilla rats but also their distribution in the biogeographic provinces where they currently occur. In contrast, late Quaternary pluvials had profound population-level effects, identified as intraspecific divergence including inferred body size changes. Limitations in live-trapping could be circumvented with longer and more intensive fieldwork or by using information from specimens housed in natural collections.

The contribution of this doctoral thesis resides in showing how an integration of these two disciplines broadens our perspective of how species respond to past environmental changes throughout their life history. It is expected that this work will encourage further research in other taxa for future conservation purposes under a similar multidisciplinary framework. The chinchilla rat studies presented here will hopefully provide a starting point for future studies, including those involving paleogenomics in *Abrocoma* fossil middens. Such studies should move beyond genetic characterization of past ecosystems and aim to understand the evolution of the genome under rapid short-term Quaternary climate oscillations.

RESUMEN

El siglo XXI trae consigo uno de los desafíos más críticos para ecólogos y biólogos de la conservación: predecir y mitigar futuras amenazas a la biodiversidad resultantes del cambio global inducido por actividades humanas. En la última década se ha sugerido que la elaboración de estrategias de conservación debería centrarse en el estudio del registro paleontológico y de paleoregistros para entender cómo la biota ha respondido a cambios ambientales del pasado que ocurrieron a diferentes escalas temporales. Sin embargo, esta frontera reciente entre paleoecología, biología de la conservación, y ciencias de la Tierra, es relativamente nueva y muy pocos estudios han integrado estas disciplinas. Las ratas chinchilla, roedores hystricognatos de la familia Abrocomidae endémicos a América del Sur, ofrecen un modelo de estudio potencial para explorar respuestas micro- y macroevolutivas de la biota a cambios ambientales pasados a escalas geológicas y mileniales cerrando la brecha entre múltiples áreas de investigación. Dos atributos de interés particular de este grupo incluyen: primero, que sus especies están distribuidas principalmente en los Andes centrales, un área donde cambios geológicos, climáticos, y ecológicos del pasado están bien documentados. Segundo, especies que habitan ambientes áridos en esta región crean depósitos orgánicos (madrigueras fósiles o paleomadrigueras) las cuales pueden permanecer inalteradas por milenios y que han sido ampliamente utilizadas en estudios paleoclimáticos y paleoecológicos.

El objetivo principal de esta tesis doctoral fue entender cómo procesos ecológicos y evolutivos influyeron en respuestas de las ratas chinchilla a cambios ambientales pasados en los Andes centrales usando métodos de la Biología Evolutiva y la Paleoecología. Las preguntas centrales en este trabajo fueron: ¿Cómo los cambios climáticos geológicos y mileniales en los Andes centrales influyeron en la diversidad y distribución de las ratas chinchilla? ¿Cómo estas respuestas se pueden asociar a procesos micro- y macroevolutivos? A partir de secuencias de ADN de un gen mitocondrial y dos genes

nucleares, primero evaluó la sistemática molecular de Abrocomidae. Reconstrucciones filogenéticas mediante métodos de Máxima Verosimilitud e Inferencia Bayesiana recuperan tres clados principales, los cuales se diferencian marcadamente en hábitat, morfología, y genética. Análisis moleculares adicionales sugieren que estos grupos podrían corresponder a diferentes géneros. Luego, utilizando métodos de coalescencia de múltiples especies e información del registro paleontológico, presento una filogenia de especies calibrada en el tiempo. Desde aquí estimo que las especies actuales de Abrocomidae se originaron durante el Mioceno medio y tardío (13 – 7 Millones de años). La divergencia de los tres clados previamente mencionados fue coetánea a la orogenia Andina y la mayor parte de la diversificación parece haber sido generada mediante especiación ecológica por adaptación a ambientes de condiciones contrastantes. Ningún episodio de diversificación ocurrió durante las edades de hielo del Cuaternario.

Mediante el uso de fecas de *Abrocoma cinerea* obtenidas desde madrigueras modernas y fósiles colectadas en el Desierto de Atacama central posteriormente presento una reconstrucción de cómo esta especie respondió a la variabilidad hidroclimática del pasado. Estudios previos en otro grupo de roedores han indicado que el diámetro de las fecas proporciona una estimación del tamaño corporal. Sin embargo, debido a limitaciones para capturar individuos vivos, esta relación no pudo ser confirmada en *A. cinerea* y por lo tanto el foco se centra en la relación entre el tamaño moderno de las fecas y la precipitación a lo largo de un gradiente latitudinal. La consiguiente correlación permitió la reconstrucción de la variabilidad de las precipitaciones en el Desierto de Atacama central en los últimos 16.000 años a partir de fecas obtenidas en madrigueras fósiles. La comparación de estos episodios pluviales a otros registros paleoclimáticos regionales y extra-regionales permitió identificar forzamientos inter-hemisféricos cruciales para proyecciones de la futura disponibilidad de agua en esta región. Este estudio además sugiere una relación entre cambios fenotípicos del tamaño corporal en *A.*

cinerea en respuesta a cambios en la precipitación, lo cuales pueden incluso ocurrir en un marco temporal de siglos.

Las estrategias de conservación bajo el cambio climático en curso en el siglo XXI, pueden ser mejoradas fuertemente al incluir un punto de vista retrospectivo de largo plazo. El uso de información de paleoregistros, secuencias de ADN, o modelamientos computarizados por sí solos limita la identificación del rango de procesos por los cuales las especies resistieron a cambios ambientales pasados. A pesar de las dificultades en capturar individuos vivos, las ratas chinchilla efectivamente proporcionan un sistema único de estudio que facilita la integración entre la Biología Evolutiva y la Paleoecología. A partir de su biogeografía histórica y de análisis en paleomadrigueros, este grupo responde de manera diferencial a cambios ambientales de acuerdo a la naturaleza y la extensión temporal de los eventos. La orogenia de los Andes centrales entre el Mioceno medio a tardío promovió divergencia la cual no sólo definió la diversidad actual de ratas chinchilla, sino que también su distribución en las provincias biogeográficas donde se encuentran actualmente. Por el contrario, las oscilaciones climáticas del Cuaternario parecen sólo haber fomentado efectos al nivel de poblaciones, identificados como divergencia intraespecífica y posiblemente por cambios en el tamaño corporal. Limitaciones en la captura de individuos pueden ser sorteadas con trabajos en terreno más largos y más intensos o mediante el uso de especímenes almacenados en colecciones naturales.

La contribución de esta tesis doctoral reside en mostrar que la integración de estas dos disciplinas amplía nuestra perspectiva sobre cómo las especies han respondido a cambios ambientales pasados a través de su historia de vida. Se espera que este trabajo motive investigación adicional en otros taxa para propósitos de conservación futura bajo un marco de trabajo multidisciplinario similar. Los estudios en ratas chinchilla aquí presentados proporcionan un punto de partida, y espero así también establecer las bases para futuros estudios, particularmente aquellos involucrando paleogenómica en madrigueras fósiles de *Abrocoma*. Estos estudios deberían ir más allá de la

caracterización genética de ecosistemas pasados y apuntar a entender la evolución del genoma bajo oscilaciones climáticas rápidas y de corto plazo del Cuaternario.

INTRODUCTION

The observed diversity and geographical distribution of species is the result of historical and contemporary processes. Plate tectonics and ecological competition are commonly described as factors that explain modern-day biogeography of species (Lomolino et al., 2010). Changes to the earth system caused by anthropogenic activities since the middle 19th century, however, are projected to severely affect global biodiversity and species distribution towards the end of this century (Dawson et al., 2011). Major drivers of change induced by human activities include land-use, nitrogen deposition, biotic exchange, and elevated concentrations of atmospheric carbon dioxide (Sala et al., 2000). Climate change indeed has been the most widely discussed anthropogenic driver, as projected magnitudes and rates of future change for the next century are unparalleled in millions of years (Foster et al., 2017; Steffen et al., 2018). How individual species and entire ecosystems will respond to future climate change is then a central question for conservation biologists seeking to safeguard the future of biodiversity (Sarkar et al., 2006; Dawson et al., 2011). Elaboration of mitigation strategies has thus centered on exploring biota responses to past environmental changes which offer a vast set of long-term unplanned natural experiments to test ecological and evolutionary theories (Fordham et al., 2016; Barnosky et al., 2017).

The study of species responses to past environmental change has been traditionally assessed by changes in the fossil record. Examples in the literature are varied and for multiple taxa, including shifts in distribution (or migrations) and evolutionary change identified either as lineage diversification or as *in situ* morphological adaptations (McFadden et al., 2005; Renaud et al., 2005; Jackson and Erwin, 2006; Taylor et al., 2009). Because these changes also remain imprinted in species' DNA in modern-day populations, additional information is provided in molecular phylogenetic reconstructions (Ridley, 2004; Futuyma, 2013). In phylogenetics, fossils of known age can be employed to estimate the time at which species diverged (Rutschmann, 2005; Drummond et al., 2006). In turn, chronological

congruence between the timing of species diversification and past environmental change can then be used to identify the drivers behind the evolutionary and biogeographic history of species (Lomolino et al., 2010). Additionally, biota responses to recent past climate change have been extensively inferred through the study of the actual geographic distribution of phylogenetic lineages, or phylogeography (Avice, 2000; Hickerson et al., 2010). Extinction, or the failure of taxa to adapt to or cope with environmental changes, has also been identified both in the fossil record and in molecular studies and linked to abrupt environmental change (Jablonski, 1994; Nee et al., 1994; McElwain et al., 2007; Purvis, 2008).

Over the last decades the growing availability of precisely-dated geological records has increased the spatio-temporal resolution of past environmental changes. Integrating the evolutionary history of biota into these geohistorical records represents a new frontier in conservation ecology aiming to identify not only the drivers but also the mechanisms and the rates at which species responded to past environmental change at multiple timescales (Nogués-Bravo et al., 2018; Fordham et al., 2020).

In South America, the evolution of terrestrial mammals represents an interesting study case to examine micro- and macroevolutionary responses of species to geologic and climatic changes occurring at long ($>10^6$ years) and short ($10^2 - 10^5$ years) temporal scales throughout the Cenozoic (the last 65 million years). A multidisciplinary approach could add novel information to existing studies on the impact of past environmental changes based on the paleontological record (Pascual, 2006) or molecular phylogenetics (Delsuc et al., 2004; Goin et al., 2010, 2012; Upham and Patterson, 2015; Gibb et al., 2016). Such information would represent a first step towards identifying current threats to biodiversity which can be applied to the elaboration of future conservation measures (Barnosky et al., 2017; Nogués-Bravo et al., 2018; Fordham et al., 2016, 2020).

Evolution of land mammals in South America

The evolution of terrestrial mammals in South America during the Cenozoic largely occurred in isolation to other landmasses, punctuated by rare episodes of waif dispersal and faunal interchange (Simpson, 1980; Croft, 2011). Living representatives of endemic mammalian lineages are only but a glimpse of the much higher taxonomic and ecological diversity that inhabited the continent throughout this era (Pascual, 2006; Goin et al., 2016). Along long-lasting endemic lineages such as xenarthrans (anteaters, sloths and armadillos) and metatherians, further expansion of past mammal diversity occurred during two different waves of immigration. The first episode occurred during the middle Eocene (~44 Mya, or Million years ago), when hystricognath rodents and anthropoid primates arrived from Africa via waif dispersal (Antoine et al., 2012; Boivin et al., 2017; Bond et al., 2015; Silvestro et al., 2019; Seiffert et al., 2020). Later, the Great American Biotic Interchange (or GABI; Marshall, 1979, 1982, Simpson, 1980), following the formation of the Isthmus of Panama, facilitated the exchange of multiple lineages between North and South America (Webb, 2006; Woodburne et al., 2010). The chronology of this event however is an ongoing debate traditionally timed at the late Pliocene around 2.8 Mya (O’Dea et al., 2016), although proposals of earlier dates also exist (Pascual, 2006; Bacon et al., 2015; Montes et al., 2015).

Environmental changes during the Cenozoic started with a protracted global transition from a greenhouse to a coolhouse between the Early Eocene (~56 Mya) to the Eocene - Oligocene boundary (~34 Mya; Zachos et al., 2008; Westerhold et al., 2020). Mammalian diversity developed gradually throughout this period (Woodburne et al., 2014), then accelerated diversification in caviomorphs and major biotic turnovers in metatherians occurred during abrupt cooling around 34 Mya (Upham and Patterson, 2015; Goin et al., 2016; Abello et al., 2018). Major phases of Andean orogeny were also chronologically congruent with abrupt diversification in land mammals (Marshall and Sempéré, 1993). Basal divergence in xenarthrans, for instance, was coeval to initial Andean orogeny during the late

Eocene (~40 Mya) and then during intense tectonic activity in the Miocene (23 - 6 Mya; Delsuc et al., 2004; Gibb et al., 2016). Large diversification within caviomorph superfamilies also started in this epoch ~15 Mya (Upham and Patterson, 2015). On the contrary, no important diversification occurred during the short-term Quaternary climate oscillations (Barnosky et al., 2005). Instead, phylogeographic patterns of taxa from varied environments indicate important population-level changes (Da Silva and Patton, 1998; Palma et al., 2005; Marin et al., 2008; Napolitano et al., 2014). Megafauna extinctions which are usually discussed under a context of Late Quaternary (~20 - 11 ka BP) environmental change were likely further exacerbated by the arrival of humans (Alroy, 2001; Barnosky and Lindsey, 2010; Lorenzen et al., 2011).

Andean uplift, because of its crucial impact on shaping current biodiversity patterns of terrestrial biota overall, remains the most important biogeographical event in South America during the Cenozoic (Antonelli et al., 2009; Hoorn et al., 2010). Evolution of land mammals in parallel to Andean uplift has been thus extensively described, particularly over its northern and southern ranges (Ortiz-Jaureguizar and Cladera, 2006; Pascual, 2006; Barreda and Palazessi, 2007). In the central Andes, however, the evolutionary history of endemic lineages throughout the Cenozoic remains largely unexplored. Studies on small mammals, the most abundant and diverse group comprising rodents, bats, and marsupials, are strikingly rare (Ramirez et al., 2007; Patton et al., 2015). Topographic uplift of this region clearly provided an arena for the diversification and dispersal of biota through vicariant events and the formation of new montane environments and corridors (Graham et al., 2009; Patterson et al., 2015). The chronology of tectonic events therefore is crucial for understanding the historical biogeography and the timing and rates of evolution in endemic biota at long temporal scales (Patterson et al., 2015). The number of studies in paleoclimate research in this region has grown over the last decades due to its links to continental atmospheric circulation (Garreaud, 2003; Vuille and Keimig,

2004). Such interest has provided a series of well-detailed records of century to millennial climate change key to explore biota responses over short-term periods.

Biogeography and past environmental change in the central Andes

The central Andes between ~12 - 24 °S is characterized by the Altiplano and the two parallel mountain ranges enclosing it, the eastern and western cordilleras. This mountain system reaches an average elevation of ~4,000 masl acting as a topographic barrier that blocks the transport of moisture from the Amazon basin (Houston and Hartley, 2003; Garreaud, 2009). Rainfall occurs primarily during the southern hemisphere summer linked to increased activity of the South American Summer Monsoon (SASM; Zhou and Lau, 1998), with an average annual precipitation of 600 - 1000 mm falling along the eastern cordillera, 50 - 400 mm along the western cordillera, and less than 50 mm along the Pacific coast (Vuille and Keimig, 2004). This topographic and climatic heterogeneity hosts multiple biogeographic provinces, environments of contrasting conditions home to endemic plant and animal taxa (Morrone, 2014). These include montane rainforests (or yungas) over the eastern cordillera, the puna in the Altiplano, and the Atacama Desert along the western Andean flank. Endemic mammalian taxa widespread prior to topographic uplift likely became progressively isolated in these environments as this mountain system developed. Estimates of diversification times in ancient endemic groups such as caviomorph rodents or marsupials should be therefore congruent to the chronology of central Andean uplift (Delsuc et al., 2004). The timing at which this tectonic process occurred however has been a matter of intense debate due to confronting geological evidence.

Two main scenarios describe central Andean uplift with alternative times and rates at which uplift occurred. Ancient and constant uplift has been proposed to have started since the Eocene-Paleocene (40 - 60 Mya; McQuarrie, 2002; Barnes and Ehlers, 2009; Lamb, 2016) or at least since the Oligocene (>25 Mya; Barke and Lamb, 2006; Ehlers and Poulsen, 2009). Alternatively, recent and

abrupt uplift is suggested to have occurred between the early and late Miocene (17 - 6 Mya) (Garzione et al., 2008, 2014; Perkins et al., 2016; Sundell et al., 2019). The evolutionary history of biota endemic to this region could provide an independent chronology to constrain these alternative geological hypotheses based on estimates of diversification times over multiple taxonomic groups (Baker et al., 2014). Estimates of diversification times in birds (Chaves et al., 2011; Hazzi et al., 2018) and nematodes (Picard et al., 2008) from the northern tropical Andes for instance, have provided strong support to previous proposals on the timing of mountain uplift for this region (Gregory-Wodzicki, 2000). In the central Andes, similar studies exist in plants (Luebert and Weigend, 2014; Böhnert et al., 2018) and arthropods (Cecarelli et al., 2016; Zuñiga-Reinoso and Pradel, 2019) although no studies have been performed in mammals. Only after comparing the timescale for the diversification of several taxa then the impact of central Andean orogeny on the evolutionary history of endemic biota could be assessed.

Interest in Quaternary paleoclimate (the last 2.3 Mya) of the central Andes has grown in the last decades because of its links with continental and inter-hemispheric atmospheric circulation (Garreaud, 2009; Vuille and Keimig, 2004). Multiple records are now available documenting century to millennial expansion and retreat of ice glaciers over the eastern cordillera and northern Altiplano (Seltzer, 1992; Thompson et al., 1998; Abbott et al., 2003) and cyclic changes in lake levels over the central and southern Altiplano (Baker et al., 2001; Bobst et al., 2001; Fritz et al., 2007; Quade et al., 2008; Placzek et al., 2013). Along these short-term episodes of environmental change, shifts in the distribution of birds (Álvarez-Varas et al., 2015), sigmodontine mice (Palma et al., 2005), and large mammals (Marin et al., 2008) were all recovered in phylogeographic analyses. Despite migrations and genetic structuring it has been stated that Quaternary climate oscillations did not result in new species of mammals but only in population-level changes (Barnosky, 2005). Testing this information is of crucial importance as the diversity and distribution of multiple mammalian lineages within are expected to be severely

threatened as multiple regional climate simulations show a reduction in summer rainfall by 30% over the coming century (Urrutia and Vuille, 2009; Minvielle and Garreaud, 2011; Thibeault et al., 2012; Neukom et al., 2015).

Chinchilla rats as a study model bridging evolutionary and paleoclimatic research

Chinchilla rats are a group of caviomorph rodents ascribed to the family Abrocomidae (Waterhouse, 1837) with two living genera *Abrocoma* (Waterhouse, 1837) and *Cuscomys* (Emmons, 1999). Species of this family are endemic to biogeographic provinces of the central Andes, found in the yungas of Peru and Bolivia and dry environments from southern Peru to northern Chile and Argentina (Patton et al., 2015). *Abrocoma bennettii* appears to be the only allopatric species, currently restricted to low-elevation semi-arid and mediterranean environments in central Chile (Mann, 1978; Patton et al., 2015). Classification of species has relied on cranial, dental and external morphology which differ remarkably according to the environment they inhabit (Glanz and Anderson, 1990; Emmons, 1999; Braun and Mares, 2002). Uncertainty exists, however, on the status of six closely-related species from arid environments (the *Abrocoma cinerea* species complex; Ellerman, 1940; Braun and Mares, 2002; Teta, 2020) and the genus at which *A. boliviensis* should be assigned (Verzi and Quintana, 2005). The paleontological record of Abrocomidae is represented by the extinct genus *Protabrocoma* from late Miocene (~9 – 6.8 Mya) formations in central- and north-western Argentina (Montalvo et al., 2008; Esteban et al., 2014; Zimics et al., 2018; Prevosti et al., 2019) and southern Bolivia (Villarroel and Marshall, 1989; Marshall and Sempéré, 1991). Overall, these ecological, morphological and paleontological precedents strongly suggest a link between central Andean uplift and the evolutionary history of abrocomids.

Besides their original descriptions and type localities, not much is known of abrocomids except for few studies on the ecology of some *Abrocoma* species (Braun and Mares, 1996, 2002; Cortés et al.,

2002; Taraborelli et al., 2011, 2015). One particularly well-known feature however, is the ability to build solid conglomerates of animal and plant debris that last for millennia in arid and semi-arid environments of South America (*i.e.*, fossil middens or paleomiddens; Betancourt and Saavedra, 2002). In Chile, paleomiddens of *A. cinerea* have been extensively employed in reconstructions of the last 50,000 years of climate change in the Atacama Desert (Betancourt et al., 2000; Latorre et al., 2002, 2003, 2006; Maldonado et al., 2005; Díaz et al., 2012; de Porras et al., 2017). These records have provided valuable information on the hydroclimatic variability of this region which is strongly consistent with other paleoclimatic records (Quade et al., 2008; Placzek et al., 2009, 2013). Recent advances in the study of fossil DNA (*i.e.*, paleogenetics and paleogenomics) moreover, have unveiled a new frontier with potential to directly assess the impact of past environmental changes on the genome of these species (Díaz et al., 2019; Wood et al., 2019; Moore et al., 2020). The study of the evolutionary history of this group therefore, offers a testable source of information on which elaboration of future conservation strategies could be based.

As an initial approach to identifying possible outcomes from current and future climate change on small mammals, this doctoral thesis explores biotic responses of chinchilla rats to past environmental changes occurring at different timescales in South America. Particular emphasis is given to abrocomids inhabiting biogeographic provinces in the central Andes where the Andean orogeny and Quaternary climate oscillations (long- and short-term environmental changes, respectively) have been well documented. Central questions to this study were: How did past geological/millennial climate change in the central Andes impact the diversity and distribution of chinchilla rats? How are these responses linked to micro- and macroevolutionary processes? It is hypothesized here that the currently observed diversity and distribution of chinchilla rats was driven by a long-term Andean orogeny, whereas only microevolutionary (*i.e.* population-level) change occurred during short-term Quaternary climate oscillations. Testing this hypothesis was performed from the perspective of two related yet

rarely interacting disciplines in the study of natural history, namely Evolutionary Biology and Paleoclimatology.

In chapter one, “*Origin, diversity and historical biogeography of chinchilla rats (Hystriognathi, Abrocomidae) from multilocus phylogeny*”, a molecular phylogenetic reconstruction of species in Abrocomidae is presented. The systematics of this family using DNA sequence data are thus shown for the first time. Additionally, using morphological information and stratigraphic ages from the paleontological record, a time-calibrated phylogenetic tree is presented. Questions addressed in this chapter included: ‘When did major episodes of diversification in chinchilla rats occurred?’ ‘Was Andean orogeny the main driver of diversification as observed in other endemic taxa to this region?’ ‘Did climate change play a role in the diversification of this group?’ Results of this chapter are first contrasted to previous species classification schemes based on external, cranial and dental morphology. Although agreement exists on the monophyletic status of the family, disagreement exists on the classification scheme for genera as suggested by marked differences in morphology, habitat use, and genetics. The Abrocomidae likely originated in the middle Miocene (~13 Mya) with subsequent diversification during the late Miocene (9 – 7 Mya). The chronology of lineage diversification is largely coeval to Andean orogeny and the role of mountain formation as a vicariant barrier compared to formation of new high-elevation environments as drivers of diversification through ecological speciation is discussed. No additional diversification is observed since the late Miocene and Quaternary climate oscillations appear to have driven intraspecific diversification likely through population-level changes.

In chapter two, “*High- and low-latitude forcings drive Atacama Desert rainfall variations over the past 16,000 years*”, biotic responses of *Abrocoma cinerea* to decade-to-century climate change were estimated from the study of paleomiddens collected in the central Atacama Desert. Similar previous studies in arid western North America have shown that variations in fecal pellet size are

related to body size changes in rodents which in turn are related to temperature changes (e.g., Bergman's Rule). Using a calibration set of modern middens collected across a latitudinal gradient we show that variation in *A. cinerea* pellet sizes are better explained by changes in precipitation. This link is then applied to measurements of pellets obtained from paleomiddens to reveal rainfall episodes over the past 16 ka BP (thousand years before present). Comparison to regional and continental paleoclimatic records shows that rainfall variability was largely driven by North-Atlantic forcing between 15.9 – 7.6 ka BP and then by a low-latitude forcing (ENSO regime) since the middle Holocene. These results provide important constraints for projections of hydroclimatic variability under future climate change. Additionally, if relation between pellet size and body size in *A. cinerea* is confirmed, new precedents on the debate for identifying environmental factors (precipitation or temperature) that control body size are provided. Moreover, it shows that morphological changes can occur within a century which is particularly relevant under scenarios for future climate change in the central Andes.

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**CHAPTER 1: ORIGIN, DIVERSITY AND HISTORICAL BIOGEOGRAPHY OF
CHINCHILLA RATS (HYSTRICOGNATHI, ABROCOMIDAE) FROM MULTILOCUS
PHYLOGENY.**

ORIGIN, DIVERSITY AND HISTORICAL BIOGEOGRAPHY OF CHINCHILLA RATS (HYSTRICOGNATHI, ABROCOMIDAE) FROM MULTILOCUS PHYLOGENY.

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ABSTRACT

Chinchilla rats (Abrocomidae) are hystricognath rodents endemic to South America found over the central Andes and central Chile including eight and two species in genera *Abrocoma* and *Cuscomys*, respectively. Systematics of Abrocomidae relying only on morphology has a long and varied history, particularly evident in the classification of six *Abrocoma* species informally called the *A. cinerea* species complex. Owing to difficulties in access and live-trapping individuals in Andean regions the systematics and evolutionary history of this group using phylogenetic methods has remained largely understudied. Here we analyze DNA sequence data from one mitochondrial and two nuclear loci sampled in specimens housed in natural history collections, covering five *Abrocoma* species along with

published sequences of *C. ashaninka*. Gene and species phylogenetic trees were recovered using maximum-likelihood and Bayesian inference approaches. We additionally performed species delimitation analyses for the *A. cinerea* species complex using single- and multi-locus approaches. Estimates of divergence times were obtained using a total evidence tip-dating approach combining a Fossilized Birth-Death Model process with multispecies coalescent inference. We recovered Abrocomidae as a monophyletic unit comprising three main clades. Marked differences in habitat, morphology, and probably also in genetics suggest these groups could represent different genera. Species delimitation analyses in the *A. cinerea* species complex recovered two main lineages although incomplete taxon sampling warns careful interpretation. We estimate that crown abrocomids originated during the middle Miocene (~12.85 Mya) likely around present-day central Chile and western Argentina. Andean orogeny was the most important driver of diversification through allopatric speciation and by formation of new environments during the late Miocene. In the central Andes, patterns of evolutionary history in endemic taxa argue for a recent and rapid topographic uplift although additional data is required for thoroughly testing this scenario.

INTRODUCTION

The Abrocomidae (Waterhouse, 1837) is a family of Hystricognathi rodents endemic to South America commonly known as chinchilla rats due to the resemblance of their fur to that of true chinchillas. Abrocomids are part of the superfamily Octodontoidea, the most taxonomically diverse group of hystricognaths that include degus (Octodontidae), tuco-tucos (Ctenomyidae) and spiny rats (Echimyidae) among other species (Patton et al., 2015; Upham and Patterson, 2015). Compared to these families however, little is known about the ecology and the evolutionary history of abrocomids. Most species of chinchilla rats are distributed across high-elevation environments in the central Andes from central Peru to northern Chile and northwestern Argentina between 15 - 25 °S (Patton et al., 2015;

Figure 1A). The intricate access to this biome and a marked proneness of chinchilla rats to be extremely difficult to observe and capture in the field, has hindered a more extensive sampling of members of this group (see for instance *Methods and Materials* in Braun and Mares, 1996). This drawback however can be somewhat alleviated through accessing specimens housed in museums or natural history collections thus providing an alternative to complement fieldwork efforts (Wandeler et al., 2007; Ward, 2012; Schindel and Cook, 2018).

Living Abrocomidae are recognized as a monophyletic group comprising 10 - 11 species comprising only two genera, *Abrocoma* and *Cuscomys* (Patton et al., 2015; Upham and Patterson, 2015). The genus *Cuscomys* consists of species *C. ashaninka* and *C. oblativa* which were described in a single locality in the yungas (mountain rainforests) of central eastern Peru (Emmons, 1999; Figure 1A). Owing to its extreme rarity, *C. oblativus* was indeed considered extinct until camera traps placed in the vicinity of Machu Picchu recently confirmed its presence (Ochoa et al., 2020). Species of *Abrocoma* occur in varied ecosystems along the central Andes reaching central Chile and Argentina, although as for *Cuscomys* most species are ascribed to point localities (Braun and Mares, 2002; Patton et al., 2015; Figure 1B). Six species are found in arid environments from the Altiplano, Atacama and Monte Desert, including *A. cinerea*, *A. budini*, *A. famatina*, *A. schistacea*, *A. vaccarum*, *A. uspallata* (Figure 1B). A single species inhabits the yungas in eastern Bolivia (*A. boliviensis*) whereas one highly parapatric species (*A. bennettii*) inhabits the semi-arid to mediterranean environments of central Chile below 2000 m (Figure 1B). This disjunct distribution between *A. bennettii* and the remainder abrocomids is of particular biogeographic interest, suggesting diversification processes were strongly linked to environmental changes driven by Andean uplift.

The natural history of abrocomids has remained largely unexplored and ecological studies have been limited to few *Abrocoma* species (Braun and Mares, 1996, 2002; Cortés et al., 2002; Taraborelli et al., 2011, 2015). The molecular systematics of this family has not yet been described and only one or

two species have been included in studies of molecular systematics addressing taxonomic relationships above the genus level (Honeycutt et al., 2003; Spotorno et al., 2004; Opazo et al., 2005; Upham and Patterson, 2015; Álvarez et al., 2017). Species classification in abrocomids has relied only on external and cranial or dental morphological traits which differ markedly according to the environments they inhabit (Glanz and Anderson, 1990; Emmons, 1999; Braun and Mares, 2002; Teta, 2020; Figure 1C). Among the six arid-adapted species however these characters have led to large uncertainty on their classification and their synonymy with *A. cinerea* into the “*A. cinerea* species complex” has been suggested (Ellerman, 1940). Subsequent studies, in turn, then dissolved this group into either separate individual species (Braun and Mares, 2002) or into two main morphotypes, one comprising *A. cinerea* and the other consisting of the remaining species in western Argentina (Teta, 2020).

Inferences about the evolutionary history of abrocomids are scarce and have only been derived from their paleontological record. This includes of the extinct abrocomid genus *Protabrocoma* (Rovereto, 1914; Kraglievich, 1927) whose earliest records date from late Miocene strata of southern Bolivia (Villarroel and Marshall, 1989; Marshall and Sempéré, 1991) and northwestern Argentina (Montalvo et al., 2008; Esteban et al., 2014; Zimics et al., 2018; Prevosti et al., 2019). Previous studies in plant and animal taxa endemic to the central Andes with distribution similar to that observed in abrocomids have explored the role past environmental changes exerted on shaping their current diversity and distribution (Luebert and Wen, 2008; Heibl and Renner, 2012; Cecarelli et al., 2016; Böhnert et al., 2018; Esquerré et al., 2019). These studies concluded that both the Andean uplift and the onset of hyperaridity in the Atacama Desert were strong vicariant barriers promoting east-west and north-south isolation, respectively, during the middle to late Miocene between 20 – 7 Mya (Million years ago). It is expected therefore that the complex topographic and climatic history of this region could have also influenced the origin, diversification and current distribution patterns of abrocomids and other endemic species (Antonelli et al., 2009; Graham, 2009; Hoorn et al., 2010).

In this work we present the first species-level molecular phylogeny of Abrocomidae using a single mitochondrial and two nuclear genes. We aimed to examine the phylogenetic relationships and to estimate divergence times between abrocomids to infer their historical biogeography. Because abrocomids are notoriously difficult to trap in the field, we complemented available fresh tissues with skin samples from vouchered specimens housed at natural history collections in museums and universities. We compared our results to previous classifications based on morphology with a special emphasis on the relationships recovered for species in the *Abrocoma cinerea* species complex. Estimates of divergence times within the family were inferred from tip-dating analyses using stratigraphic age information of stem fossils recently described for Abrocomidae (Verzi et al., 2016; Arnal et al., 2017). We then compare our divergence date estimates with those in other taxa endemic to the central Andes attempting to provide chronological constraints for past environmental changes relevant for the evolution of terrestrial biota in this region.

MATERIALS AND METHODS

Sample collection and DNA extraction

We analyzed 20 individuals comprising five out of the eight *Abrocoma* species currently recognized (Patton et al., 2015). Samples were obtained from natural history collections of museums and universities (Figure 2 and Table 1). Tissues sampled consisted of fresh liver preserved at -80 °C and/or ethanol at room temperature, as well as dry skin tissues from museum voucher specimens (Table 1). To be consistent with type localities and current classification of abrocomid species (Figure 1B), specimens captured during the 1940's in La Rioja and San Juan provinces (northwestern Argentina) were assumed to be species of *A. famatina* and *A. schistacea*, respectively (Braun and Mares, 2002).

DNA extraction of tissues was performed at the Laboratorio de Biología Evolutiva (LBE), Department of Ecology at the Pontificia Universidad Católica de Chile using a standard phenol-chloroform protocol (Sambrook et al., 1989), then stored at -20 °C. Because DNA from museum specimens is known to be fragmented and at low concentrations (Wandeler et al., 2007; Hernández-Triana et al., 2014; Mitchell, 2015), extractions and amplifications were performed in separated clean rooms to avoid potential external contamination. DNA extraction of skin tissues was performed under a laminar flow cabinet following bleach rinsing (10% bleach) of the cabinet bench and pipettes and UV light sterilization of pipettes and pipette tips (Cooper and Poinar, 2000; Beja-Pereira et al., 2009). DNA extraction of fresh tissues was conducted on a separated bench outside the laminar flow cabinet and at different days from procedures involving museum samples. Negative controls were performed during each batch of extractions. DNA quality (the degree of DNA fragmentation) was checked visually on 1% agarose electrophoresis gels stained with SYBR safe (Invitrogen, Thermo Fisher) using four microliters of DNA extraction. Nucleic acid concentrations were quantified using a NanoDrop spectrophotometer (Thermo Fisher Scientific).

DNA Amplification, sequencing, and alignment

Sequences of one mitochondrial (Cytochrome b, *cytb*) and two unlinked nuclear loci (the exon 10 of the Growth Hormone Receptor, *GHR*, and; the Recombination Activating Protein 1, *RAG1*) were obtained from each individual. These genes were selected based on their demonstrated use in previous studies of molecular systematics in caviomorphs at the species level (Rowe and Honeycutt, 2002; Honeycutt et al., 2003; Galewski et al., 2005; Opazo et al., 2005; Patterson and Velazco, 2008; Rowe et al., 2010; Upham and Patterson, 2012, 2015; Upham et al., 2013). The amplification scheme aimed to amplify small overlapping fragments (140 – 330 bp long) of each marker in museum samples, and the entire sequences in fresh tissues (Figure 3; Mitchell, 2015). Primer sequences were either obtained

from the literature or custom-designed based on nucleotide sequence information from the first few fresh tissues sequenced (Table 2).

PCR reactions totaled 50 uL containing 2.0 uL of DNA template, 5.0 uL 10x reaction buffer, 1.0 uL of 10 mM premixed deoxynucleotide triphosphates (dNTPs; 200 uM each nucleotide in final reaction), 1.5 uL of 25 mM MgCl₂, 38.3 uL of double-distilled H₂O (dH₂O), 0.2 uL of 5 U/uL Invitrogen™ Platinum Taq™ DNA Polymerase (Thermo Fisher Scientific), and 1.0 uL of each 10 uM primer (Table 3). Thermal cycler conditions followed guidelines recommended by Invitrogen for 50-uL reactions using Platinum Taq™ (Pub. No. MAN0000925 Rev. B.0) including an extra final extension step of 5 minutes at 72°C before the final step. PCR products were then purified and sequenced in Macrogen (Seoul, South Korea; <http://www.macrogen.com>) or MCLAB (San Francisco, CA, US; <http://www.mclab.com>). Resulting sequences were edited and aligned using the ClustalW algorithm with default settings in Geneious software (v11.1.5; <http://www.geneious.com>).

Phylogenetic Analyses

Phylogenetic relationships between species of Abrocomidae were established using character-based methods of Maximum Likelihood (ML) and Bayesian Inference (BI). Although I also performed Maximum Parsimony analysis (not shown), this phylogenetic approach did not recover enough resolution on the phylogenetic trees, mainly due to the limited amount of parsimony informative sites, the limited amount of samples per species, and the low number of species that compose Abrocomidae. For these major reasons, phylogenetic analyses favored the use of the above probabilistic calculations and exploration of the tree space under Maximum Likelihood and Bayesian analyses which also were less computationally demanding (Yang and Rannala, 2012). Prior to the analysis, we included the only available sequences of the genus *Cuscomys* in Genbank for the species *C. ashaninka* (Table 4). Outgroup selection was based on information from previous studies of molecular systematics in

caviomorph families which recovered Octodontidae and Chinchilloidea as the closest family and superfamily, respectively, to Abrocomidae (Upham and Patterson, 2012, 2015; Álvarez et al., 2017). Within these groups nucleotide sequences available in Genbank from *Octodontomys gliroides* (Octodontidae) and *Chinchilla lanigera* (Chinchilloidea), the closest species to Abrocomidae, were thus included as outgroup taxa (Table 4). Selection of the most appropriate nucleotide substitution model for each gene alignment was performed using jModelTest (v2.1.10; Darriba et al., 2012; Guindon and Gascuel, 2003) under the Bayesian Information Criterion (BIC; Schwarz, 1978). This criterion has been reported to provide more accurate estimates of branch lengths, which are particularly relevant for divergence time estimations (Minin et al., 2003; Abdo et al., 2005). Model selection under this criterion suggested the use of TIM2+I+G for *cytb*, and the K80+I (Kimura, 1980) for *GHR* and *RAG1*, respectively. Phylogenetic analyses for both, ML and BI were performed for the individual gene alignment and the combined dataset using a gene partitioning scheme where parameters for each nucleotide substitution model were estimated independently.

Maximum Likelihood (ML)

Phylogenetic inference under a ML approach was performed using RAxML-NG (Kozlov et al., 2019) using the “all-in-one” mode with the ‘*--all*’ command including some minor modifications to the default options. To explore the tree space more thoroughly, and due to the reduced number of sequences, we performed 2000 starting tree searches with 1000 random and 1000 parsimony-based trees. To check whether the analyses converged to a local optimum with low likelihood, the number of unique topologies for each run was determined using the Robinson-Foulds distance with the ‘*--rfdist*’ command. By default RAxML-NG employs the MRE-based bootstrapping test to automatically determine the sufficient number of bootstrap replicates (Pattengale et al., 2010). A cutoff value based on the weighted Robinson-Foulds distance is estimated every 50 bootstrap inferences, and once this

value drops below 0.03 (*i.e.* average distances below 3%) the analysis stops. When this cutoff value was not reached additional 1000 bootstrap replicates were conducted and then convergence was assessed using the ‘*--bsconverge*’ command. Branch support was mapped onto the best-scoring ML tree and then visualized in Figtree (v.1.4.4; Rambaut, 2017).

Bayesian Inference (BI)

Bayesian analyses of individual and combined gene alignments were conducted in MrBayes v.3.2.6 (Ronquist et al., 2012) with four independent runs of the MCMC (Monte Carlo Markov Chain) for 10 million generations sampled every 1000 generations. For the combined dataset we unlinked partition parameters, so they were estimated independently for each gene partition, and rates were set as variable across loci allowing partitions to evolve under different rates. Assessment of convergence was first performed visually in Tracer v.1.7.1 (Rambaut et al., 2018) by inspecting values of Effective Sampling Size (ESS), plots of marginal distributions, and trace mixing behavior of the estimated parameters. Tree topology convergence was diagnosed using RWTY (Warren et al., 2017) by inspecting density distributions and treespace plots of the independent runs. The consensus tree obtained was then visualized in FigTree (v.1.4.4; Rambaut, 2017) after discarding the initial 25% of the trees as burn-in.

Species delimitation analyses

Testing of species delimitation for morphospecies comprising the *A. cinerea* species complex was conducted through analyses of molecular delimitation of species using two different approaches. First, we performed single-locus species delimitation using two different tree-based likelihood models: the Generalized Mixed Yule Coalescent (GMYC; Pons et al, 2006; Fujisawa and Barraclough, 2013)

and the Bayesian implementation of Poisson tree processes (bPTP; Zhang et al., 2013). Both analyses were performed submitting phylogenetic trees recovered using *cytb* sequences in the Exelisis Lab's web server (GMYC – <https://species.h-its.org/gmyc/>; bPTP – <https://species.h-its.org/ptp/>). Input topologies contained only a singleton sample, *C. ashaninka*. For GMYC, the ultrametric tree obtained in BEAST2 (see below) was employed for single and multiple threshold analyses, checking the significance of the delimitation model with respect to the null hypothesis of a single species. For bPTP, delimitation search using a non-dated tree obtained in RAxML-NG was performed for 500,000 Markov Chain Monte Carlo (MCMC) generations, with thinning set to 100 and burn-in of initial samples to 0.25 (25%). The convergence of bPTP was visually checked in the trace plot. Maximum likelihood and Bayesian solutions for bPTP delimitation were considered.

Second, we performed multilocus species delimitation using the Bayesian Phylogenetics and Phylogeography software (BPP v. 4.1.3; Yang, 2015; Flouri et al., 2018). BPP uses a Bayesian modeling approach to estimate posterior probabilities of species assignments using multi-locus data under the Multispecies Coalescent (Rannala and Yang, 2003). The A10 analysis (species delimitation using a fixed guide tree) was performed using relationships derived from the species tree obtained in BEAST2 (see below) as a guide tree. We used a diffuse prior of $\alpha = 3$ for both θ and τ priors, and $\beta = 0.01$ for both nucleotide diversity (for θ) and node height (for τ). To explore the sensitivity of the BPP analysis to different prior settings, we tested different prior sets by setting $\alpha = 21$ (a suggested informative prior) and by varying the β parameter by one order of magnitude. The MCMC run was set to 100,000 samples with burn-in of 8,000 samples and sampling frequency equal to 2. Convergence was assessed by comparing the consistency of posterior distributions in independent runs using the two alternative species delimitation algorithms for each prior set (Yang, 2015; Flouri et al., 2018).

Time estimates of diversification

Divergence times were inferred using StarBEAST2 (v.2.6.2; Ogilvie et al., 2017), a Bayesian implementation of the multispecies coalescent (MSC) that jointly infers gene and species trees from multiple sequence alignments and is available in BEAST2 (Bouckaert et al., 2019). The latest version of StarBEAST2 includes the ability to combine tip-dating using the Fossilized Birth-Death (FBD) process for obtaining divergence time estimations (Heled and Bouckaert, 2013; Heath et al., 2014). This integrative FBD-MSC approach provides a model for the distribution of speciation times, tree topology, and distribution of lineage samples before the present by integrating fossil occurrence times to impose a time structure on the trees. Calibration information for the FBD process is based on the occurrence times of eight stem fossils of Abrocomidae (Arnal and Vucetich, 2015; Verzi et al., 2016; Arnal et al., 2017; Table 5).

Tip-dating analyses using only information of occurrence times was performed by creating individual gene alignments including only Abrocomidae species and stem fossil species whose sequences were made up entirely of missing data. All partitions were unlinked and therefore substitution site parameters and clock rates were estimated independently for each gene alignment. Because currently available information to estimate population sizes is insufficient and estimates obtained from the runs could be unrealistic, this option was left as default and not considered in the results. Preliminary runs using an uncorrelated lognormal relaxed-clock approach resulted in very low estimates of among-branch rate variation (standard deviation ≈ 0.2), suggesting use of a strict clock instead is appropriate.

Prior distributions on parameters of substitution models were all kept as default, whereas clock rate distribution priors were drawn from a lognormal distribution with mean (m) and standard deviation (sd) values approximating previous estimations for nuclear (m=0.001; sd=0.1) and mitochondrial (m=0.01; sd=0.1) loci (Hugall et al., 2007). Time estimates for the origin of Abrocomidae were

constrained by proposed times for the initial diversification of Octodontoidea (32 Mya; Uphman and Patterson, 2015) and occurrence times of the oldest Abrocomidae stem fossil (29 Mya; Table 5). The proportion of sampled extant species included in this analysis was set to 0.8, based on the number of extant abrocomids (Emmons, 1999; Braun and Mares, 2002). Because diversification rate is generally low (few extant species and many fossils), we set an exponential distribution prior with $m = 1.0$, adding the highest probability near zero. Beta prior distributions were employed in the proportion of sampled fossils setting α and β to 2.0 ($m=0.5$) thus allocating low probabilities to extreme values (i.e., close to 0 or 1), while turnover rate was estimated using the default uniform prior distribution. To further constrain the true age of the fossil specimens, we also sampled the age of each fossil using a uniform distribution prior with lower and upper limits defined by their occurrence times (Table 5). Topological constraints were also included by specifying two monophyletic taxon sets corresponding to all members of Abrocomidae (extant and extinct) and the crown group.

Before the MCMC run the resulting *xml* file was modified replacing the *TipDatesRandomWalker* node operator by a *SampledNodeDateRandomWalker* operator, which is compatible with trees containing sampled ancestors obtained under the FBD process (Barido-Sottani et al., 2018). Four independent MCMC runs (including one run sampling from the prior) of 70 million generations were executed in BEAST2 with parameters, gene trees, and species trees being sampled every 7,000 generations. Assessment of convergence was performed as for BI phylogenetics analyses using both Tracer and RWTY. Gene and species trees from the different independent runs were combined using the Logcombiner package with a 20% of burn-in. Because morphological character data for the fossil taxa was missing, these lineages can attach to any lineage in the tree presenting inadequate phylogenetic relationships. We thus pruned off stem fossil species using the *FullToExtantTreeConverter* post-processing application, and then Maximum Clade trees with mean node heights were obtained using Treeannotator. Each of these three packages is included in the

BEAST2 software package. Gene trees were visualized and exported from FigTree v.1.4.4 (Rambaut, 2017), while the time-calibrated species tree was plotted with a geological time scale starting at the Pleistocene using the *phyloch* (Heibl, 2008) and *strap* (Bell and Lloyd, 2015) packages in R (RStudio Team, 2020).

RESULTS

DNA sequences

Sequencing of mitochondrial and nuclear loci resulted in 1140 bp, 837 bp and 1107 bp for *cytb*, *GHR* and *RAG1*, respectively, totaling an alignment of 3084 bp. Owing to either low DNA concentration or high fragmentation of DNA in historical samples (those collected prior to year 2000), individuals missing more than 50% of information in any two gene sequences were excluded from the analyses. Instead, samples with small sequence gaps (~50 bp) observed for *cytb* and *GHR* sequences and a larger gap of 174 bp in *RAG1* sequences did not alter the results as observed in trials previous to the analyses. Alignment of *cytb* sequences was the variable with 62.02% of invariant sites, compared to the more conserved nuclear sequences of *GHR* and *RAG1* containing 81.6% and 88.62% of invariant sites, respectively.

Phylogenetic relationships

Bayesian and maximum likelihood analyses of the combined dataset recovered a single tree for Abrocomidae, that strongly support the monophyly of the family (BS = 100; PP = 1.0; Figure 4). A remarkable finding was the nesting of *C. ashaninka* amidst the three well-supported major clades of *Abrocoma*, and not as a distinct lineage as expected from morphological classifications. The analyses recovered *A. bennettii* as the most basal lineage, followed by *C. ashaninka* which is sister to a

reciprocally monophyletic group including species of the *A. cinerea* species complex: *A. famatina/cinerea* – *A. uspallata/schistacea*. Bootstrapping convergence in ML was reached after 50 replicates while parameter and tree topology convergence in BI analyses was reached after 10 million generations. Nodal support values were large across the tree (BS = 96 – 100; PP = 0.95 – 1.00) although medium to weak bootstrap support (74 – 84) was recovered in the basal split of the *A. cinerea* species complex.

Phylogenetic reconstructions using individual gene alignments recovered were moderately congruent (Figure 5). Monophyly of the family was strongly supported in each tree although sister relationships between species were not that consistent across trees and multiple unique topologies were suggested for each individual gene tree. In ML analyses, multiple topologies resulted from differences in branch length rather than branching order as indicated by RF distances (≤ 1.0) and visual inspection of best-scoring trees. Similarly, inspection of the treespace in RWTY for BI analyses indicated that tree searches for *cytb* and *GHR* were mostly focused in a reduced group (4 – 6 trees) while tree search in RAG1 was more diffuse. Bootstrapping convergence was reached after 50 replicates for *cytb* and *GHR*, and after 550 replicates for *RAG1*. ESS values and plots of posterior distributions for individual gene alignments in Tracer and RWTY indicated convergence was reached at 10 million generations. Increasing runs to 30, 50, and 80 million generations slightly improved treespace exploration yet topologies and branch lengths remained unaltered. Consensus trees were identical for *GHR* and *RAG1* in ML and BI analyses while a slightly different tree topology was obtained for *cytb* (not shown).

The *A. cinerea* species complex

Results of the species delimitation analysis in GMYC delimited two entities (likely species) under analyses using both, single threshold and multiple thresholds. These corresponded to *A. schistacea* and *A. uspallata* as one entity, and *A. cinerea* and *A. famatina* as the other. In both methods

the model was significantly better than the null hypothesis in the likelihood ratio test (Figure 4). In the multiple threshold analysis however, the most recent bifurcations within *A. bennettii* was also considered to represent a separate entity. The bPTP model in turn also delimited two entities within the *A. cinerea* species complex using both maximum likelihood and Bayesian solutions (Figure 4). Posterior probabilities for species delimitation in bPTP were above 0.93.

In BPP, species delimitation within the *A. cinerea* species complex also favored a two-species model (coded 100, posterior = 0.72) similar to results obtained in GMYC and bPTP analyses. This model was selected over scenarios for three (models 110 or 101, posterior probabilities = 0.17 and 0.08, respectively), four (model 111, posterior probability = 0.02) and a single unique species (model 000, posterior probability ~ 0). Because the number of species and loci in this analysis is reduced, prior variation by one order of magnitude had substantial impact on the posterior estimates of the tree with the maximum probability. Independent replicates using the designated α and β priors however, consistently reproduced similar posterior estimates therefore indicating convergence of the runs was reached. High posterior estimates obtained in this analysis for the basal split of this group (~0.99) compared to values for additional splits between putative species (~0.1–0.09) give further support to a two-species model for the *A. cinerea* species complex.

Diversification times

Results of the MCMC runs performed on BEAST2 using StarBEAST2 recovered a species tree with an identical topology to that obtained in ML and BI analyses using the combined dataset (Figure 6A). Inferred dates for the Abrocomidae family suggested a middle Miocene origin at 12.85 Mya (95% HPD: 10.03–15.87), with subsequent divergence during the late Miocene. Splitting between *Cuscomys* and the *A. cinerea* species complex was estimated at 9.35 Mya (95% HPD: 7.24–11.55) and radiation of arid-adapted species estimated at 7.22 Mya (95% HPD: 5.34–9.3). Middle and late Pleistocene

episodes of diversification are suggested at 0.52 Mya (95% HPD: 0.07–0.89) and 0.15 Mya (95% HPD: 0–0.33) for further divergence between the *A. uspallata*-*A. schistacea* and *A. cinerea*-*A. famatina* clades, respectively. Strong support was obtained for every node of this species tree with PP values equal to 1.0.

Parameters estimated on the FBD model suggested a net diversification rate of $6.146\text{E-}2$ (95% HPD: $1.22\text{E-}3$ –0.13), turnover rate of 0.668 (95% HPD: 0.34–0.99), and sampling proportion of 0.334 (95% HPD: 0.05–0.65). Inspection of plots of posterior distributions for parameters and tree topologies suggested that stationary distribution was reached after 70 million generations. As in BI phylogenetic analyses, exploration of the treespace varied among runs and increasing the number of generations up to 200 million did not alter tree topology. High ESS values (>1000) were recovered for most parameters whereas lower values (400–700) were obtained in some FBD parameters. Because no morphological information for fossil taxa was included in the analyses these low values were therefore expected. Comparisons of marginal density distributions including the run sampling from the prior indicated that FBD parameters and diversification times were effectively estimated using the combined information from the modern DNA sequences and occurrence times of fossil taxa. Prior distribution and taxon clade settings employed to calibrate the tree were therefore highly informative, providing accurate age estimates of diversification for Abrocomidae. Estimates of strict clock rates in substitution changes per million years for each locus based on the DNA sequences and fossil occurrences correspond to $1.008\text{E-}2$ for *cytb*, and to $1.012\text{E-}3$ and $1.003\text{E-}3$ for *GHR* and *RAG1*, respectively.

DISCUSSION

Systematics of Abrocomidae

Previous works related to the molecular systematics between families and superfamilies of caviomorpha including Abrocomidae, have been limited to the use of two or three species of this family (Upham and Patterson, 2012, 2015; Álvarez et al., 2017). Despite including both fresh tissues and skin samples from historical specimens our taxon sampling was still incomplete owing to difficulties on live-trapping (Braun and Mares, 1996) and also to restrictions from museum collections housekeeping the few individuals available for analyses. This partial sampling of the family therefore prevents us from making strong conclusions and we remain cautious in interpreting our results. We nonetheless here present the most complete study on the molecular systematics of Abrocomidae performed up to date, expecting to provide the basis for future research on the natural history of this understudied group of rodents.

Our results agree with previous classifications relying on morphological traits which suggested Abrocomidae as a single taxonomic unit (Glanz and Anderson, 1990; Emmons, 1999; Braun and Mares, 2002). Contrary to morphology-based classifications however, our molecular phylogenetic analyses recovered *Cuscomys* as a lineage nested within *Abrocoma* (Figures 4 and 6A), and not as a separate taxon. A recent study using molecular and morphological data recovered a relatively similar nesting position of *Cuscomys* derived from *A. boliviensis* and sister to a clade splitting *A. cinerea* and *A. bennettii* (Álvarez et al., 2017). The taxonomic placement of *A. boliviensis* in studies of molecular systematics however is largely uncertain due to the limited nucleotide data available for analysis (only 430 bp of *cytb* in Genbank). Based on similarities in dental morphology indeed previous studies suggested that *A. boliviensis* should be moved to genus *Cuscomys* (Verzi and Quintana, 2005). Additional studies of molecular systematics in Abrocomidae with a more inclusive taxon sampling might be therefore necessary to solve these conflicts with morphology-based delimitations in

taxonomic categories. Likewise, classification of species in the *A. cinerea* species complex has remained a long-standing controversy which we here attempt to address.

Species delimitation in the *A. cinerea* species complex has relied only on morphological evidence. Species delimitation using molecular approaches however, are not exempt of controversies (Fujisawa and Barraclugh, 2013; Sukumaran and Knowles, 2017) and results derived from these analyses should be interpreted cautiously. Classification schemes in the *A. cinerea* species complex have moved from considering them either separate individual species (Thomas, 1919; Braun and Mares, 2002), multiple sub-species of *A. cinerea* (Ellerman, 1940), or two clearly distinguishable morphotypes (Teta, 2020). Our results using single- and multilocus data under maximum likelihood and Bayesian approaches were similar to more recent studies in identifying only two main entities (Figure 4). This arrangement is similar to that recently described using morphological data (Teta, 2020) with a slight difference on the taxonomic position of *A. famatina*. The same individuals (namely, MACN 49.247 and MACN 49.248) can be recovered either as part or sister to *A. cinerea* depending on whether morphological or molecular information, respectively, is used. Additional studies including the other two arid-adapted species (*A. budini* and *A. vaccarum*) with more extensive individual sampling will therefore be necessary to clarify the two-entities classification scheme of the *A. cinerea* species complex.

Systematics of Abrocomidae therefore, remains far from being resolved and additional questionings appear when ecological (*i.e.* distributional ranges), morphological and molecular information is considered. A strong correspondence is observed between species classification (Figure 4) and the biogeographic provinces inhabited by them, namely the yungas, prepuna, Monte Desert, and mediterranean central Chile (Figure 1A). This correspondence is also notorious in the morphological adaptations described for terrestrial (*A. bennettii*), scansorial (arid-adapted *Abrocoma* species), and arboreal (*Cuscomys* and *A. boliviensis*) habits described for each group. Abrocomidae therefore might

as well be composed of three major evolutionary lineages differing markedly in ecology, genetics, and morphology. If this were the case we then wondered whether these groups different species or might consist of entire different genera. As a preliminary approach to address this question, we estimated *cytb* sequence divergence values for species pairs between these groups, for which inter-population to inter-generic ranges have been described in multiple mammalian taxa (Baker and Bradley, 2006). In abrocomids, *cytb* sequence divergence among the three main lineages is >18% (Table 6) which is considered to reflect inter-generic differences (Baker and Bradley, 2006). Testing this taxonomic hypothesis however requires an even more integrative taxonomic approach including multiple lines of evidence in addition to an improved species sampling (Dayrat, 2005; Padial et al., 2010; Schlick et al., 2010). We however hypothesize that, under this three major lineages scenario, *A. boliviensis* should be recovered in the same lineage as *Cuscomys* based on previous observations in dental morphology (Verzi and Quintana, 2005) and on fieldwork observations over eastern Bolivia (Tarifa et al., 2009).

Historical biogeography of Abrocomidae

The disjunct distribution of abrocomids is a biogeographical feature also shared by plant taxa found in sclerophyll forests in central Chile with some species also found in the yungas, northwestern Argentina, and southeastern Brazil (Landrum, 1981; Marquínez et al., 2009; Chacón et al., 2012; Murillo et al., 2016). Divergence times in these taxa were estimated between the early and middle Miocene (18 - 13 Mya), suggesting a common biogeographical history (Hinojosa and Villagrán, 1997). Previously, it was suggested that subtropical forests extended continuously across South America during the Oligocene and Miocene (Landrum, 1981), later becoming fragmented owing to several environmental events. These include Andean uplift (Marquínez et al., 2009; Chacón et al., 2012), increasing aridity (Ortiz-Jaureguizar and Cladera, 2006), and an Atlantic marine transgression (the Paranaense Sea; Pascual, 1996). The origin of crown Abrocomidae at 12.85 Mya and the basal position

of *A. bennettii* (Figure 6A) led us to hypothesize that an ancestral abrocomid population was likely distributed across present-day central Chile and central western Argentina around the middle Miocene (Figure 7A). Isolation into eastern and western populations would have occurred then through vicariance by the Andes mountain formation (Scott et al., 2018; Figure 7B), a scenario also hypothesized for other octodontids with similar distribution and diversification times (Suarez-Villota et al., 2016). The western Andean population (current *A. bennettii*) would have established its current distribution by expanding north- and southwards since then (Figure 7B-D).

Ancestral abrocomid populations isolated over the eastern Andean flank likely expanded northwards reaching the southern Altiplano and the eastern cordillera between the late and early Miocene (Figure 7B). The eastern Andean flank by this time has been hypothesized to have reached only half of its current height (Gregory-Wodzicki, 2000; Figure 6B). Timing and rate of topographic uplift in this region indeed has been quite controversial (Ehlers and Poulsen, 2009; Garzzone et al., 2014; Perkins et al., 2016; Scott et al., 2018) and our estimated origin of *Cuscomys* by 9 Mya could provide a chronological constraint to alternative geological hypotheses. Based on proposals of late Miocene rapid uplift (Garzzone et al., 2014) and onset of convective rainfall (Poulsen et al., 2010) we therefore suggest that yungas-like environments already existed around 10 Mya. In these environments adaptation to montane forests would have promoted differentiation from populations distributed over the Andean plateau through allopatric (most likely peripatric) speciation (Figure 7B). Following our proposal of a sister relationship between *A. boliviensis* and *Cuscomys*, we also hypothesize that the former constitutes the basal lineage within this group. Origin of *Cuscomys* therefore, would have been posterior to this event and resulted from populations migrating northward as montane forests expanded isolating populations between the yungas in Bolivia and Peru (*i.e.* parapatric speciation; Figure 7B). Similar scenarios of northward expansion and subsequent differentiation have been also described previously for nematodes (Picard et al., 2008) and more recently for plants (Böhnert et al., 2022).

Uplift of the eastern cordillera was also crucial in the origin of the *A. cinerea* species complex by promoting development of arid conditions over the central Andes (Ortiz-Jaureguizar and Cladera, 2006; Poulsen et al., 2010). Onset of convective precipitation promoted a strong east-west gradient of increasing aridity which led to replacement of open grasslands with a small proportion of forested areas into more steppe-like environments over the southern Altiplano (Croft et al., 2011; Sweet and Johnson, 2015). More pronounced aridity since 7.5 Mya is suggested by the expansion of C4 plants (Latorre et al., 1997) likely reinforced later by changes in atmospheric circulation (Insel et al., 2009; Rohrmann et al., 2016). Evidence of abrocomids occupying this region is provided by the temporal and geographical extension of multiple paleontological records of the extinct genus *Protabrocoma* (Prevosti et al., 2019; Chiesa et al., 2019). Results of our phylogenetic analyses and molecular species delimitation, suggest that two lineages of the *A. cinerea* species complex evolved independently. In lizards and coleopteran with similar distributions, a proposed mechanism accounting for the same deep phylogenetic break was attributed to a vicariant barrier during the Paranean Sea (Flores and Roig-Juñent, 2001; Yoke et al., 2006). The extension of this transgression into northwestern Argentina however, is not well-supported (del Río et al., 2018) and additional geological and biological information is therefore necessary to understand the origin of this deep phylogenetic break in co-distributed species.

Global yet brief (<1 Mya in temporal extension) climatic changes occurring since the late Miocene did not promote further diversification in Abrocomidae (Figure 6A and 6C). Middle and late Pleistocene estimates of divergence are therefore interpreted as intra-specific lineage divergence in entities identified in species delimitation analyses. This low diversification trend is consistent with most caviomorph families (Upham and Patterson, 2015) and with previous studies in mammals suggesting that millennial-scale environmental change did not drive speciation but population-level changes instead (Barnosky, 2005). Indeed, except for genera *Ctenomys* and *Proechymis* (Octodontoidea), most caviomorph genera (40%) are represented by only few species (Ojeda et al.,

2015). Abrocomids however, provide an interesting opportunity to study the genetic legacy of Quaternary climate oscillations through fossil deposits commonly known as paleomiddens (Betancourt and Saavedra, 2002; Pearson and Betancourt, 2002). These organic remains are so well-preserved that endogenous DNA has been extracted and analyzed in metagenomics studies in paleomiddens from the Atacama and North American deserts (Díaz et al., 2019; Moore et al., 2020). Reconstruction of millennial-scale genetic variation in populations of *Abrocoma* species as a response to past climate change could be therefore crucial to understand and predict microevolutionary responses of small mammals to current and future climate change (Fordham et al., 2020; Moore et al., 2020).

Biological constraints to central Andean uplift

The chronology and rate of central Andean topographic uplift is a decades-long debate comprising multiple studies with conflicting evidence leading to alternative geological hypotheses (Figure 6B). In short, the debate centers on whether topographic uplift was a steady protracted process since the Oligocene or earlier (>25 Mya; McQuarrie et al., 2005; Barnes and Ehlers, 2009; Lamb, 2016; Sundell et al., 2019) or if, on the contrary, it consisted of rapid and recent pulses of uplift since the middle Miocene (<15 Mya; Barke and Lamb, 2006; Ghosh et al., 2006; Garzzone et al., 2008; Perkins et al., 2016). As a mean to constrain these geological hypotheses, use of large-scale genetic data of biota endemic to the central Andes has been suggested (Baker et al., 2014). A revision of estimates of diversification times in plants grouped the influence of the Andes into four major categories: (i) as a source of new high-elevation habitats; (ii) as a vicariant barrier; (iii) as a north-south corridor, and; (iv) as a generator of new environmental conditions outside de Andes (Luebert and Weigend, 2014). The chronologies of each of these categories however encompass a wide range of ages although some patterns persist. For example, high-Andean lineages being older in the south

compared to the northern Andes (as speculated in Gregory-Wodzicki, 2000) or east-west disjunct distributions being caused by vicariance during Andean uplift.

Estimates of divergence times for central Andean endemic fauna are scant, particularly for mammals, yet some of the aforementioned patterns reviewed in plants still hold. Middle Miocene Andean-related biogeographic events described include east-west vicariance in scorpions (Cecarelli et al., 2016), colonization of high-elevation environments by birds (McGuire et al., 2014; Sweet and Johnson, 2015) and nematodes (Picard et al., 2008), and dispersal to surrounding biomes by lizards (Esquerré et al., 2018) and butterflies (Da Silva et al., 2016). Expansion and diversification of these taxa occurred later during the late Miocene. Our estimated diversification times are consistent with biogeographic events occurring in other animal taxa both regarding the formation of a geographic barrier (vicariance) and the generation of new high-elevation environments. As in plants (Luebert and Weigend, 2014) time estimates of diversification in animal taxa also argue for a model of recent and rapid topographic uplift of the central Andes (Gregory-Wodzicki, 2000; Ghosh et al., 2006; Garzzone et al., 2008, 2014). Compared to plants however, studies in animal taxa suggest an important role of ecological speciation rather simple vicariance as shown by new high-elevation environments promoting diversification in butterflies (Elias et al., 2009), terrestrial doves (Sweet and Johnson, 2015) and montane-adapted abrocomids (this study). More studies are necessary not only to better constrain chronology of central Andean uplift but also to better understand the biogeographic processes leading to the currently observed diversity and distribution of South American biota.

CONCLUSIONS

Results presented here correspond to the first study of the molecular systematics of Abrocomidae using mitochondrial and nuclear DNA nucleotide sequences. As in previous studies using morphological external traits we recovered a single monophyletic group although disagreements exist

on species-level classification. In the *A. cinerea* complex for instance, molecular species delimitation analyses suggested that the four species included in our analyses can be grouped into two entities (likely species), closely resembling a recent classification proposal based on qualitative and quantitative morphological characters. More interestingly however our study suggested the presence of three main evolutionary lineages in Abrocomidae which differ markedly in habitat, morphology, and genetics. These include *A. bennettii*, the montane species of the genus *Cuscomys*, and arid-adapted species of the currently known *A. cinerea* species complex. Based on *cytochrome b* sequence divergence as a preliminary estimate of genetic differences between these groups we suggest that lineages might represent different genera. Additional studies with a more intensive taxon and individual sampling are required to confirm these observations under an integrative taxonomic framework which, owing to difficulties in live-trapping individuals of these species, will involve remarkable efforts. Meanwhile, specimens from natural history collections could provide additional required morphological and molecular data for species not included in this work.

Origin of crown Abrocomidae was estimated during the middle Miocene at 12.85 Mya with further lineages originating during the late Miocene between 9 – 7 Mya. As in most families of caviomorph rodents (with some exceptions), no additional diversification has occurred since the Pliocene. Based on these time estimates, the geographical and temporal extension of the extinct genus *Protabrocoma*, and on the biogeographical history of taxa with similar disjunct distributions we presented a hypothetical biogeographic history for abrocomids. We here suggest that Andean uplift was the main diversification driver through allopatric (vicariant) speciation and also through ecological speciation as new high-elevations environments formed. Causes behind the independent evolution of two genetically independent yet morphologically similar lineages in the *A. cinerea* species complex are not clear. Lastly, Andean orogeny influenced the diversification of South American biota and their chronology offers a mean to test geological hypotheses regarding timing and rate of uplift. Although it

could be argued that a recent and rapid model of uplift is supported, dated phylogenies for animal and plant endemic to the central Andes are still scarce and similar studies are required to provide additional support to this proposal.

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FIGURES AND TABLES

Figure 1. Study area and species of the Abrocomidae family. **A.** Biogeographic provinces of the central Andes (Morrone, 2014; layers available in Löwenberg-Neto, 2014) and associated type localities for species of Abrocomidae (black dots) based on information from Braun and Mares (2002) and Emmons (1999). **B.** Topographic relief of the central Andes (1:50m Raster Data from <http://www.naturalearthdata.com>) indicating the eastern and western cordilleras surrounding the Altiplano plateau. Also shown are type localities (black dots) of Abrocomidae species and estimated distributional ranges available for *A. bennettii* and *A. cinerea* (source: <http://www.mma.gob.cl/>). **C.** *Cuscomys ashaninka*. **D.** *Abrocoma cinerea*. **E.** *Abrocoma bennettii*.

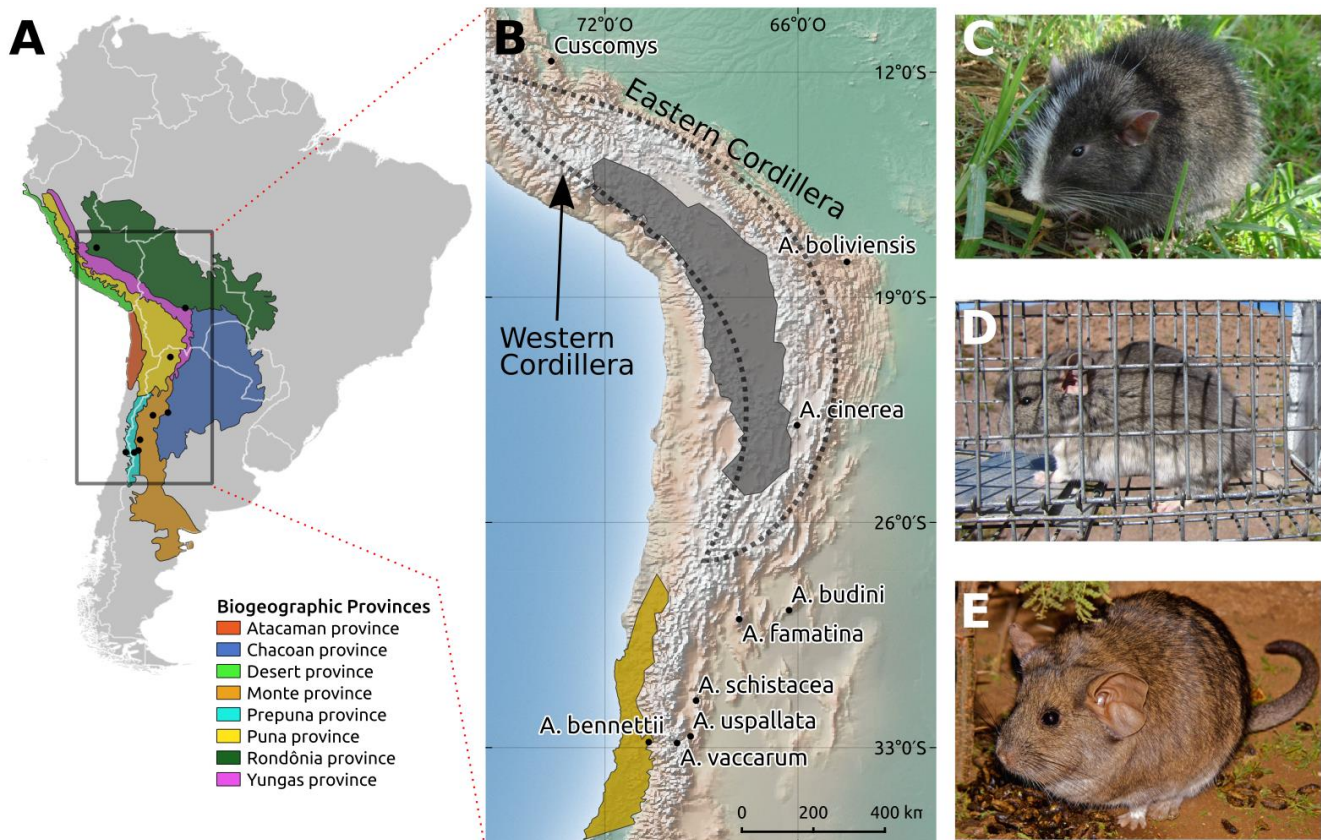


Figure 2. Sampling localities of *Abrocoma* specimens included in this study (detailed information in Table 1). Shaded areas correspond to the geographic range of *A. bennettii* (red) and *A. cinerea* (dark gray) (source: www.mma.gob.cl). The software used to create this map was QGIS v3.14-Pi, with use of the STRM30 elevation model (Data: US Geological Survey). Topographical relief is shown with elevation colors based on climate, with humid lowlands in green and arid lowlands are brown (1:50m Raster Data; source: <http://www.naturalearthdata.com>)

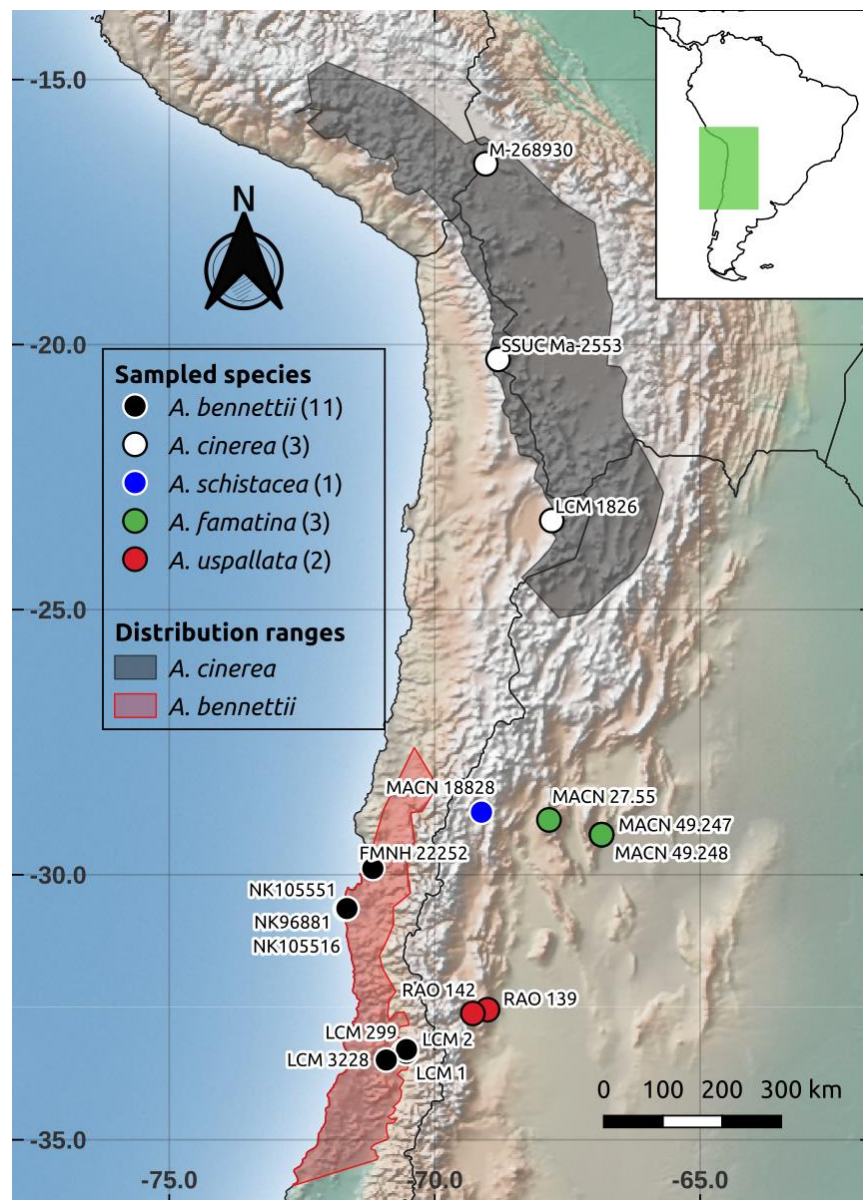


Figure 3. Schematic overview of gene amplification. Each single locus is shown in the 5' to 3' direction with size proportional to their length (in bp) as shown in Geneious (<http://www.geneious.com>). Gray bars below the genes correspond to the small overlapping fragments amplified in historical specimens (previous to 2000's). Detailed information of primers and primer combinations are available in Table 3.

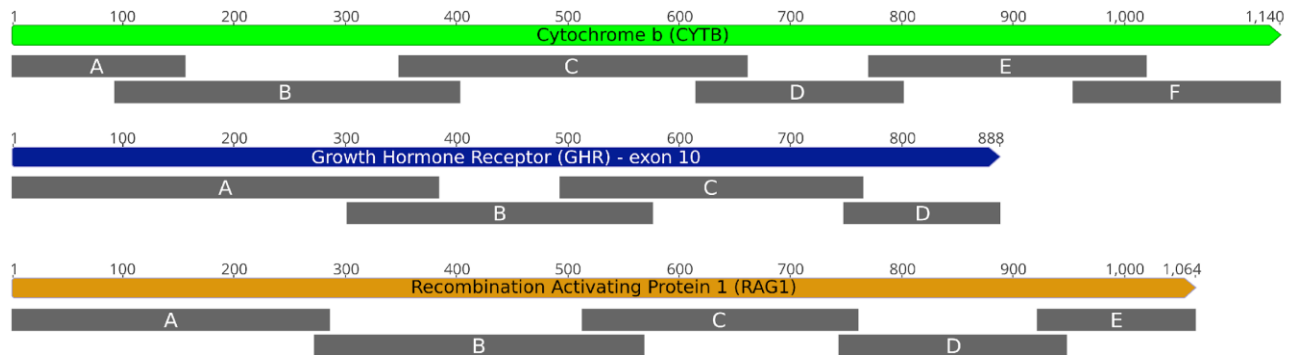


Figure 4. Phylogenetic relationships within Abrocomidae using the combined nuclear and mitochondrial genes. The topographic image of the sampling region is shown as a reference. Bootstrap (BS) and posterior probability (PP) nodal support is indicated as BS/PP. Tree topologies are identical in both partitioned ML and BI analyses. Shown is the tree generated in BI analyses. Scale is in expected number of substitutions per site. Each individual in the tree is linked to a site in the map by a designated letter at the end of each tip label and by match in colors between branches and sites.

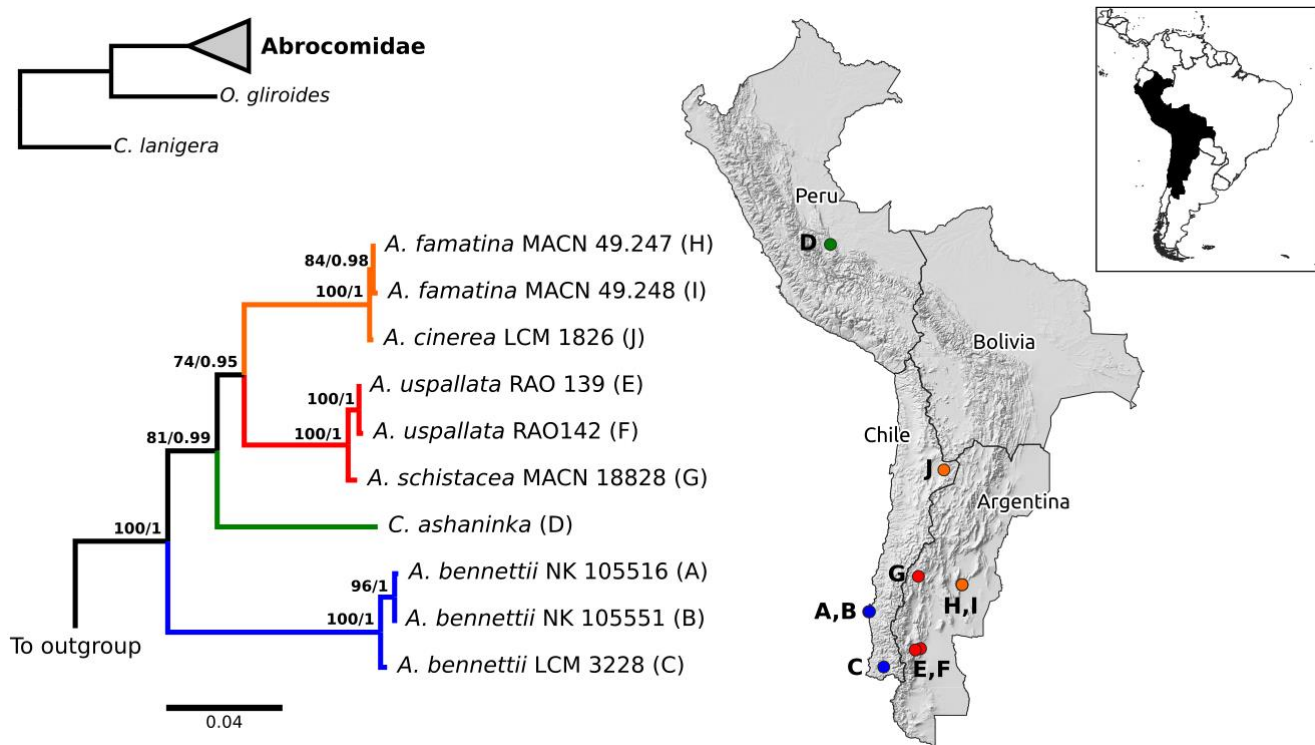


Figure 5. Maximum likelihood gene trees. **A.** *Cytochrome-b* tree (1140 bp, TIM2+I+G). **B.** Growth Hormone Receptor exon 10 (837 bp, K80+I). **C.** Recombination Activating Protein 1 (1107 bp, K80+I). Bootstrap (BS) and posterior probability (PP) nodal support is indicated above nodes as BS/PP. Individual gene tree topologies are identical in both ML and BI, except for a branching pointed out in the cytochrome-b tree (marked with an *). Scale is in expected number of substitutions per site. NR: node not recovered in BI.

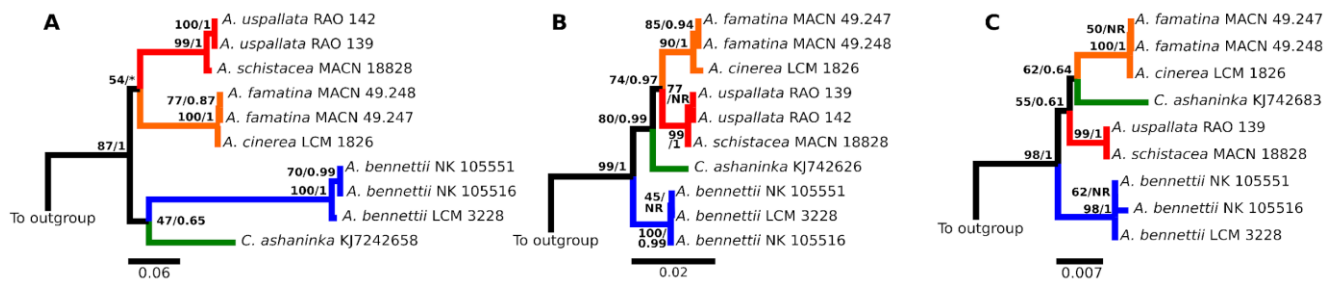


Figure 6. Ultrametric timetree and main environmental events discussed in this study. A. Maximum clade-credibility timetree of extant Abrocomidae species. All posterior probability values of internal nodes are 1.00. The 95% credibility intervals for node ages are shown with blue translucent bars. **B.** Paleoelevational reconstructions and timing of the main topographic features of the central Andes. **C.** Benthic foraminifer oxygen isotope dataset from ocean drilling cores as a proxy of global climate (Westerhold et al., 2020). The tree was plotted with a geological time scales since the Pleistocene using the *phylochron* (Heibl, 2008) and *strap* (Bell and Lloyd, 2015) packages in R (RStudio Team, 2020) using South American Land Mammal Ages as a reference (Cione et al., 1995; Woodbourne et al., 2014).

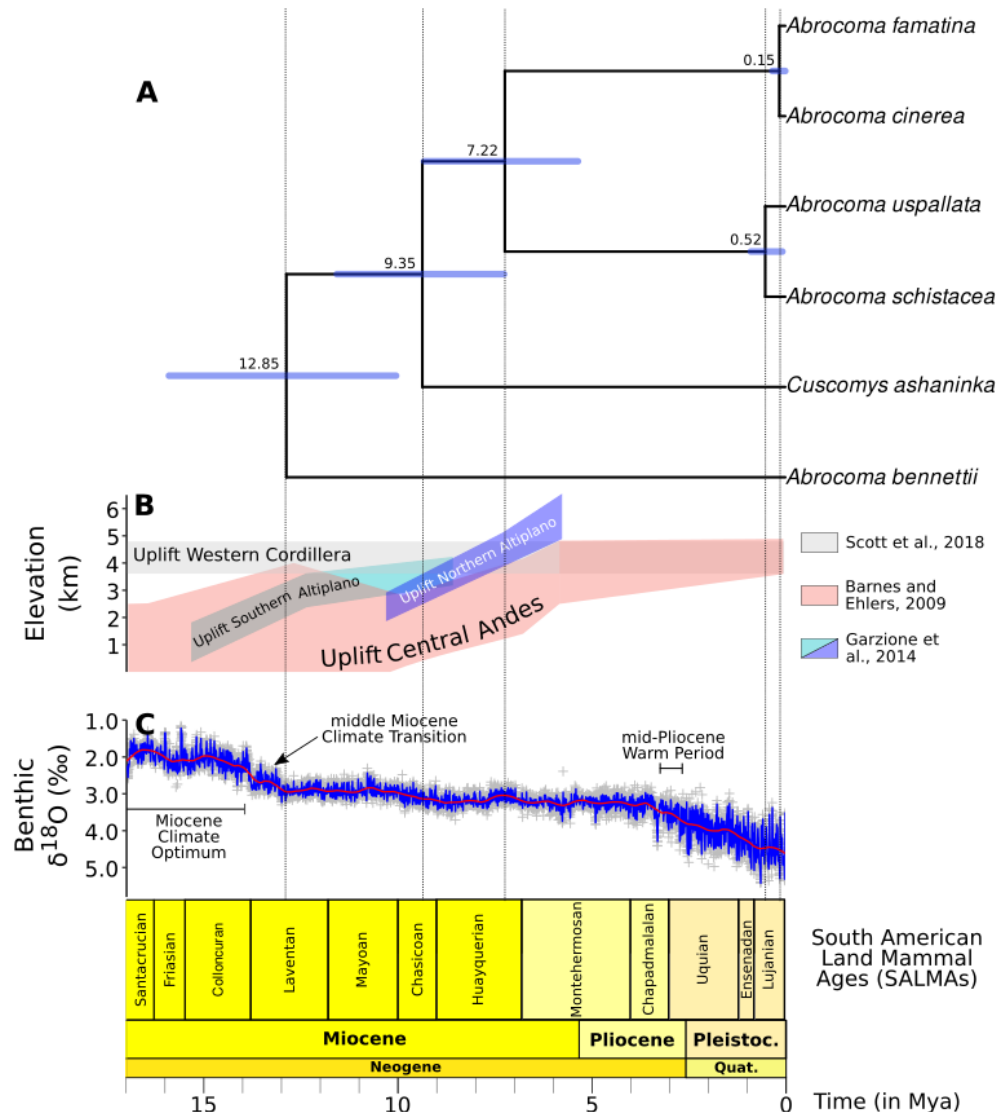


Figure 7. Historical biogeographical events for Abrocomidae diversification. The four maps are schematic representations of events discussed in the text. These events are marked with numbers in circles and mentioned in the inner boxes.

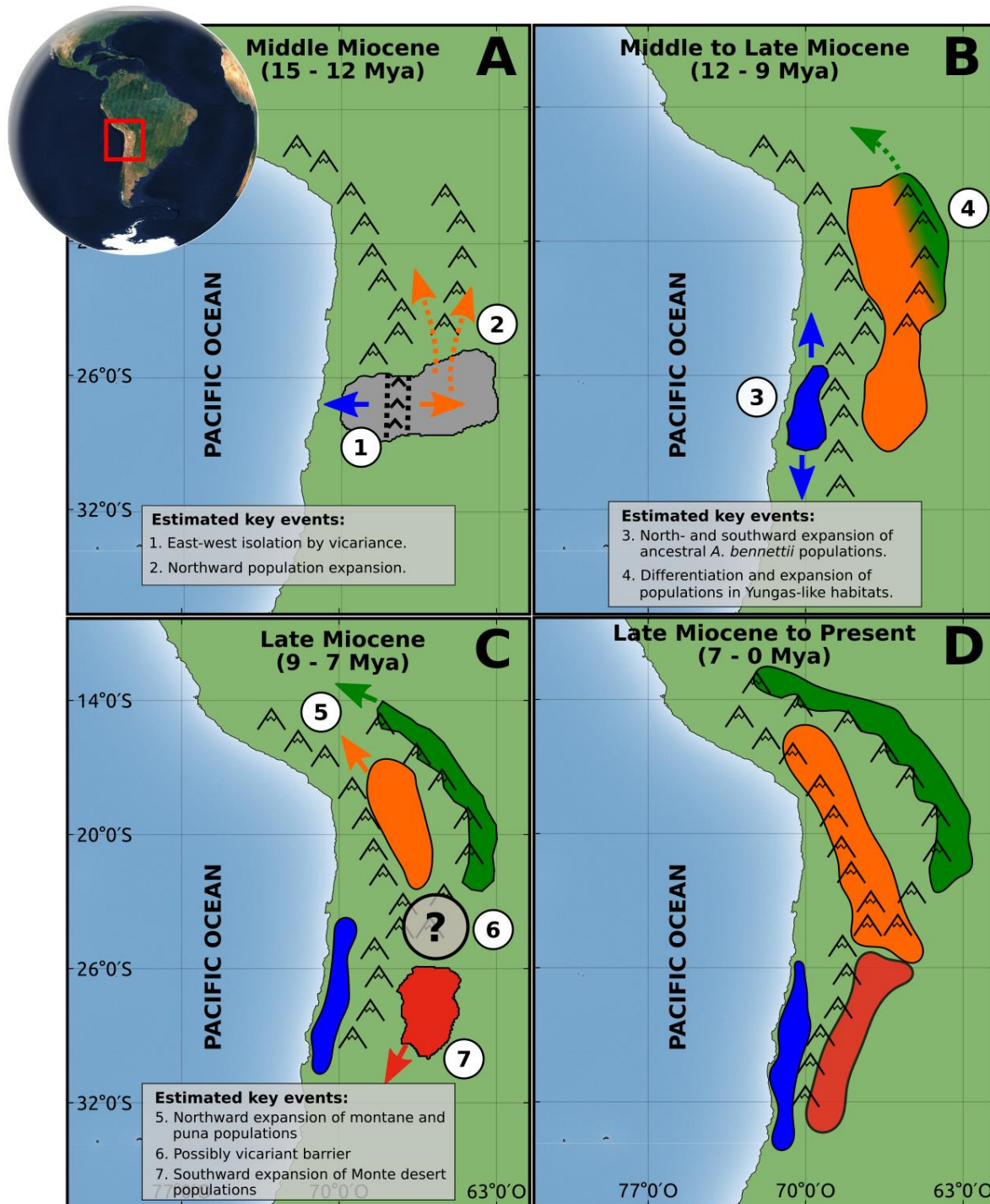


Table 1. Information of *Abrocoma* specimens used in this study. Source of samples appear as superscript numbers next to Sample IDs and include: (1) the Field Museum of Natural History; (2) Colección de Flora y Fauna Profesor Patricio Sánchez-Reyes (Pontificia Universidad Católica de Chile); (3) Laboratorio de Citogenética de Mamíferos (Universidad de Chile); (4) American Museum of Natural History; (5) Museo Argentino de Ciencias Naturales Bernardino Rivadavia; (6) Instituto Argentino de Investigaciones en Zonas Áridas (IADIZA). Sample type corresponds to liver tissues (L) or skins from vouchers (S). ^aSpecies originally described as *A. cinerea*. ^bSpecies originally described as *Abrocoma* sp. ^cGeoreference values were estimated from locality information. *NI*: Not informed.

Species	Sample ID (and type)	Locality	Country	Capture date	Latitude (°S) ^c	Longitude (°W) ^c
<i>A. bennettii</i>	FMNH 22252 (S) ¹	Romero, Coquimbo	Chile	Jul 11, 1923	-29.88	-71.17
<i>A. bennettii</i>	NK 105516 (L) ²	Parque Nacional Fray Jorge, La Serena	Chile	Oct 23, 2002	-30.65	-71.69
<i>A. bennettii</i>	NK 105551 (L) ²	Parque Nacional Fray Jorge, La Serena	Chile	Oct 24, 2002	-30.64	-71.65
<i>A. bennettii</i>	NK 96881 (L) ²	Parque Nacional Fray Jorge, La Serena	Chile	Jul 29, 2001	-30.64	-71.65
<i>A. bennettii</i>	FMNH 119583 (S) ¹	2.5 km NE Cerro Manquehue, Santiago	Chile	Nov 24, 1975	-33.35	-70.60
<i>A. bennettii</i>	LCM 1 (L) ³	Los Domínicos, Santiago	Chile	Late 1980	-33.37	-70.54
<i>A. bennettii</i>	LCM 2 (L) ³	Los Domínicos, Santiago	Chile	Late 1980	-33.37	-70.54
<i>A. bennettii</i>	LCM 299 (L) ³	La Dehesa, Santiago	Chile	Late 1980	-32.29	-70.53
<i>A. bennettii</i>	LCM 300 (L) ³	La Dehesa, Santiago	Chile	Late 1980	-32.29	-70.53
<i>A. bennettii</i>	LCM 305 (L) ³	La Dehesa, Santiago	Chile	Late 1980	-32.29	-70.53
<i>A. bennettii</i>	LCM 3228 (L) ³	Quebrada de la Plata, Santiago	Chile	Late 1980	-33.50	-70.91
<i>A. cinerea</i>	M-268930 (S) ⁴	Ingavi, 8 km W of San Andrés de Machaca	Bolivia	Aug 03, 1983	-16.59	-67.79
<i>A. cinerea</i>	SSUC Ma-2553 (L) ²	Salar del Huasco, Tarapacá	Chile	Abr 18, 2015	-20.28	-68.81
<i>A. cinerea</i>	LCM 1826 (L) ³	Tumbre, Antofagasta	Chile	Late 1980	-23.32 ^c	-67.79
<i>A. famatina</i>	MACN 27.55 (S) ⁵	Sierra Famatina, La Rioja	Argentina	Jul 10, 1927	-28.97	-67.85
<i>A. famatina</i> ^b	MACN 49.247 (S) ⁵	La Rioja	Argentina	1949	-29.25 ^c	-66.86
<i>A. famatina</i> ^b	MACN 49.248 (S) ⁵	La Rioja	Argentina	1949	-29.25 ^c	-66.86
<i>A. schistacea</i> ^a	MACN 18828 (S) ⁵	Reserva San Guillermo, Cerro Inés, San Juan	Argentina	Mar 28, 1982	-28.82 ^c	-69.12
<i>A. uspallata</i>	RAO 139 (L) ⁶	Road to Villavicencio, Mendoza	Argentina	<i>NI</i>	-32.55 ^c	-69.01

Species	Sample ID (and type)	Locality	Country	Capture date	Latitude (°S) ^c	Longitude (°W) ^c
<i>A. uspillata</i>	RAO 142 (L) ⁶	Cerro 7 colores road, Uspallata, Mendoza	Argentina	<i>NI</i>	-32.62	-69.28

Table 2. PCR primers information. Gene position are based on the following reference sequences: ¹Cytochrome b extraction from complete mitochondrial genome of *Octodon degus* (Genebank accession ID NC_020661); ²Partial GHR exon 10 sequence of *Abrocoma bennettii* (JN414754); ³Partial RAG1 exon 1 sequence of *Octodon bridgesi* (KJ742676).

Cytochrome b				
Primer ID	Direction	Sequence 5' to 3'	Gene Position ¹	Source
MVZ 05	Forward	CGAAGCTTGATATGAAAAACCATCGTTG	14139F	Smith and Patton, 1993
MVZ 06	Reverse	GCTGTGTCTGATGTGTAGTGTAT	14369R	Smith and Patton, 1993
MVZ 03	Forward	GCTTCCATCCAACATCTCAGCATGATG	14256F	Smith and Patton, 1993
MVZ 04	Reverse	GCAGCCCCTCAGAATGATATTTGTCCTC	14621R	Smith and Patton, 1993
MVZ 35	Forward	TCTCAGAAACCTGRAAYATYGG	14516F	Smith and Patton, 1993
MVZ 26	Reverse	AGATCTTTGATTGTGTAGTAGGGGT	14876R	Smith and Patton, 1993
MVZ 23	Forward	TACTCTTCCTCCACGAAACWGGNTC	14780F	Smith and Patton, 1993
MVZ 16	Reverse	AAATAGGAARTATCAYTCTGGTTTRAT	15019R	Smith and Patton, 1993
LBE 35	Forward	CTAGGAGAYCCTGACAAYTACA	14938F	This study
H15767	Reverse	ATGAAGGGATGTTCTACTGGTTG	15233R	Spotorno et al., 2004
LBE 36	Forward	AAACAACGTAGYATATCATTYCG	15121F	This study
LBE 34	Reverse	TCATTTTGGTTTACAAGACCA	15376	This study

Growth Hormone Receptor exon 10

Primer ID	Direction	Sequence 5' to 3'	Gene Position ²	Source
GHR 50F	Forward	TTCTAYARYGATGACTCYTGGGT	28F	Adkins et al., 2001
GHR 12R	Reverse	GACTCAGTTTTACCAATAAAAAGTAGTTGTGG	416R	Upham et al., 2013

GHR 11F	Forward	GGAGAAGCAGATCTCTTGTGCCTTG	277F	Upham et al., 2013
LBE 23	Reverse	GGCACTGTCTTTGATGAAGTTTGC	600R	This study
GHR 13F	Forward	GGCAAACATGGACTTTTATGCTCAAGTAAGC	462F	Upham et al., 2013
GHR 15R	Reverse	CAGAGGTATAATCTGGGAGGGCCATTTC	793R	Upham et al., 2013
LBE 24	Forward	CTGAGAAGTCTGGGGCTGCG	728R	This study
GHREND	Reverse	CTACTGCATGATTTTGTTTCAGTTGGTCTGTGCTCAC	OFF	Adkins et al., 2001

Recombination Activating Gene 1

Primer ID	Direction	Sequence 5' to 3'	Gene Position ³	Source
RAG1F1705	Forward	GCTTTGATGGACATGGAAGAAGACAT	OFF	Teeling et al., 2000
LBE 25	Reverse	CTCACTGCTCTTCATGGCCT	306R	This study
RAG1_3F	Forward	GACTGCCATCCTCAGCCCCGC	252F	Upham et al., 2013
LBE 27	Reverse	GGCTGAGACCCCTTTCACTCGAC	591R	This study
LBE 26	Forward	AGCCACACTGAGAACCTGGA	493F	This study
LBE 29	Reverse	CGGCTTCAGGTTTCATCTTCTTC	783R	This study
LBE 28	Forward	AAGGAAAAGATGGCAGGCCA	728F	This study
LBE 30	Reverse	AGAGGGAGTCTGGGCACTC	967R	This study
LBE 31	Forward	TTTACCTGAAGATGAAGCCC	902F	This study
RAG12864	Reverse	GAGCCATCCCTCTCAATAATTTCAGG	OFF	Teeling et al., 2000

Table 3. Primer pair combinations and fragment information. Fragment length corresponds to the size of the amplified PCR product without considering primers.

Gene	Fragment ID	Primer Combo	Fragment Length (bp)	Bp spanned
Cytochrome b	A	MVZ05 / MVZ06	180	0 – 156
	B	MVZ03 / MVZ04	311	93 – 403
	C	MVZ35 / MVZ26	314	348 – 661
	D	MVZ23 / MVZ16	187	315 – 801
	E	LBE35 / H15767	251	770 – 1020
	F	LBE36 / LBE34	211	954 – 1140
Growth Hormone Receptor	A	GHR50F / GHR12R	334	0 – 334
	B	GHR11F / LBE23	275	252 – 526
	C	GHR13F / GHR15R	273	443 – 715
	D	LBE24 / GHREND	141	698 – 838
Recombination Activating Gene exon 1	A	RAG1F1705 / LBE25	312	0 – 287
	B	RAG13F / LBE27	297	272 – 568
	C	LBE26 / LBE29	249	513 – 761
	D	LBE28 / LBE30	206	743 – 948
	E	LBE31 / RAG1R2864	143	922 – 1064

Table 4. Genbank accession numbers and source information of additional sequences included in the analyses. *Cytochrome b sequence extracted from a whole mitochondrial genome.

Species	<i>cytb</i>	<i>GHR</i>	<i>RAG1</i>
Family Abrocomidae			
<i>Cuscomys ashaninka</i>	KJ742658	KJ742626	KJ742683
Family Octodontidae			
<i>Octodontomys gliroides</i>	AF370706	AG520649	KF590663
Superfamily Chinchilloidea			
Family Chinchillidae			
<i>Chinchilla lanigera</i>	NC021386*	AF332036	KF590658

Table 5. Crown and stem fossil information. Age ranges were obtained from the Paleobiology Database website (www.pbdb.org) and confirmed by the cited literature.

Fossil species	Age range (Mya)	Reference
<i>Caviocricetus spp.</i>	17.5 – 21	Vucetich and Verzi, 1996; Arnal and Vucetich, 2015
<i>Deseadomys arambourgi</i>	21 – 29	Wood and Patterson, 1959
<i>Dudumus spp.</i>	16.3 – 21	Arnal et al., 2014; Arnal and Vucetich, 2015
<i>Protabrocoma spp.</i>	3.6 – 11.62	Prevosti, et al., 2019; Chiesa et al., 2019
<i>Prospaniomys spp.</i>	16.3 – 21	Arnal and Vucetich, 2015
<i>Protacaremys spp.</i>	15.5 – 21	Arnal and Vucetich, 2015
<i>Protacaremys denisae</i>	13.8 – 15.5	Vucetich et al., 1993
<i>Spaniomys spp.</i>	15.97 – 23.03	Arnal and Vucetich, 2015

Table 6. Estimates of evolutionary divergence between *cytochrome-b* sequences. Shown is average (in bold) and range (parentheses) of *cytb* sequence divergence within and among pair of species as percentage. Analyses were conducted using the Kimura 2-parameter model (Kimura, 1980). The rate variation among sites was modeled with a gamma distribution (shape parameter = 1.02). Analyses were conducted in MEGA X (Kumar et al., 2018). ^aIncluding individuals of *A. famatina*. ^bIncluding individuals of *A. uspillata*. NA: Not enough individuals for analysis. *Estimates were based only on divergence between two individuals.

	1	2	3	4	5	6
1. <i>A. bennettii</i>	1.25 (1.68 – 1.90)					
2. <i>A. cinerea</i> ^a	22.64 (22.36 – 22.79)	0.49 (0.37 – 0.65)				
3. <i>A. schistacea</i> ^b	23.70 (23.46 – 24.13)	15.98 (15.24 – 16.38)	1.30 (0.29 – 1.96)			
4. <i>C. ashaninka</i>	24.84 (24.76 – 26.96)	17.72 (17.29 – 18.23)	20.52 (20.23 – 20.78)	NA		
5. <i>O. gliroides</i>	32.58 (32.08 – 33.06)	28.62 (28.05 – 29.98)	25.18 (24.76 – 25.73)	28.05*	NA	
6. <i>C. lanigera</i>	35.03 (34.57 – 35.55)	32.05 (31.47 – 32.04)	31.51 (31.02 – 32.14)	32.89*	33.57*	NA

CHAPTER 2: HIGH AND LOW LATITUDE FORCING DRIVE ATACAMA DESERT

RAINFALL OVERT THE PAST 16,000 YEARS

High and low latitude forcing drive Atacama Desert rainfall over the last 16,000 years

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ABSTRACT

Late Quaternary precipitation dynamics in the central Andes have been linked to both high and low latitude atmospheric teleconnections. We use present-day relationships between fecal pellet diameters from ashy chinchilla rats (*Abrocoma cinerea*) and mean annual rainfall (MAR) to reconstruct the timing and magnitude of pluvials (wet episodes) spanning the last 16,000 years in the Atacama Desert based on 81 ^{14}C -dated *A. cinerea* paleomiddens. A transient climate simulation shows that pluvials identified at 15.9 – 14.8, 13.0 – 8.6, and 8.1 – 7.6 ka BP can be linked to North Atlantic (high-latitude) forcing (e.g., Heinrich Stadial 1, Younger Dryas and Bond cold events). Holocene pluvials at 5.0 – 4.6, 3.2 – 2.1 and 1.4 – 0.7 ka BP are not simulated, implying low-latitude internal variability forcing (i.e., ENSO regime shifts). These results help constrain future central Andean hydroclimatic variability and hold promise for reconstructing past climates from rodent middens in desert ecosystems worldwide.

INTRODUCTION

The dry central Andes in South America (15 – 27° S), encompassing the semiarid Altiplano and high Andes > ~3600 m and the adjacent hyperarid Atacama Desert, are potentially vulnerable to future warming. Regional climate simulations under extreme greenhouse warming (GHW) scenarios indicate a reduction in summer rainfall by 30% over the coming century (1, 2), bringing about severe impacts on ecosystems and human societies (3, 4). The central Andes, however, are remote and topographically complex with only sparse weather observations, making it difficult to discriminate different climate outcomes from independent lines of evidence. Precisely identifying episodes of past rainfall variability and their myriad drivers could improve forecasts of future hydroclimatic variability, as well as aiding to understand past human-environment interactions in this region. Paleoclimatic records spanning the last 50 ka BP (thousands of years before present) have shown that major hydroclimatic variations occurred

during the late Quaternary (5 – 7). The timing of these changes, however, suggests a complex set of forcing mechanisms that could be responding to regional (5, 8) and/or inter-hemispheric drivers (6).

The Atacama Desert and Pacific slope of the Andes have been particularly sensitive to past rainfall variability, which left an indelible footprint on the coupled environmental and cultural history of the Atacama (9). Permanent arid to hyperarid conditions in this region have been interrupted in the past by the incursion of wet events that are widely replicated in multiple late Quaternary paleoecological (10, 11) and paleohydrological (7, 8, 12) records. The largest of these events over the last 100 ka BP, both in terms of magnitude and spatial extent, was the Central Andean Pluvial Event (CAPE) originally constrained from >15.9 – 9.7 ka BP (thousands of years before present) (8) and later expanded to 18 – 9 ka BP based on additional records (11, 13). As currently defined, the CAPE consists of two extensive pluvials (CAPE I and CAPE II) interrupted by a dry phase between c. 14 – 13 ka BP (8). Increased precipitation during the two CAPE pluvials have been attributed to either increased local summer insolation (14) or to permanent or semi-permanent “La Niña-like” states (5, 11) driven by anomalously cool tropical Pacific sea surface temperatures (SSTs) and are referred to here as low latitude forcing. Conversely, prolonged dry periods are thought to have resulted from El Niño-like conditions. More recent evidence suggests that changes in North Atlantic SSTs (*i.e.*, high latitude forcing) during Heinrich Stadial 1 (HS1) could have played a much larger role during the CAPE, likely through southward displacements and intensification of the South American Summer Monsoon (SASM; 6, 15). Hence, periods of decreased SST in the North Atlantic throughout the Holocene such as during Bond events (16) could have impacted precipitation regimes in the central Andes.

Hydroclimatic variability throughout the Holocene following the CAPE has been largely attributed to low latitude forcing. During the middle Holocene (~8 – 4 ka BP) for instance, most records indicate prevailing hyperarid conditions that may have significantly impacted human settlements (9, 17). ENSO activity was indeed severely limited between 5 – 4 ka BP, most likely driven by orbital changes (18 – 20). Major ENSO regime shifts have also been linked to hydroclimatic

variability during the Medieval Climate Anomaly (MCA) and the Little Ice Age (LIA) between 1.0 – 0.8 and 0.75 – 0.55 ka BP, respectively (21). Discrepancies exist, however, on whether El Niño or La Niña prevailed during the MCA with the opposite ENSO stage following afterwards during the LIA (22 – 24). Changes in SASM intensity have also been suggested for these same periods in the Bolivian and Peruvian Andes (25, 26). More recent “historic” pluvials during the early 19th and mid-20th centuries described in records from the Altiplano and the Atacama have been attributed to dominant La Niña conditions (27).

Modern precipitation in the central Andes occurs predominantly (>80%) during the austral summer, with two different upper air forcing mechanisms causing an anti-phased pattern in the northern and southern extents of this region (28). Precipitation in the north (15 – 23° S) results from advection of tropical moisture from the Amazon basin and the tropical Atlantic (29) and its interannual variability depends on both the intensity of the SASM (30) and SST changes in the tropical Pacific (28). Further south (24 – 27° S), convective activity is modulated by the strength and location of the Bolivian high (31), which relies on the moisture content of lowlands east of the Andes (i.e., the Gran Chaco) (28). Moisture in the Gran Chaco depends on the intensity of the SASM and the transport of warm, moist air from the Amazon basin by the South American Low-Level Jet (SALLJ) but also on extratropical cold air incursions (32). Intensification of the SASM is therefore crucial for rainfall episodes in the central Andes, yet its contribution to past pluvials has received little attention.

Here, we present a new proxy record of rainfall variability from the central Atacama Desert (22–23° S; Figure 1A) that spans the last 16,000 years. Our record is based on a new quantitative method that estimates past changes in rainfall using a correlation between Mean Annual Rainfall (MAR) and fecal pellet average diameters of present-day ashy chinchilla rats (*Abrocoma cinerea*) in northern Chile. We then apply the inverse correlation as a transfer function to *A. cinerea* pellets obtained from a series of radiocarbon-dated fossil middens (or paleomiddens) to develop a record of the magnitude and temporal extension of past rainfall episodes. Paleomiddens are amalgamations of plant and animal

debris encased in crystallized urine (amberat), which enhances their preservation for tens of thousands of years in caves and rock shelters of arid environments and have been studied extensively to infer past climates in arid regions of western North and South America (33). To establish the extent of either high- or low-latitude forcing of past hydroclimatic variability, we compare our results to other regional and extra-regional paleoclimate records and to a transient climate simulation of rainfall in the Atacama Desert that spans the last 22,000 years, which is mostly driven by high latitude forcing (34).

Fossil fecal pellets and past climate change

Why would fecal pellet size be related to climate? Changes in body size profoundly affect the life history, ecology and evolution of organisms and is a heritable and easily measured morphological trait in animals that scales allometrically with fecundity, energetic requirements, diet, territory, and home range size (35). Identification of the environmental factors that drive long-term (i.e., at millennial scales) body size changes is therefore of particular interest for the ecology and evolution of species. Fecal pellet size (diameter) is correlated positively with body size in modern packrats (*Neotoma cinerea*), and negatively with ambient temperature, and have been used to estimate body size variations in packrats in response to temperature variations during the late Quaternary as a test of Bergmann's Rule (36, 37). In other arid lands, however, modern studies indicate that the relationship between mammal body size and environmental factors is variable and that precipitation (through net primary production, or NPP) rather than temperature may be the main limiting factor (38).

In the hyperarid Atacama Desert (21 – 24 °S) paleomiddens built by ashy chinchilla rats (*Abrocoma cinerea*) are identified by the size and shape of their copiously abundant fecal pellets (Supplementary Figure S1). At present this species occurs at elevations > 3500 m where mean annual rainfall (MAR) and temperature (MAT) are c. 60-70 mm/yr and 5-6 °C, respectively (39; Figure 1A). Several late Quaternary radiocarbon-dated middens record downslope displacements of this species,

relative to its modern range into what is currently known as “absolute desert” between 2400 – 3100 m (10; Figure 1B). As with *Neotoma* middens, fecal pellets from *Abrocoma* middens also exhibit large variations in size and have been linked to past changes in precipitation (40). Contrary to North American packrats, however, estimating body size changes in *A. cinerea* from fecal pellet diameters is hindered because individuals of this species are very shy, difficult to capture and observe in the field, and do poorly in laboratory experiments that control for diet and ambient conditions (temperature and relative humidity). Based on similar studies with *Neotoma*, we assume that a relation exists between fecal pellet size and body size in *A. cinerea* and use this theoretical link to test for modern correlations with temperature and/or precipitation along an environmental gradient in northern Chile between 18 - 24 °S (Figure 1A and see *Modern calibration* section in Materials and Methods).

RESULTS

Past rainfall anomalies over the last 16,000 years in the central Atacama

Our record (Figure 2) shows that persistently very wet and almost uniform conditions prevailed from 15.9 – 14.8 ka BP (e.g., during the CAPE I) followed by a conspicuous absence of paleomiddens between 14.8 to 13.1 ka BP. This conspicuous lack of middens could be due to several causes, including a very dry period which would have forced midden building rodents upslope from our midden sites but we remain cautious with our interpretations until more evidence is available (see also *Criteria for defining the timing of wet and arid phases* in Materials and Methods). In contrast, rainfall was much more variable from 13.0 – 8.6 ka during the CAPE II (Figure 2) characterized by large centennial-scale fluctuations of very wet (from 100 to 60 mm/yr, the largest anomalies in our record) to mildly-wet or dry periods (60 to 10 mm/yr) until 8.6 ka BP. Aridity increased gradually from a very wet period at 9.3 ka BP to near modern conditions at 8.4 ka BP. A wet phase ensued at 8.1 ka BP, reaching a maximum of $\sim 88 \pm 11$ mm/yr around 7.5 ka BP. This was followed by a ~ 2500 yr gap in our record

bounded by similar-to-present and positive rainfall anomalies at 7.4 and 5.0 ka BP, respectively. As with the previous gap, one possible explanation for the lack of middens from 7.4 – 5.0 ka BP is the prevalence of extremely arid conditions.

A brief wet episode occurred at 5.0 ka BP followed by increasingly large wet anomalies during the late Holocene. Sustained but decreasing rainfall from 2.5 – 1.7 ka BP was followed by increased rainfall variability from 1.4 – 0.76 ka BP with large wet anomalies ($\sim 83 \pm 11$ mm/yr) at 0.86 ka BP, coeval with the Medieval Climate Anomaly (MCA, between 1.0 – 0.7 ka BP; 21). Some of the largest changes in rainfall anomalies occur in paleomiddens with almost identical calibrated ^{14}C dates. For example, an 83 ± 11 mm/yr anomaly occurs at 0.862 ka BP (960 ± 15 ^{14}C yr BP), followed by an $\sim 11 \pm 20$ mm/yr anomaly from another midden dated to 0.857 ka BP (1015 ± 15 ^{14}C yr BP). One possible explanation is that these changes could be due to large decadal-scale variability in precipitation, which would not be resolvable by direct AMS dating of individual middens (Supplementary Table S3 and Supplementary Figure S5). Four middens dated to between 0.5 – 0.1 ka BP (e.g., during the Little Ice Age or LIA; 21) have anomalies indistinguishable from present-day values, except during the last 200 yr when a slight increase (45 – 50 mm/yr anomaly) in rainfall estimated from two middens matches a regional recent historical pluvial event in the early 1800s (27, 40).

We used a global transient climate simulation (34) of the last 22,000 years to further analyze rainfall in the Atacama Desert (centered at 24° S) (Figure 3I). This simulation shows two major pluvials with >20% increase in rainfall during the late Pleistocene, from 22 – 14.5 ka BP and from 13.8 – 11.4 ka BP. The simulation further shows a precipitation minimum from 14.3 – 14.0 ka BP. After 11.3 ka BP, precipitation rises almost linearly throughout the Holocene, from an average deficit of -15% to modern values. A less intense pluvial interrupts this secular trend between 8.9 – 7.6 ka BP although average rainfall was still below the present-day average.

DISCUSSION

Our evidence for extensive pluvials at 15.9 – 14.8 ka BP and 13.0 – 8.6 ka BP in the central Atacama (15 – 27° S) further constrains the temporal extension of the CAPE. Our improved chronology also shows that pluvials during the early Holocene were possibly absent between 7.5 – 5 ka BP and resumed during the middle to late Holocene. These younger pluvials were much shorter in duration (<1 ka) that gradually started at ~5 ka BP and intensified at 2.5 and 1.1 ka BP. To what extent were variations in present-day climate mechanisms (e.g., ENSO) responsible for causing these regional changes versus changes in summer insolation? And to what extent is high latitude forcing responsible for these pluvials?

Local changes in summer insolation (the amount of solar radiation at the top of atmosphere, typically at 20° S for the central Andes) were among the first mechanisms proposed to explain the formation of paleolakes in the central Andes (14, 41). The timing of the pluvial events seen in our record, however, shows no support for local orbital insolation forcing as these occur during an insolation minimum (at 11 ka BP) (Figure 3A). Late Holocene Atacama pluvials, however, increased in magnitude over time, similar to other paleo-ENSO records (Figure 3E, F; 42, 43) pointing to a possible role for increasing insolation through its impact on ENSO (18).

Until recently, past changes in rainfall described in different paleorecords from the Atacama were attributed to permanent or semi-permanent “La Niña-like” states to explain large increases in precipitation during the late Quaternary (5, 8, 44). Wet events (or “pluvials”) occurring during these periods of low-latitude forcing should thus be characterized by ‘cold phases’ in the tropical Pacific and strengthened west-east SST gradients. Our timing of the 15.9 – 14.8 ka BP pluvial (CAPE I) does indeed occur during “La Niña-like” conditions (11). Yet our record shows that this was not the case during the second part of the CAPE II (11 – 9.6 ka BP) or at 7.5 ka BP. Additional explanations are clearly necessary apart from such low latitude forcing.

Recent studies have examined how changes in North Atlantic SSTs impact rainfall variability over the central Andes (15, 25, 26, 45). Indeed, a correlation between North Atlantic cooling and precipitation increases over the central Andes during the Holocene has been previously suggested (46). Two major mechanisms are likely involved in regulating inter-hemispheric temperature contrasts in the Atlantic and its subsequent impacts on central Andean climate: (i) a southward displacement of the Intertropical Convergence Zone (ITCZ); and (ii) enhanced moisture transport from the tropical Atlantic (47). These changes lead to a southward displacement and intensification of the SASM thus increasing available moisture in the Amazon basin, leading to increased easterly advection over the central Andes (48). Several paleo-records of SASM intensity have been correlated with North Atlantic SSTs over the last decade (49, 50), and link massive ice discharges in the North Atlantic to corresponding increases in rainfall over the central Andes (15, 46). An intensified and southerly displaced Bolivian High resulting from a southerly shifted SASM could partly explain the intensity and magnitude of CAPE I (6).

We support the hypothesis that the CAPE likely resulted from an intensified SASM triggered by cooling of the North Atlantic by massive ice discharges during HS1 (between 16 – 14 ka BP) and the Younger Dryas event (YD, between 12.8 – 11 ka BP). This, in turn, drove an intensification and southward shift of the SASM (49, 51, 52; Figure 3B, D). These two periods of increased and widespread SASM activity were partly coeval with the two CAPE phases: CAPE I during HS1 and the first half of CAPE II during the YD (Figure 3G). Furthermore, records of Equatorial Pacific SSTs suggest La Niña-like conditions (53, 54), which would have even further increased precipitation over the central Andes. The Atacama rainfall transient climate simulation also suggests cold North Atlantic forcing during this interval (Figure 3I). One key difference, however, is that ice discharge was far less intense during the YD compared to HS1 (55), which would have resulted in a less-intensified SASM during the CAPE II (51). This difference in SASM intensity appears to have impacted most of the central Andes, with deep paleolakes in the Altiplano and increased, sustained rainfall over the Atacama

during the CAPE I, and shallow paleolakes and increased but variable rainfall during the CAPE II (Figure 3G–I).

Precipitation increases appear to have been more intense in the southern Altiplano during CAPE II which has been attributed to changes in moisture source (5, 7, 8, 13). If the CAPE II involved an intensification and southward displacement of the Bolivian high, as with the CAPE I, then this would shift precipitation maxima southwards with moisture transport from the central Brazil-Gran Chaco region (6). This implies that the differences observed between the CAPE phases likely resulted from weakened and/or more variable monsoonal activity during the CAPE II compared to the CAPE I and not from changes in moisture source, which is consistent with the transient climate simulation (Figure 3I) and our MAR anomaly record (Figure 3H).

Our results imply that hydroclimatic variability in the Atacama appeared to switch from high- to low-latitude forcing during the middle Holocene. The positive anomaly peaks in our record between 11 – 7.5 ka BP correlate with SASM intensification during Bond events (45, 52), suggesting that a high-latitude control remained even after the end of the CAPE II (Figure 3D, H). This relationship breaks down as the Laurentide ice sheet disappeared around 7 – 7.5 ka BP along with possibly reduced ENSO activity between 10 – 6 ka BP (Figures 3E, F) (19, 42, 43, 56). The middle to late Holocene pluvials were remarkably similar in terms of intensity and temporal extension to changes in ENSO events frequency and intensity (Figure 3E, F) implying a switch to low-latitude forcing sometime between 8 – 5 ka BP.

Increased orbital insolation since 5 ka BP resulted in enhanced ENSO activity through its impact on equatorial Pacific SSTs (Figure 3A, F) (18, 19). SASM intensification between 3 – 2.4 ka BP, however, could have also been driven by high-latitude forcing (52) through southward displacement of the ITCZ (57). No single driver, however, appears to explain all the rainfall variations over the last few millennia in the central Atacama, and these events are noticeably absent from the

transient simulation. Because these modes of variability are internal and intrinsic to the climate system, their exact timing cannot be reproduced by a climate model, which can only respond to a given external forcing or driver. Nevertheless, a stronger low-latitude forcing is more clearly visible during the Common Era (i.e., last 2 ka BP) as the timing seen in our record (with positive rainfall anomalies during the MCA and negative ones at the onset of LIA) corresponds with major ENSO regime shifts. Indeed, the nature of hydroclimatic variability over the central Andes during the MCA and the LIA is a topic of ongoing debate, much of it centered on which ENSO phase predominated during each period. Wet conditions during the MCA have been attributed to continuous La Niña-like states (with subsequent El Niño dry conditions during the LIA: 11, 22, 58), whereas the opposite (El Niño followed by La Niña-like conditions, i.e., 23, 59) has also been suggested.

In the Atacama, evidence points to a pluvial event during the MCA (11, 60), although some recent studies also show evidence for pluvials during the LIA (12, 61). As most records point to a weak SASM during the MCA which later strengthened during the LIA (25, 62, 63; Figure 3D), a wet Atacama during the MCA would imply a low-latitude driver for hydroclimatic variability that favored moisture advection across the central Andes. Although a recent “historic pluvial” could also be driven by changes in ENSO regimes (27), the timing of these changes indicates a more complex set of forcing mechanisms with differing regional impacts (64).

Finally, increased moisture availability from 13 – 8.6 ka BP in the Atacama Desert may have attracted the first human settlers that were expanding at the time across the different ecosystems of the central Andes (9). Increased environmental stress drove human societies to abandon certain territories while dispersing to others from 8 – 5 ka BP, where they developed different socio-ecological strategies including camelid domestication (17). Although shorter in duration, the late Holocene pluvial events (<1 ka BP) had significant impacts on human societies that thrived in the Atacama hyperarid core (9, 57). Major technological improvements for coastal and inland food procurement and processing,

coupled with major socio-cultural changes including investments in permanent hamlets with solid and multi-functional architectures, irrigated and fertilized desert farming, major population growth, and increased social complexity and inequalities were all accelerated by these late Holocene pluvials (9, 65, 66).

CONCLUSIONS

Hydroclimatic changes in the central Andes during the Holocene have been a matter of debate for decades and regional differences between the western Andes and the Bolivian and Peruvian Altiplano have been suggested (25, 26, 46). Putting aside complexities in dating and interpretations of these different proxies, unraveling hydroclimatic variability in the region requires understanding the relative contributions of high- and low-latitude forcing mechanisms during the Holocene. Depending on timescales, we propose that changes in north Atlantic SSTs were as relevant as those occurring over the tropical Pacific in controlling rainfall variability over the central Andes (Figure 3), and neither driver can independently explain our entire record. For instance, Holocene rainfall variability in the Atacama resulting from SASM modifications alone would generate pluvials that would only track austral summer insolation as shown by the transient climate simulation, instead of becoming less frequent and more intense as seen in our record (Figure 3D, I).

We link episodes of massive ice discharge during HS1 and YD, and brief discharges during Bond Events until 7 ka BP to: (i) increased Atlantic trade winds and southward displacement of the ITCZ; (ii) intensification and southward displacements of the SASM, and (iii) pluvials in the Atacama Desert. This implies that these pluvials likely had a North Atlantic driver instead of the La Niña-like states which had been previously proposed for the CAPE from 16 – 7 ka BP. Indeed, the alteration of the Bolivian high as a response to these atmospheric changes during CAPE I likely caused the most

intense pluvial (CAPE I) in the central Andes over the last 100 kyr, providing the best conditions for inland late Pleistocene human societies. It is reasonable to assume that similar mechanisms operated during the YD and subsequent Bond events throughout the Holocene. Although changes in equatorial Pacific SSTs could have additive effects coupled with episodes of North Atlantic cooling, our record suggests that ENSO-regime drivers became the dominant control of precipitation only since the middle Holocene, likely linked to increased solar insolation and its influence on the tropical Pacific.

Paleomiddens are used widely to reconstruct past climate and ecological change throughout the world's arid regions, but the discontinuous nature of the midden record has hampered comparisons with other continuous proxies. By pooling several paleomidden series from nearby localities (such as throughout a basin) covering a large geographical area and time scale, our study overcomes this restriction by providing an increased number of samples available for replication. We show that rodent fecal pellets from ancient middens can be used to obtain quantitative estimates of past climate change. Here, we identify the timing and magnitudes of multiple wet and dry episodes in the Atacama Desert over the last 16,000 years and propose different mechanisms of climatic forcing. We note that the methods used could be readily exported to other arid regions of South America where chinchilla rat middens have been collected, which could provide further examination of the timing of events observed here.

Our results here highlight the complexity of the controls of climate variability over the central Andes. Although our interpretations are simplified they are essential for assessing if models of future climate change can correctly estimate the full range of future regional hydroclimatic responses. These will be critical for regional governance and development of sustainable policies for the decades to come.

MATERIALS AND METHODS

Midden collection & processing

We selected and analyzed a total of 81 previously collected chinchilla rat (*Abrocoma cinerea*) middens (10, 13, 44) in northern Chile (Figures 1A and 1B; Supplementary Table S1). Midden agents (i.e., the species of rodents that build middens) were identified based on fecal pellet size and shape (Supplementary Figure S1; 67). Following standard procedures (68) indurated middens were placed in 10 l buckets of water for 5 – 7 days to remove the crystallized urine (amberat), then wet-sieved and dried at 50 – 60° C in a drying oven. Fecal pellets and other organic debris (plant macrofossils, vertebrate bones, and insect remains) were sorted and stored for various research purposes. Radiocarbon dating was performed on all middens by either conventional or accelerator mass spectrometry (AMS) using between 0.1 – 0.3 g for AMS or 3 – 10 g for conventional dating of fecal pellets (Supplementary Table S1). Midden ^{14}C ages were calibrated at two-sigma with the Southern Hemisphere curve (SHCal13; 69) using the CALIB 7.0.2 program (70) to thousands of calendar years before 1950 (ka) to facilitate comparisons across records. Out of the total set of available middens, 13 were employed to establish correlations with modern climate variables (Supplementary Table S2), and 68 middens were employed for our mean annual rainfall anomaly reconstruction (Supplementary Table S3). To ensure that local rainfall in the vicinity of the middens was the only source of water, the middens employed in this study (both modern and fossil) were collected away from water sources (wetlands, point springs, etc.).

Pellet measurements

After separation from other materials, the width of the largest ~200 pellets (or ~20% of those available, whichever was greater) was measured to the nearest 0.1 mm using a digital caliper

(Mitutoyo, USA) following protocols previously described for woodrat (*Neotoma cinerea*) middens in North America (36, 71). Statistics on the largest pellets were employed instead of total measurement statistics as this allows for discrimination of the confounding effect of juveniles (71). Measuring 10 – 20% of the sample is sufficient to characterize the largest pellets, above this threshold maximum pellet size does not vary with sample size (36). When fewer than 200 pellets were present, all were measured. The mean, standard deviation, standard error, and 95% confidence interval of the all the measurements (N_{TOT}) and the largest 20% of the pellets measured (N_{20}) were calculated.

Modern calibration and past estimations of Mean Annual Rainfall (MAR)

Modern middens were defined here as those directly dated with ^{14}C resulting in ages <150 cal yr BP or containing “bomb radiocarbon”. These middens were mostly collected and archived during fossil midden surveys carried out between 1996 and 2012 covering an extensive latitudinal range (18 – 26° S). During these collection campaigns, approximately 1,600 middens have been recovered and are currently stored at the Laboratory of Paleoecology and Paleoenvironments of the Pontificia Universidad Católica de Chile. Application of criteria such as sufficient number of measurements (i.e. >200 largest pellets or ~20% of those available), discarding middens collected in proximity to nearby water sources other than rainfall, and limiting the dataset to those collected within the latitudinal range covered by weather stations (see below), results in only 13 middens that could be employed to establish the relationship between modern MAR and pellet diameter values.

Mean daily temperatures and monthly accumulated rainfall data in northern Chile (17 – 30°S) was retrieved from weather stations of the DGA (Dirección General de Aguas) available at the Center for Climate and Resilience Research website (MAT: <http://www.cr2.cl/datos-de-temperatura/>; MAR: <http://www.cr2.cl/datos-de-precipitacion/>). We included only those above the inversion layer boundary at ca. 800 m asl, spanning the longest continuous period possible without any gaps (Supplementary

Table S4). Due to differences in collection of rainfall and temperature data between stations, we applied different filters for each dataset. For temperature we employed stations spanning a 13-year period (1976 – 1989) between 17 – 28°S with more than 76% of available data, except for stations located where gaps in elevation or latitude existed. Stations with less than 300 days of data information were also discarded. In the case of rainfall data, we employed stations covering a 30-year period (1987 – 2016) including stations with more than 98% of data between 17 – 24°S. We considered water years from 1 November to 31 October as it groups both summer and the following winter rainfall peaks into the same year. After filtering both datasets, we performed analyses of variance (ANOVAs) to identify whether elevation or latitude better explained changes in temperature or rainfall.

We found that MAT varies inversely with elevation but very little with latitude between 17 – 25° S (Supplementary Figure S2A), in agreement with previous research (72). MAR presents a more complex relationship varying in both latitude and elevation (Supplementary Figure S2B), decreasing towards the Pacific coast and southwards until ~24° S, the southernmost region where summer rainfall regularly occurs (73). Linear regressions to estimate temperature were then established on a yearly basis as a function of elevation ($MAT = a - b * Elevation$), and of latitude and elevation to estimate rainfall ($MAR = a * Latitude + b * Elevation + c$). These annual equations captured between 80 – 94% and 57 – 96% of the variance, for MAT and MAR respectively. We thus derived average MAT and MAR values for each modern midden site using latitude and elevation information (Supplementary Figures S2C and S2D). Estimates of means and error values of MAT and MAR for each modern midden site are included in Supplementary Table S2. N_{20} was measured in each *A. cinerea* modern midden and then plotted against MAR and MAT estimates for each site (Supplementary Figure S3) which then enables us to link changes in pellet diameters as a function of these climatic variables (Eqs. 1 & 2).

Simple linear regression models show that MAR (Eq. 1) is a better predictor of changes in N_{20} pellet diameters than MAT (Eq. 2) in the Atacama Desert (Supplementary Figure S3). We then use the inverse correlation as a transfer function to calculate past quantitative MAR estimates from fecal pellet measurements obtained from our paleomiddens (Figure 1C).

$$\text{Modern } N_{20} = 2.57409 * (\text{MAR}) + 0.01185; \text{ Multiple } r^2 = 0.8013; P < 0.001 \text{ (Eq. 1)}$$

$$\text{Modern } N_{20} = 6.0875 - 0.2324 * \text{MAT}; r^2 = 0.2324; P > 0.001 \text{ (Eq. 2)}$$

Estimation of past rainfall anomalies

Fecal pellet measurements from 68 radiocarbon-dated paleomiddens collected from seven localities in the central Atacama Desert were used to estimate past rainfall anomalies (estimated past MAR minus present-day MAR at the same site; Figure 1A and Supplementary Tables S1 and S3). Pellet diameters slightly decrease linearly with age, and a correction was applied to all N_{20} average measurements from paleomiddens (Supplementary Figure S4). Accuracy of MAR estimates was assessed by calculating the difference in anomaly estimates between same-age midden pairs (within <10 ^{14}C yr difference of each other) collected from multiple sites and/or elevations (Supplementary Figure S5). As most paleomiddens were collected along the hyperarid margin of the Atacama where no active *A. cinerea* populations exist today, a positive bias exists in our record implying that may be better at tracking wet phases rather than dry ones (see *Criteria for defining the timing of wet and arid phases in Materials and Methods*).

For estimation of rainfall anomalies, diameters from 16,071 fecal pellets were measured from 68 individually ^{14}C -dated rodent middens (i.e., those older than 0.15 ka) collected from seven localities in the central Atacama Desert (Figure 1B; Supplementary Table S3). Because pellet diameters slightly decrease linearly with age (Eq. 3; Supplementary Figure S4), a correction was firstly applied to all N_{20}

average values for obtaining quantitative estimates of MAR in each midden. This decrease appears to be linear at least for the last 16 ka but may level off for older middens. This will need to be further explored with a larger dataset of much older paleomiddens.

$$\text{Paleomidden } N_{20C} = \text{Paleomidden } N_{20} + 0.03 * [\text{midden calibrated age in ka}] \text{ (Eq. 3)}$$

After correcting for changes in diameter with time, we then established a simple linear regression model based on the inverse relationship between modern fecal pellet diameters and MAR, which permits the prediction of MAR estimates using corrected paleomidden N_{20} mean values as a predictor variable (Eq. (4); Figure 1C).

$$\text{MAR} = 67.62 * [\text{Paleomidden } N_{20C}] - 148.63; r^2 = 0.80; P < 0.001 \text{ (Eq. 4)}$$

Estimates of MAR values and 95% confidence and prediction intervals were thus obtained from each midden and rainfall anomalies were calculated using modern MAR estimates for each paleomidden site (Supplementary Table S3). Replicability of MAR estimates was assessed by calculating the difference in anomaly estimates between same-age midden pairs (within $<10^{14}\text{C}$ yr difference of each other) collected from multiple sites and/or elevations (Supplementary Figure S5).

The use of a linear regression model was confirmed after checking for parametric assumptions through analyses of residuals and additional validation was obtained in R (74) using the *gvlma* package (75). Diagnostic evaluation of the regression model was performed by splitting the modern MAR and pellet diameters dataset into an 80:20 (training:test) subset for comparison of observed and predicted MAR values. These analyses suggested a min-max accuracy of 0.97 and a mean absolute percentage deviation of 0.029. Although a log function provides a slightly better fit ($\text{AIC} = 109.2314$) compared to a lineal function ($\text{AIC} = 110.9961$), we opted for the linear function as (i) visual inspection of the log

curve data remains linear within the range of values covered by the dataset with no indications of reaching a plateau, and (ii) a linear function provides a simpler way to interpret MAR estimates based on pellet diameter without data transformation. Additionally, MAR estimates using both functions do not differ significantly and therefore use of a lineal model is appropriate under the dataset employed. We do call for caution, however, as pellet diameters (and therefore body size) are restricted to increase indefinitely with increasing rainfall and thus a log model would be more biologically reasonable. Testing for this prediction should be explored in further studies using a wider range of fecal pellet diameters along a wider latitudinal gradient and/or from other regions of arid South America where *A. cinerea* occurs.

Criteria for defining the timing of wet and arid phases

Wet episodes are defined when MAR anomalies remained above our level of uncertainty (conservatively established at >40 mm/yr- see Supplementary Figure S5). Such wet events differ significantly from the modern baseline (see previous section). Arid to hyperarid phases were established based on either: 1) low MAR anomaly estimates (<40 mm/yr) or, 2) tentatively by the absence of any middens for prolonged periods of time (i.e., >1000 yrs, see Figure 2). The reasoning for this is that many of our paleomiddens were originally collected with the purpose of establishing major vegetation changes along the hyperarid upper margin of the absolute desert (Figure 1B), an area sparsely vegetated today with very low bioproductivity and no active *A. cinerea* populations (10, 39). As these areas would have been too dry for middens to form in the past during extended droughts, this could likely create the “gaps” in our record. Hence, a lack of middens for prolonged periods of time could be a response to very arid conditions. This also implies that our record is “positively biased” in that it does a much better job at tracking wet phases than dry ones. A possible test would be to develop a similar record at higher elevations (>3500 m) where *A. cinerea* populations remain active today.

Transient Simulation of Atacama Desert Rainfall

We used the TraCE 21k simulation (34) to analyze rainfall in the Atacama Desert over the last 16,000 years to enable comparison of our results to other regional paleoclimatic records. TraCE is a simulation of the Transient (i.e., continuous) Climate of the last 21,000 years. The transient climate simulation performed was centered at 24 °S using a fully coupled model (National Center for Atmospheric Research Community Climate System Model version 3) that is forced by time-varying orbital parameters, greenhouse gases, time-varying ice-sheet extent and topography, and freshwater forcing to the oceans from the retreating ice sheets (34). The model thus simulates local impacts of major high-latitude drivers such as the HS1 and YD stadials as well as the Antarctic Cold Reversal.

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Author contributions: CL, FJGP and JLB designed, conducted the research, and wrote the paper. MIR and AM contributed with additional data and helped writing the paper. MR provided the climate models and wrote the paper. JH, CMS and JQ provided additional data, discussions, and writing. The work by JLB was done while serving as a Scientist Emeritus with the U.S. Geological Survey. **Competing interests:** The authors declare no competing financial interests. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Data and materials availability: All data are included as supplementary tables to this paper.

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FIGURES AND TABLES

Figure 1. A. Map of study area showing major trends in Mean Annual Rainfall (MAR) which positively correlates with elevation and negatively correlates with latitude. Modern midden sites (red stars; QLH = Quebrada La Higuera, SHO = Salar del Huasco; CDT = Cordón de Tuina) and DGA meteorological stations (white triangles) are also shown, as well as the current distributional range of *Abrocoma cinerea* (hatched shading). Map was created using QGIS 3.16 software using the STRM30 elevation model (Source: U.S. Geological Survey) and monthly precipitation data spanning 50 years (1950-2000) (Source: 76). **B.** Satellite image of the eastern slope of the Calama basin in the central Atacama Desert showing paleomidden sites (black circles) along with isohyets (abbreviations of paleomidden sites are: CDM = Cerros de Minta, CDA = Cerros de Aiquina, CDT = Cordón de Tuina, ACO = Arroyo Coya, EHT = El Hotel, BSA= Barros Arana, PVI = Pampa Vizchachilla) (Supplementary Table S4). **C.** Scatterplot of modern *A. cinerea* fecal pellet diameters and MAR showing the linear model employed for estimating MAR in paleomiddens ($MAR = 67.62 * [Paleomidden N_{20C}] - 148.63$; $r^2 = 0.80$; $P < 0.001$; prediction accuracy = 0.97). Shaded area corresponds to the 95% interval confidence of the model, and error bars represent the 95% standard error confidence interval.

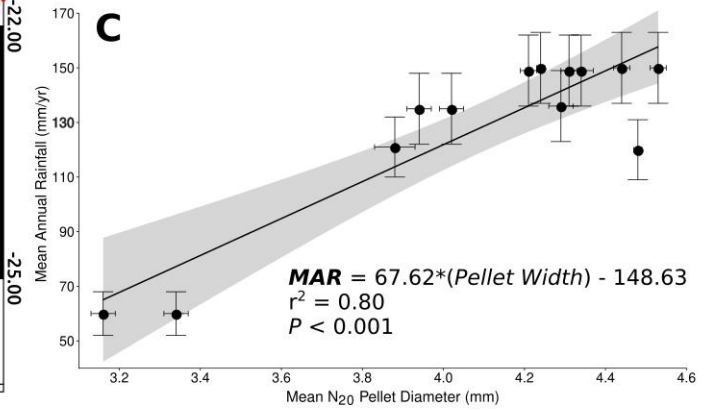
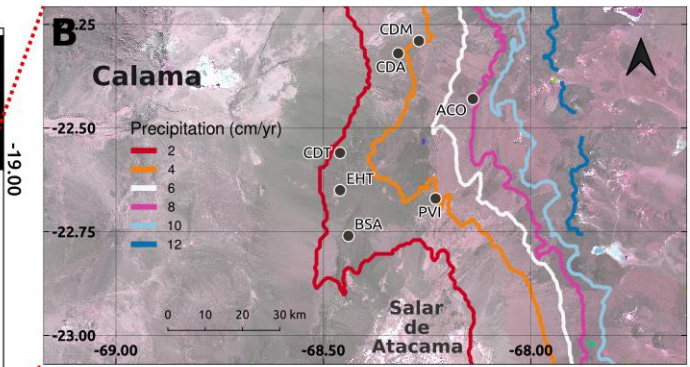
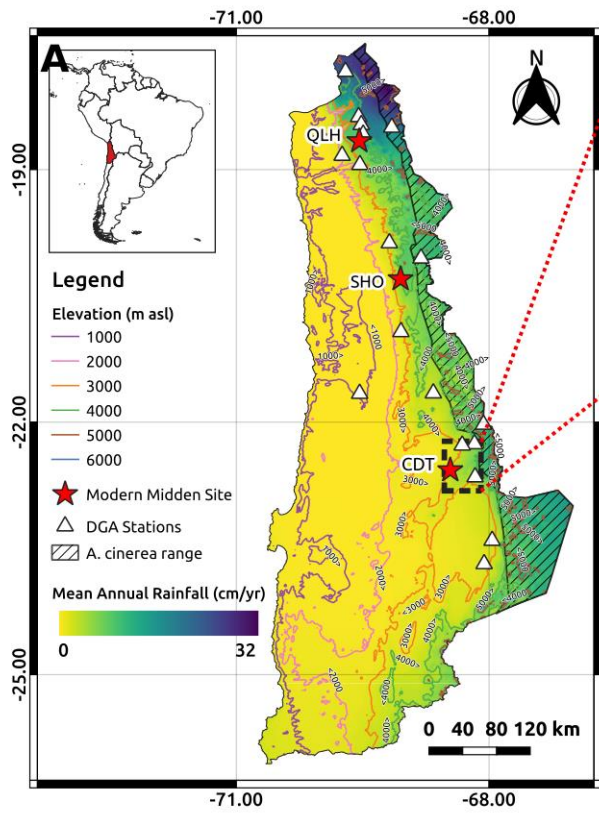


Figure 2. Temporal variation of *A. cinerea* pellet diameters (top) and estimated rainfall anomalies (bottom) in the central Atacama. **Top:** Plot of corrected pellet diameter from paleomiddens over the past 16,000 years. Error bars represent the 95% standard error confidence interval and horizontal bars represent calibrated age errors at two-sigma. **Bottom:** Plot of Mean Annual Rainfall anomalies estimated from corrected pellet diameters from paleomiddens (top) using the linear model shown in Figure 1C. Hydroclimatic phases for the Atacama are indicated in blue (wet) or red (dry) shading (see Results and Discussion). Major climate events relevant for the Atacama as established by previous research (8 and 13 for CAPE, and 21 for the MCA and the LIA) are shown for reference. Quaternary Epochs and Stages follow the International Stratigraphic Chart v.2019 (<http://www.stratigraphy.org>).

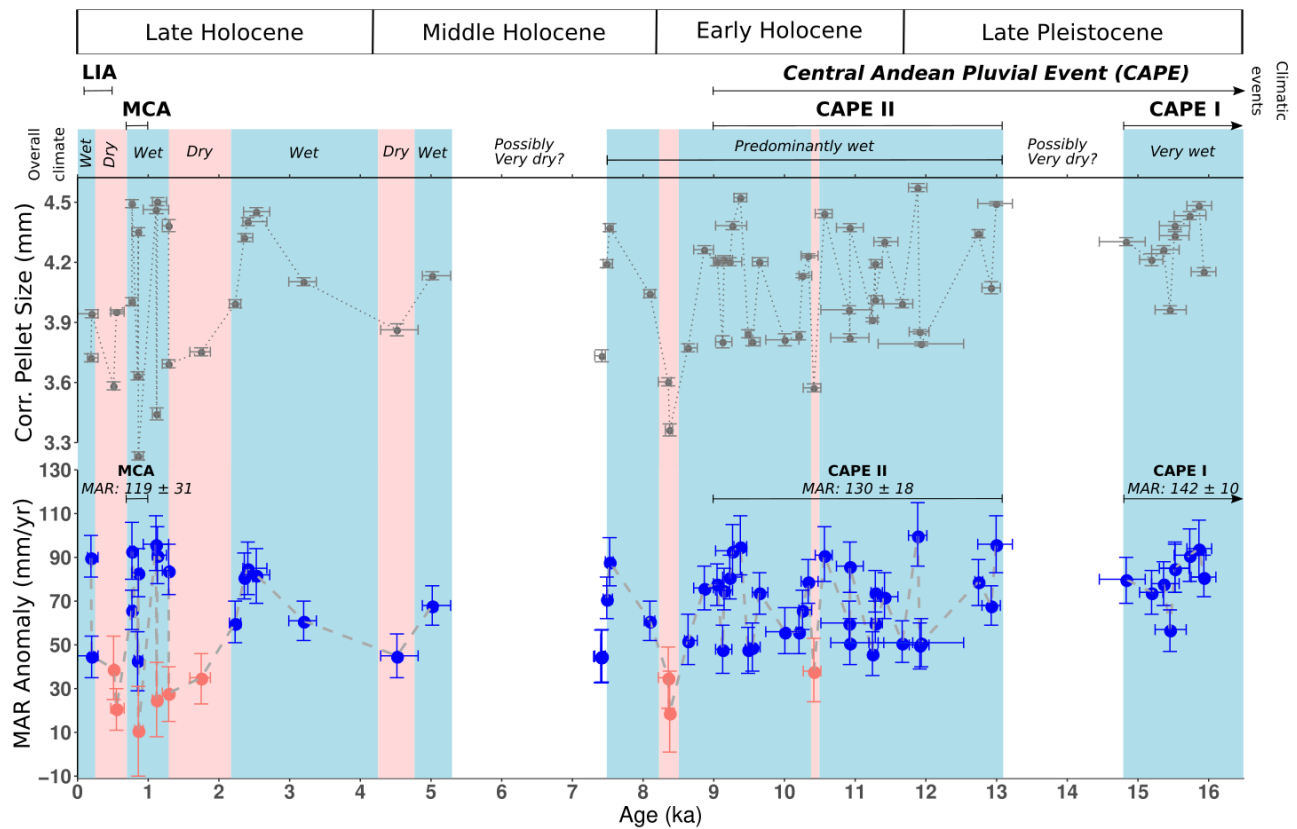
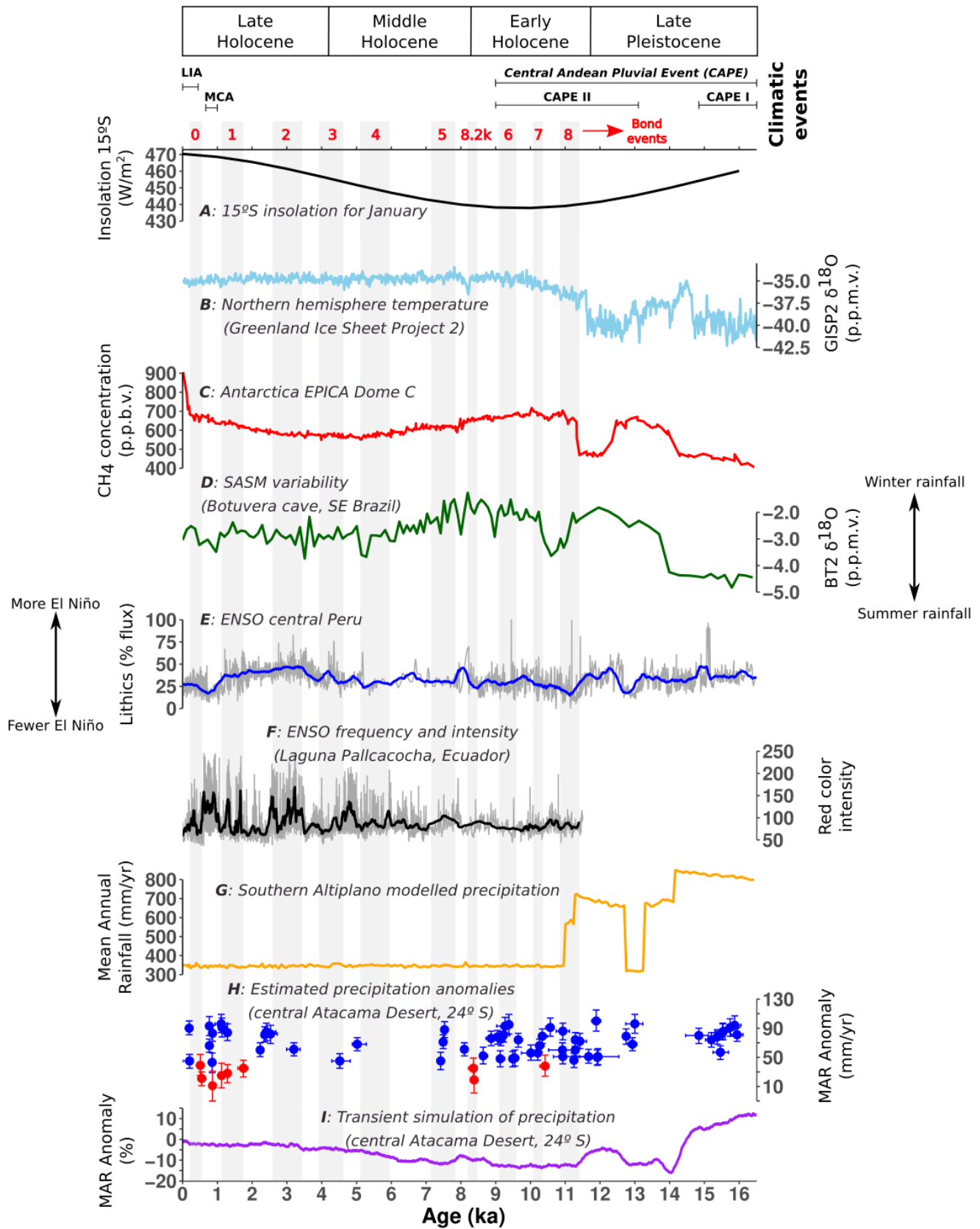


Figure 3. Comparison of regional and extra-regional paleoclimate records. **(a)** Mid-month January (summer) insolation 15°S (77). **(b)** $\delta^{18}\text{O}$ from GISP2 Greenland ice core (78). **(c)** CH_4 ice core record from EPICA Dome C Antarctica (79). **(d)** $\delta^{18}\text{O}$ speleothem record from Botuverá cave in southeast Brazil (49). **(e)** lithics concentration in a marine sediment core offshore central Peru (43). **(f)** Modeled precipitation of the southern Bolivian Altiplano (15). **(g)** Mean Annual Rainfall anomalies in the central Atacama Desert (this study). **(h)** A transient simulation of precipitation (Trace21K) over the central Atacama (24°S) plotted as 100 yr running average anomalies from present-day climate (this study). Bond events 0 – 8 and the 8.2k event are shown by vertical gray shading (16). Timing of major regional climatic events follows 8 and 13 for CAPE, and 21 for the MCA and the LIA. Quaternary Epoch Stages are after the International Stratigraphic Chart v.2019 (<http://www.stratigraphy.org>).



SUPPLEMENTARY MATERIAL

Table S1. Midden collection information. Calibrated age in calendar years before 1950 obtained in CALIB 7.1. Lab Code corresponds to the laboratories where samples were sent for radiocarbon dating (UGAMS = University of Georgia AMS; UCIAMS = Keck-CCAMS Group, Irvine, California, USA; GX = Geochron Labs; AA = Arizona–NSF Accelerator Facility).

#	Midden ID	Latitude (°S)	Longitude (°W)	Elevation (masl)	¹⁴ C Age	Calibrated Age	+2σ	-2σ	Lab Code
<u><i>Barros Arana</i></u>									
1	BSA 442A	-22.7557	-68.4393	3440	10130 ± 25	11670	150	260	UCIAMS-107892
2	BSA 442B	-22.7557	-68.4393	3440	9895 ± 25	11250	70	40	UCIAMS-107891
3	BSA 442C	-22.7557	-68.4393	3440	10025 ± 25	11420	190	150	UCIAMS-107893
<u><i>Cerros de Aiquina</i></u>									
4	CDA 186A	-22.3325	-68.3212	3240	10935 ± 30	12750	60	50	UCIAMS-97083
5	CDA 502	-22.3271	-68.3260	3108	11105 ± 35	13000	130	130	UCIAMS-97091
6	CDA 503	-22.3280	-68.3258	3134	8230 ± 25	9130	130	100	UCIAMS-97084
7	CDA 505	-22.3326	-68.3236	3165	12795 ± 40	15200	160	170	UCIAMS-97085
8	CDA 506A	-22.3331	-68.3222	3189	7325 ± 25	8100	70	80	UCIAMS-97078
9	CDA 506B	-22.3331	-68.3222	3189	8030 ± 25	8870	130	150	UCIAMS-97079
10	CDA 507A	-22.3330	-68.3222	3189	1400 ± 20	1290	20	90	UGAMS-8963
11	CDA 535	-22.3238	-68.3312	2967	13300 ± 35	15940	170	180	UGAMS-8971
12	CDA 545A	-22.3311	-68.3251	3196	2420 ± 25	2410	270	70	UGAMS-8964
13	CDA 550A	-22.3190	-68.2896	3352	1395 ± 20	1290	20	90	UCIAMS-97077
14	CDA 561B	-22.3300	-68.3216	3100	9230 ± 30	10340	140	100	UCIAMS-8968
15	CDA 562A	-22.3300	-68.3215	3101	6545 ± 25	7420	50	100	UCIAMS-97087
16	CDA 563B	-22.3313	-68.3182	3173	4475 ± 20	5020	260	140	UCIAMS-97081
17	CDA 571	-22.3155	-68.3248	3164	2390 ± 25	2360	120	40	UGAMS-8966

#	Midden ID	Latitude (°S)	Longitude (°W)	Elevation (masl)	¹⁴ C Age	Calibrated Age	+2σ	-2σ	Lab Code
18	CDA 574C	-22.3246	-68.3286	3115	8640 ± 25	9550	110	50	UGAMS-8969
19	CDA 574F	-22.3246	-68.3286	3115	7600 ± 30	8380	40	60	UGAMS-8970
20	CDA 575	-22.3326	-68.3237	3111	6695 ± 25	7530	50	60	UCIAMS-97075
21	CDA 591A	-22.3307	-68.3223	3210	9160 ± 30	10260	130	50	UCIAMS-97089
22	CDA 595A	-22.3157	-68.3264	3140	8240 ± 30	9150	120	120	UGAMS-8967
23	CDA 595B	-22.3157	-68.3264	3140	2245 ± 20	2230	80	80	UCIAMS-97082
24	CDA 616A	-22.3185	-68.2892	3355	200 ± 20	200	90	200	UCIAMS-97090
<i><u>Cerros de Minta</u></i>									
25	CDM 481B	-22.2967	-68.2520	3250	4070 ± 80	4520	300	230	GX-25658
26	CDM 482A	-22.2959	-68.2531	3250	3060 ± 70	3200	180	210	GX-27821
27	CDM 484	-22.2923	-68.2669	3300	2490 ± 70	2530	190	180	GX-27822
28	CDM 485	-22.2940	-68.2627	3300	1860 ± 60	1750	130	160	GX-27823
<i><u>Cordón de Tuina</u></i>									
29	CDT 386C	-22.5686	-68.4612	3190	9630 ± 140	10920	320	400	GX-24205
30	CDT 386M1	-22.5686	-68.4612	3190	130 ± 20	90	170	10	--
31	CDT 386M2	-22.5686	-68.4612	3190	130 ± 20	90	170	90	--
32	CDT 387	-22.5647	-68.4626	3079	8940 ± 70	10010	200	270	GX-26748
33	CDT 389C	-22.5676	-68.4456	3180	9630 ± 95	10930	270	270	GX-24210-LS
34	CDT 391C1	-22.5599	-68.4377	3150	1240 ± 100	1110	180	180	GX-25419
35	CDT 391C2	-22.5599	-68.4377	3150	10280 ± 150	11940	600	610	GX-24211
36	CDT 401	-22.6181	-68.4685	3153	920 ± 15	770	30	40	UCIAMS-123135

#	Midden ID	Latitude (°S)	Longitude (°W)	Elevation (masl)	^{14}C Age	Calibrated Age	+2 σ	-2 σ	Lab Code
37	CDT 435	-22.5558	-68.4637	3166	8155 ± 20	9050	80	50	UCIAMS-123277
38	CDT 437A	-22.5742	-68.4712	3112	8295 ± 20	9230	170	100	UCIAMS 107881
39	CDT 437B	-22.5742	-68.4712	3112	9290 ± 25	10420	100	150	UCIAMS 107882
40	CDT 438A2	-22.5969	-68.4487	3278	6635 ± 20	7490	80	50	UCIAMS 107885
41	CDT 438B	-22.5969	-68.4487	3278	8510 ± 20	9490	40	40	UCIAMS 107886
42	CDT 439-2.0	-22.5964	-68.4490	3295	1265 ± 20	1130	130	70	UCIAMS 107887
43	CDT 440A	-22.6097	-68.4769	3118	7905 ± 20	8640	130	50	UCIAMS 107888
44	CDT 440C1	-22.6097	-68.4769	3118	9060 ± 25	10210	30	40	UCIAMS-123137
45	CDT 440C2	-22.6097	-68.4769	3118	1000 ± 15	850	70	50	UCIAMS 107889
46	CDT 440D	-22.6097	-68.4769	3118	515 ± 15	510	20	10	UCIAMS 107890
<i><u>El Hotel</u></i>									
47	EHT 383	-22.6644	-68.4649	3141	8320 ± 90	9270	200	240	GX-24200-LS
48	EHT 384B	-22.6641	-68.4644	3219	11190 ± 120	13000	230	260	GX-24202-LS
49	EHT 453B1	-22.6602	-68.4628	3243	9395 ± 25	10570	110	130	UCIAMS-133903
50	EHT 453B2	-22.6602	-68.4628	3245	9950 ± 25	11290	100	60	UCIAMS-107896
51	EHT 454X	-22.6539	-68.4584	3272	960 ± 15	860	40	90	UCIAMS-133904
52	EHT 454Y	-22.6539	-68.4584	3272	915 ± 15	770	30	30	UCIAMS-133897

#	Midden ID	Latitude (°S)	Longitude (°W)	Elevation (masl)	¹⁴ C Age	Calibrated Age	+2σ	-2σ	Lab Code
53	EHT 462	-22.6502	-68.4659	3254	9630 ± 35	10930	190	190	UCIAMS-133896
54	EHT 464_1	-22.6523	-68.4575	3276	13030 ± 40	15530	210	220	UCIAMS-133901
55	EHT 464_2	-22.6523	-68.4575	3276	12580 ± 40	14840	270	380	UCIAMS-133899
56	EHT 466A	-22.6627	-68.4645	3238	13155 ± 40	15740	230	220	UCIAMS-133898
57	EHT 466B	-22.6627	-68.4645	3228	13030 ± 35	15530	200	220	UCIAMS-107898
58	EHT 468	-22.6609	-68.4679	3231	7575 ± 20	8360	40	140	UCIAMS-107899
59	EHT 469A	-22.6617	-68.4695	3224	1250 ± 15	1120	50	60	UCIAMS-107900
60	EHT 469C	-22.6617	-68.4695	3224	1015 ± 15	860	70	50	UCIAMS-107901
61	EHT 470A	-22.6597	-68.4648	3240	13245 ± 35	15870	180	170	UCIAMS-107903
62	EHT 470B	-22.6597	-68.4648	3240	10240 ± 25	11890	130	130	UCIAMS-107904
63	EHT 475	-22.6496	-68.4579	3279	12980 ± 45	15460	230	210	UCIAMS-133900
65	EHT 477	-22.6480	-68.4604	3271	10270 ± 30	11920	130	150	UCIAMS-133905
66	EHT 478A	-22.6478	-68.4608	3266	8750 ± 25	9650	120	100	UCIAMS-133902
67	EHT 478B	-22.6478	-68.4608	3266	8395 ± 25	9380	90	90	UCIAMS-107905
68	EHT 500	-22.6500	-68.4657	3255	12925 ± 35	15370	220	170	UCIAMS-123139
<i><u>Quebrada La Higuera</u></i>									
69	QLH 86	-18.6604	-69.5464	3454	105 ± 15	Postbomb	--	--	--

#	Midden ID	Latitude (°S)	Longitude (°W)	Elevation (masl)	¹⁴ C Age	Calibrated Age	+2σ	-2σ	Lab Code
70	QLH 285	-18.6602	-69.5445	3457	30 ± 15	Postbomb	--	--	--
71	QLH 281	-18.6601	-69.5442	3459	85 ± 15	Postbomb	--	--	--
72	QLH 183	-18.6612	-69.5429	3468	140 ± 15	90	160	90	--
73	QLH 182A	-18.6609	-69.5425	3469	110 ± 15	Postbomb	--	--	--
74	QLH 182B	-18.6609	-69.5425	3469	120 ± 20	80	170	80	--
<i><u>Salar del Huasco</u></i>									
75	SHO 116	-20.3028	-69.0460	3746	70 ± 30	PostBomb	--	--	--
76	SHO 120C	-20.3023	-69.0456	3756	60 ± 34	PostBomb	--	--	--
77	SHO 123	-20.3021	-69.0456	3758	110 ± 30	PostBomb	--	--	--
78	SHO 161-2A	-20.3096	-69.0787	3486	80 ± 25	PostBomb	--	--	--
79	SHO 164	-20.3090	-69.0783	3513	90 ± 30	PostBomb	--	--	--
<i><u>Single-point Localities*</u></i>									
80	ACO 321	-22.4309	-68.1415	3823	570 ± 70	550	110	80	GX-23851
81	PVI 404	-22.6719	-68.2342	3125	220 ± 20	190	100	50	GX-24913

Table S2. Modern midden dataset used for calibration. ^{14}C Age of middens are shown in Table 1 and MAR and MAT estimates and associated standard errors for each midden locality were obtained from Table S6. N_{TOT} corresponds to the total number of pellets measured in each midden, while N_{20} represents the 20% higher used for establishment of linear relations with climatic variables at each site (Figure 1C). SE = 95% standard error confidence interval.

Midden ID	MAT \pm SE ($^{\circ}\text{C}/\text{yr}$)	MAR \pm SE (mm/yr)	N_{TOT}	N_{TOT} Mean \pm SE (mm)	N_{20}	N_{20} Mean \pm SE (mm)
QLH 86	8.8 ± 0.07	149 ± 13	235	3.81 ± 0.02	47	4.34 ± 0.03
QLH 285	8.8 ± 0.07	149 ± 13	230	3.86 ± 0.02	46	4.21 ± 0.02
QLH 281	8.8 ± 0.07	149 ± 13	235	4.00 ± 0.01	47	4.31 ± 0.02
QLH 183	8.7 ± 0.07	150 ± 13	235	4.08 ± 0.02	47	4.44 ± 0.02
QLH 182A	8.7 ± 0.07	150 ± 13	235	3.94 ± 0.01	47	4.24 ± 0.01
QLH 182B	8.7 ± 0.07	150 ± 13	235	4.15 ± 0.02	47	4.53 ± 0.02
SHO 161-2A	8.6 ± 0.08	120 ± 11	207	4.17 ± 0.01	41	4.48 ± 0.01
SHO 164	8.5 ± 0.08	121 ± 11	180	3.46 ± 0.02	36	3.88 ± 0.05
SHO 116	7.3 ± 0.09	135 ± 13	200	3.46 ± 0.02	40	3.94 ± 0.03
SHO 120C	7.3 ± 0.09	135 ± 13	200	3.62 ± 0.02	40	4.02 ± 0.03
SHO 123	7.3 ± 0.09	136 ± 13	202	3.92 ± 0.02	40	4.29 ± 0.03
CDT 386M1	10.1 ± 0.06	60 ± 8	200	2.56 ± 0.03	40	3.16 ± 0.03
CDT 386M2	10.1 ± 0.06	60 ± 8	179	2.77 ± 0.03	35	3.35 ± 0.03

Table S3. Paleomidden dataset information. Age is indicated in ka with two-sigma ranges. N_{TOT} corresponds to the total number of pellets measured in each midden, N_{20} represents the 20% higher used for estimating MAR for each midden. Modern MAR values for each midden locality were obtained using elevation and latitude information for each site as input in the linear equations described in the methods. SE = 95% standard error confidence interval. CI and PI correspond to the 95% confidence and predicted interval, respectively.

Midden ID	Age (ka)	+2 σ	-2 σ	N_{TOT}	N_{20}	N_{20} Mean \pm SE	Modern MAR \pm SE	Estimated MAR	95% CI	95% PI
CDA 535	15.9	170	180	209	41	3.69 ± 0.02	52 ± 7	133	129 – 143	99 – 167
EHT 470A	15.9	180	170	234	47	4.02 ± 0.02	61 ± 8	156	143 – 169	120 – 191
EHT 466A	15.7	230	220	210	42	3.98 ± 0.02	61 ± 8	152	140 – 164	117 – 187
EHT 464_1	15.5	210	220	272	55	3.93 ± 0.02	64 ± 9	149	137 – 160	114 – 184
EHT 466B	15.5	200	220	207	41	3.88 ± 0.02	61 ± 8	146	135 – 156	111 – 180
EHT 475	15.5	230	210	200	40	3.52 ± 0.02	64 ± 9	121	111 – 130	86 – 155
EHT 500	15.4	220	170	219	44	3.82 ± 0.02	63 ± 8	141	131 – 151	106 – 175
CDA 505	15.2	160	170	206	41	3.77 ± 0.03	63 ± 8	137	128 – 147	103 – 172
EHT 464_2	14.8	270	380	213	43	3.87 ± 0.02	64 ± 9	144	133 – 154	109 – 178
CDA 502	13.0	130	130	200	40	3.70 ± 0.03	60 ± 8	128	119 – 137	94 – 162
EHT 384B	13.0	230	260	227	45	4.12 ± 0.01	60 ± 8	156	143 – 169	121 – 192
CDA 186A	12.8	60	50	208	41	3.98 ± 0.02	68 ± 9	146	135 – 157	112 – 181
CDT 391C2	11.9	600	610	200	40	3.45 ± 0.01	58 ± 8	109	98 – 120	74 – 144
EHT 477	11.9	130	150	203	40	3.51 ± 0.01	63 ± 9	113	103 – 123	79 – 147
EHT 470B	11.9	130	130	237	47	4.23 ± 0.02	61 ± 8	162	147 – 176	126 – 198
BSA 442A	11.7	150	260	211	42	3.66 ± 0.02	71 ± 9	123	113 – 132	88 – 157

Midden ID	Age (ka)	+2σ	-2σ	N_{TOT}	N₂₀	N₂₀ Mean \pm SE	Modern MAR \pm SE	Estimated MAR	95% CI	95% PI
BSA 442C	11.4	190	150	217	43	3.98 \pm 0.02	71 \pm 9	144	133 – 154	109 – 178
EHT 453B2	11.3	100	60	225	45	3.87 \pm 0.02	62 \pm 8	136	127 – 146	102 – 170
EHT 476	11.3	100	60	200	40	3.69 \pm 0.02	63 \pm 9	124	115 – 133	90 – 158
BSA 442B	11.3	70	40	205	41	3.59 \pm 0.01	71 \pm 9	117	107 – 127	83 – 151
CDT 389C	10.9	270	270	200	40	3.51 \pm 0.02	60 \pm 8	111	100 – 122	77 – 146
EHT 462	10.9	190	190	220	44	4.06 \pm 0.02	62 \pm 8	148	137 – 160	114 – 183
CDT 386C	10.9	320	400	200	40	3.65 \pm 0.02	60 \pm 8	121	111 – 130	86 – 155
EHT 453B1	10.6	110	130	213	43	4.14 \pm 0.02	62 \pm 8	153	141 – 165	118 – 188
CDT 437B	10.4	100	150	264	53	3.28 \pm 0.02	56 \pm 8	94	80 – 109	58 – 130
CDA 561B	10.3	140	100	215	43	3.94 \pm 0.01	60 \pm 8	139	129 – 149	105 – 173
CDA 591A	10.3	130	50	225	45	3.84 \pm 0.01	66 \pm 8	132	123 – 141	98 – 166
CDT 440C1	10.2	30	40	212	42	3.54 \pm 0.02	55 \pm 8	112	101 – 122	77 – 146
CDT 387	10.0	200	270	200	40	3.53 \pm 0.03	54 \pm 8	110	100 – 121	76 – 145
EHT 478A	9.7	120	100	208	42	3.93 \pm 0.02	63 \pm 8	137	127 – 146	103 – 171
CDA 574C	9.6	110	50	197	39	3.53 \pm 0.02	61 \pm 8	110	99 – 121	75 – 144
CDT 438B	9.5	40	40	200	40	3.58 \pm 0.02	65 \pm 9	112	102 – 123	78 – 147
EHT 478B	9.4	90	90	204	41	4.26 \pm 0.02	56 \pm 8	158	145 – 172	123 – 194
EHT 383	9.3	200	240	228	45	4.12 \pm 0.02	56 \pm 8	149	137 – 160	114 – 184
CDT 437A	9.2	170	100	208	42	3.94 \pm 0.02	62 \pm 8	137	127 – 146	103 – 171
CDA 595A	9.2	120	120	210	42	3.96 \pm 0.02	62 \pm 8	137	128 – 147	103 – 172
CDA 503	9.1	130	100	208	41	3.55 \pm 0.03	59 \pm 8	110	99 – 121	75 – 144
CDT 435	9.1	80	50	217	43	3.95 \pm 0.02	65 \pm 8	137	127 – 146	103 – 171
CDA 506B	8.9	130	150	229	45	4.01 \pm 0.02	65 \pm 8	141	131 – 151	106 – 175

Midden ID	Age (ka)	+2 σ	-2 σ	N _{TOT}	N ₂₀	N ₂₀ Mean \pm SE	Modern MAR \pm SE	Estimated MAR	95% CI	95% PI
CDT 440A	8.6	130	50	204	41	3.53 \pm 0.02	55 \pm 8	108	96 – 119	73 – 142
CDA 574F	8.4	40	60	201	40	3.13 \pm 0.03	61 \pm 8	80	62 – 98	42 – 118
EHT 468	8.4	40	140	166	33	3.37 \pm 0.02	61 \pm 8	96	82 – 110	61 – 132
CDA 506A	8.1	70	80	214	42	3.82 \pm 0.02	65 \pm 8	126	117 – 135	92 – 160
CDA 575	7.5	50	60	195	39	4.16 \pm 0.02	60 \pm 8	148	137 – 160	114 – 183
CDT 438A2	7.5	80	50	207	41	3.99 \pm 0.02	65 \pm 9	136	127 – 146	102 – 170
CDA 562A	7.4	50	100	200	40	3.53 \pm 0.03	60 \pm 8	105	93 – 117	70 – 140
CDA 563B	5.0	260	140	257	51	4.00 \pm 0.02	64 \pm 8	132	123 – 141	98 – 166
CDM 481B	4.5	300	230	158	31	3.74 \pm 0.03	69 \pm 9	114	104 – 124	79 – 148
CDM 482A	3.2	180	210	206	41	4.02 \pm 0.02	69 \pm 9	130	121 – 139	96 – 164
CDM 484	2.5	190	180	200	40	4.39 \pm 0.02	72 \pm 9	154	141 – 166	119 – 189
CDA 545A	2.4	270	70	230	46	4.35 \pm 0.02	65 \pm 8	150	139 – 162	115 – 185
CDA 571	2.4	120	40	235	47	4.27 \pm 0.02	64 \pm 8	145	134 – 156	110 – 179
CDA 595B	2.2	80	80	208	41	3.94 \pm 0.02	62 \pm 8	123	113 – 132	88 – 157
CDM 485	1.8	130	160	200	40	3.72 \pm 0.02	72 \pm 9	106	95 – 118	72 – 141
CDA 507A	1.3	20	90	207	41	4.36 \pm 0.03	65 \pm 8	149	137 – 160	114 – 184
CDA 550A	1.3	20	90	205	41	3.67 \pm 0.02	74 \pm 9	102	90 – 115	67 – 137
CDT 439-2.0	1.1	130	70	219	44	4.49 \pm 0.02	66 \pm 9	157	144 – 170	122 – 192
EHT 469A	1.1	50	60	208	40	3.43 \pm 0.03	61 \pm 8	85	69 – 102	48 – 122
CDT 391C1	1.1	180	180	200	40	4.45 \pm 0.02	58 \pm 8	154	142 – 167	119 – 189
EHT 454X	0.9	40	90	219	44	4.34 \pm 0.02	63 \pm 9	147	136 – 158	112 – 181
EHT 469C	0.9	70	50	195	39	3.22 \pm 0.02	61 \pm 8	71	50 – 92	32 – 110
CDT 440C2	0.9	70	50	211	42	3.62 \pm 0.02	55 \pm 8	98	85 – 112	63 – 134

Midden ID	Age (ka)	+2σ	-2σ	N_{TOT}	N₂₀	N₂₀ Mean \pm SE	Modern MAR \pm SE	Estimated MAR	95% CI	95% PI
CDT 401	0.8	30	40	244	49	4.00 \pm 0.02	57 \pm 8	123	114 – 132	89 – 157
EHT 454Y	0.8	30	30	212	42	4.49 \pm 0.02	63 \pm 9	156	143 – 169	121 – 192
ACO 321	0.6	110	80	891	178	3.95 \pm 0.01	99 \pm 11	120	110 – 129	86 – 154
CDT 440D	0.5	20	10	200	40	3.58 \pm 0.02	55 \pm 8	95	81 – 109	59 – 131
CDA 616A	0.2	90	200	200	40	3.95 \pm 0.02	75 \pm 9	119	110 – 129	85 – 153
PVI 404	0.2	100	50	1018	203	3.73 \pm 0.02	55 \pm 8	104	92 – 116	69 – 139

Table S4. DGA climatic stations employed in this study.

#	Station name	Latitude (°S)	Longitude (°W)	Elevation (m asl)	Dataset
1	Humpalca	-17.835	-69.704	3980	Rainfall
2	Pacollo	-18.177	-69.509	4185	Temperature
3	Putre	-18.199	-69.560	3545	Temperature
4	Central Chapiquia	-18.372	-69.548	3350	Rainfall
5	Belen	-18.467	-69.517	3240	Rainfall
6	Guallatire	-18.498	-69.155	4240	Rainfall
7	Tignamar	-18.581	-69.494	3230	Rainfall
8	Codpa	-18.832	-69.744	1870	Rainfall, Temperature
9	Esquia	-18.942	-69.533	2170	Rainfall
10	Poroma	-19.872	-69.183	2880	Rainfall
11	Coyacagua	-20.053	-68.808	4013	Rainfall, Temperature
12	Guatacondo Dga	-20.927	-69.046	2460	Rainfall
13	Cebollar	-21.531	-68.339	3730	Temperature
14	Lequena	-21.655	-68.661	3320	Rainfall
15	Quillagua	-21.660	-69.536	802	Rainfall
16	Parshall N2	-21.943	-68.516	3318	Temperature
17	Inacaliri	-22.028	-68.066	4040	Rainfall, Temperature
18	Conchi Embalse	-22.052	-68.624	3010	Temperature
19	Linzor	-22.230	-68.023	4100	Temperature
20	Turi	-22.241	-68.288	3070	Temperature
21	Toconce	-22.259	-68.173	3310	Rainfall
22	Ayquina	-22.275	-68.318	3031	Rainfall
23	Caspana	-22.337	-68.212	3260	Temperature
24	Chiu-Chiu	-22.338	-68.637	2524	Temperature
25	El Tatio	-22.371	-68.013	4370	Temperature

#	Station name	Latitude (°S)	Longitude (°W)	Elevation (m asl)	Dataset
26	Coya Sur	-22.394	-69.623	1250	Temperature
27	Calama	-22.449	-68.904	3300	Temperature
28	Rio Grande	-22.652	-68.166	3250	Rainfall
29	San Pedro	-22.905	-68.200	2450	Temperature
30	Baquedano	-23.334	-69.840	1032	Temperature
31	Camar	-23.407	-67.963	2700	Rainfall
32	Peine	-23.684	-68.058	2460	Rainfall, Temperature
33	Lautaro Embalse	-27.798	-70.003	1110	Temperature

Figure S1. Midden building rodent species found in northern Chile (top), along with their associated fecal pellets (middle), and estimated distributional ranges (bottom; from 39) ordered from left to right by the relative frequency at which paleomiddens built by these species are found. Scale bar for fecal pellet photographs is 5 mm. Rodent photographs courtesy of Michael Weymann (*A. cinerea* and *L. viscacia*) and Edwin Riveros (*P. xanthopygus*).

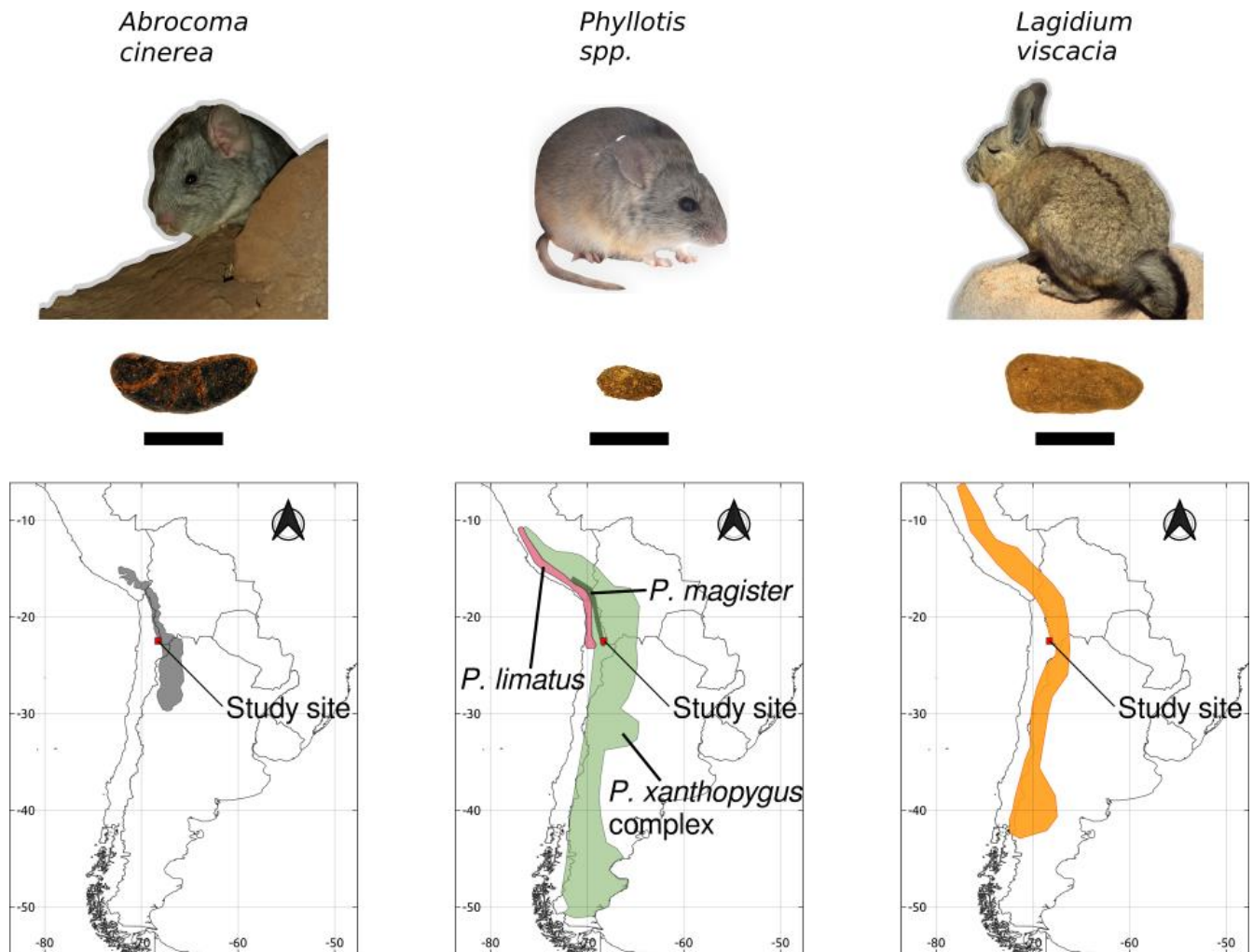


Figure S2. Regional patterns of present-day temperature and rainfall and estimation of midden site values. **A.** Relationship between elevation (m asl) and MAT for the year 1989. Points represent mean annual estimates and numbers indicate DGA weather station as in Table S4. Shaded area represents the 95% confidence interval of the model. A general form of the equation employed to estimate annual MAT values for middens sites between 1976–1989 is shown, with parameters a and b particular to each year. The minimum and maximum variance explained throughout the period is also shown. **B.** Relationship between latitude (°S) and MAR also for 1989 by way of comparison. Points and shaded area as in A. The general form of the regression function employed to estimate annual MAR values in modern middens between 1987 – 2016 is shown, with parameters a , b , and c particular to each year. Note that MAR varies with both elevation and latitude, although only one relationship is shown. The minimum and maximum variance explained throughout the period is also shown. **C.** Annual estimates of MAT values for four modern middens based on the general equation shown in A. Total means for the period 1976–1989 are indicated for each midden and correspond to values reported in Table S2. **D.** Annual estimates of MAR values for three modern middens based on the general equation described in B. Total means for the period 1987 – 2016 are indicated for each midden and correspond to values reported in Table S2.

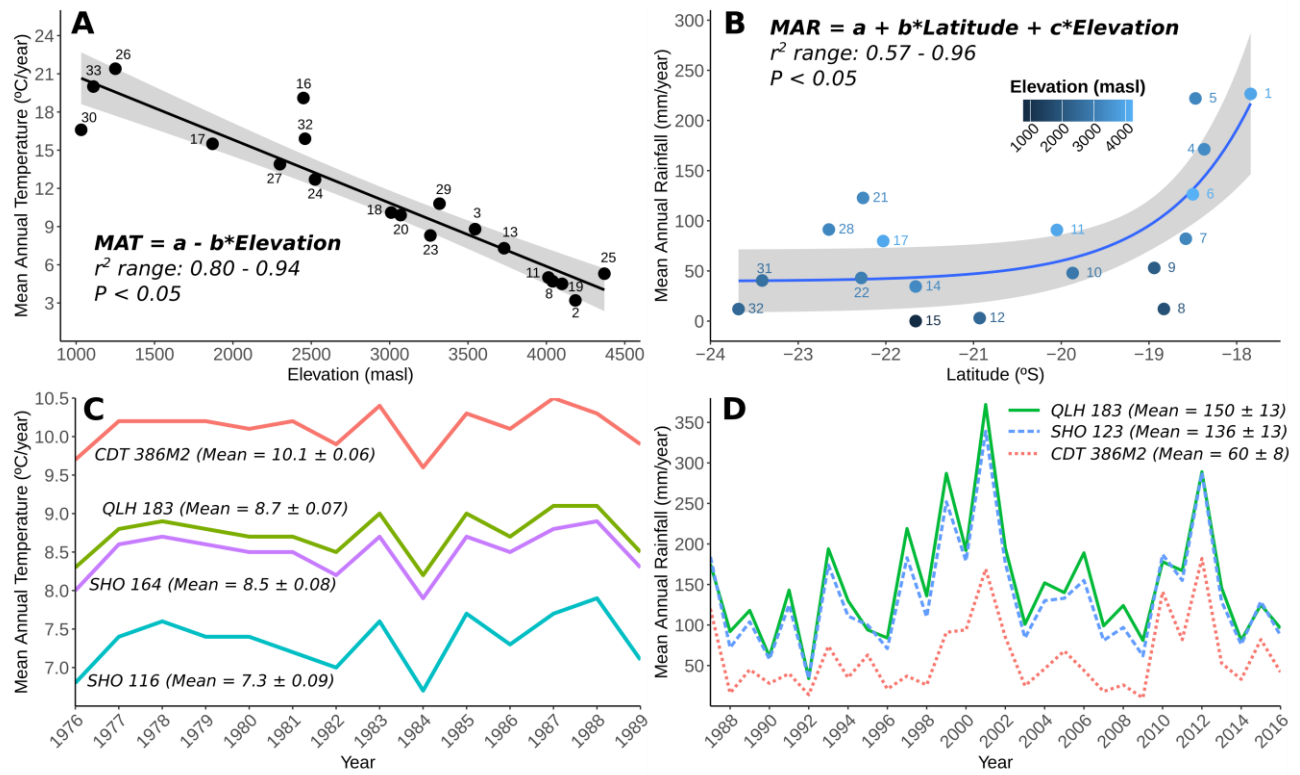


Figure S3. Scatterplots and linear relationships of variations in N₂₀ pellet diameters as a function of MAR (left) and MAT (right). Shaded area corresponds to the 95% interval confidence of the model and bars around points represent the 95% standard error confidence interval.

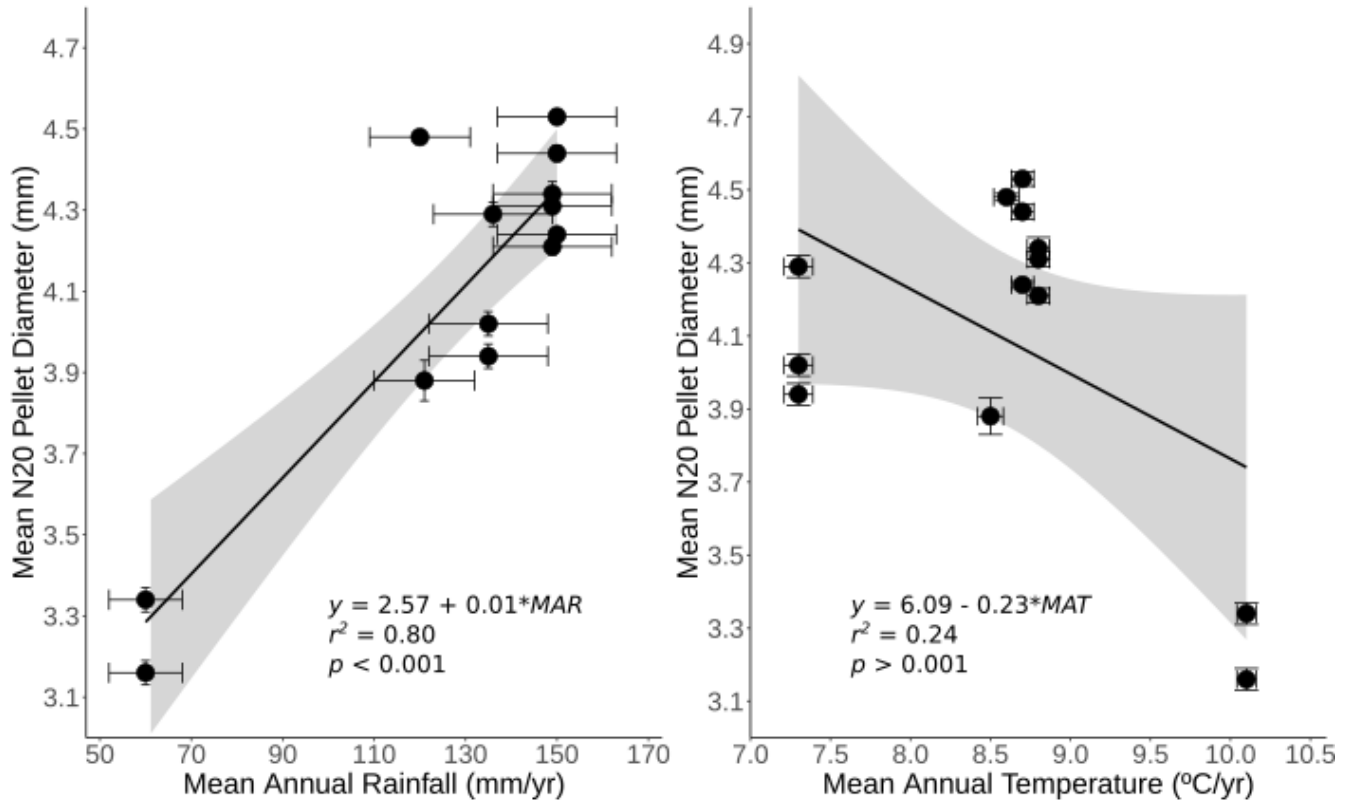


Figure S4. Taphonomic effect on fecal pellet diameters as they age. Points represent the highest peaks in pellet measurements sampled every thousand years in two basins, as represented by two localities where the midden record is sufficiently continuous during the last 16 ka. A linear model describing an increase in pellet sizes towards the present is observed in both sites (dashed lines) with similar slopes. Pooling all information allows for estimation of a correction factor using a constantly decreasing size in fecal pellets with time (average slope = -0,03 mm/ka). Midden site information is available in Table 1.

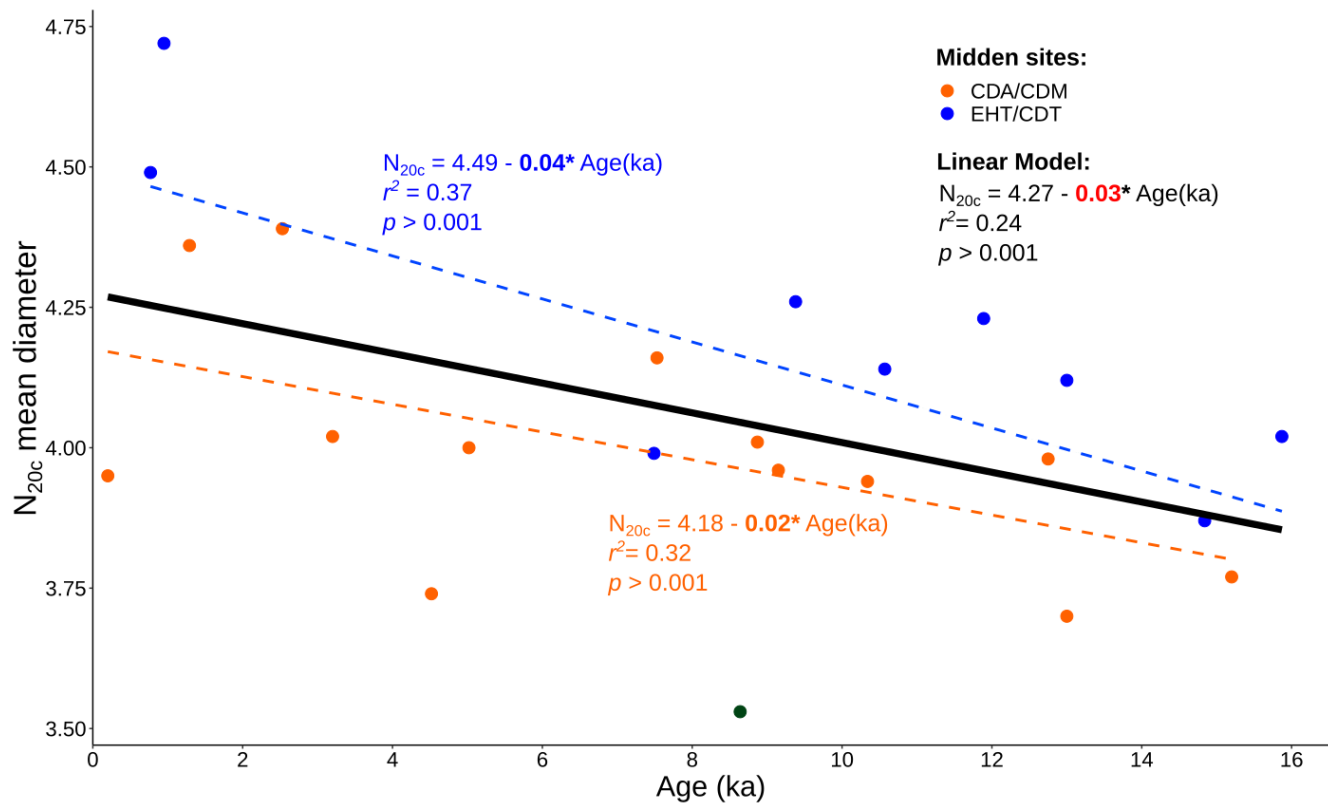
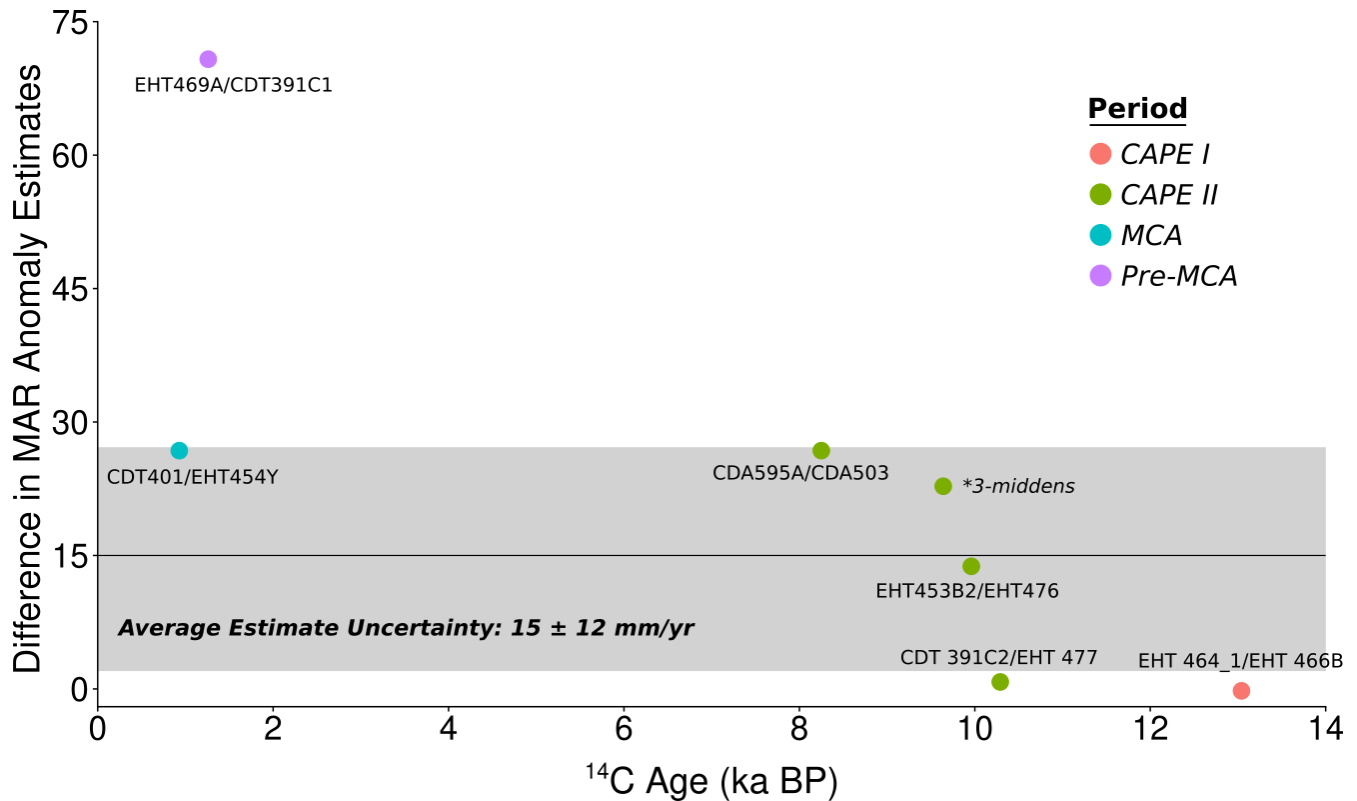


Figure S5. Uncertainty of MAR Anomaly estimates as established by a scatterplot of standardized MAR differences (in mm/yr) for pairs of paleomiddens practically identical in age (i.e., no more than 10^{14}C years apart from each other). Midden sample numbers are indicated next to each point. The “*3-middens” represents the average difference in MAR anomalies between three middens all dated to 9630 ^{14}C yr (CDT389C, CDT386C, and EHT462). *Note:* Paleomiddens dated using conventional radiocarbon dating (the ‘GX’ series in Table S1) were excluded from this analysis due to large errors in age. The “pre-MCA” pair of paleomiddens was excluded from the average for reasons given in the



Discussion section.

GENERAL CONCLUSIONS

Using a combined approach from the disciplines of Evolutionary Biology and Paleoecology, this doctoral thesis shows how chinchilla rats, hystricognath rodents endemic to the central Andes, responded to past environmental changes. Overall, these biotic responses depended largely on the nature and temporal extension of events. Initial diversification of the family occurred during the Middle and Late Miocene (13 – 7 Mya) coeval with Andean uplift, likely driven by allopatric speciation by mountain formation (*i.e.*, vicariance). Ecological speciation instead seems to have driven additional diversification through adaptation in newly formed high-elevation environments. Short-term late Quaternary climatic oscillations, in turn, do not appear to have been a strong diversification driver. Apparently, however, initial stages of genetic divergence occurred since the middle Pleistocene (0.5 Mya) in the *A. cinerea* species complex. Populations of *A. cinerea* over the central Atacama Desert in northern Chile likely experienced phenotypic changes in body size associated with hydroclimatic variability since the last glacial termination (past 16 ka BP). These results provide perhaps one of the most remarkable outcomes from this study: morphological change in abrocomids can occur within centuries in response to abrupt environmental change whereas genetic divergence seems to occur at a much more protracted rate in response to intensive but long-term environmental change, although not without certain important caveats as discussed below.

Studies on molecular systematics or population genetics in abrocomids are particularly difficult to pursue due to species and individual sampling. Difficulties in access to areas inhabited by most species, plus shyness and/or rareness during live-trapping, pose important limitations which were circumvented by sampling specimens available in natural collections. Unfortunately, access to sampling was denied for some collections, arguing a lack of previous positive results using museum samples, despite acknowledging fieldwork difficulties associated with collecting chinchilla rats and the absence of any prior molecular surveys using museum specimens. I strongly support avoiding

unnecessary destructive sampling of museum specimens whenever possible, yet sampling vouchered specimens of Abrocomidae remained the only alternative after 3-4 unsuccessful field work seasons. It is expected then that this study, where DNA from specimens almost 100-years old was successfully retrieved, can be employed as a reference for further studies on Abrocomidae systematics. Molecular phylogenetic analyses from this work, using both relatively recent and historical samples, suggested that systematics in Abrocomidae might be more complex than morphology-based classification schemes previously proposed. Additionally, estimates of diversification times from a time-calibrated phylogeny provided strong support for the central hypothesis: currently observed diversity and geographical distribution in abrocomids was reached during Andean orogeny and not throughout Quaternary climate oscillations. Improved sampling, either through more intense fieldwork or widest access to museum specimens are expected to confirm/reject classification schemes presented in this work and also test estimates of diversification times here obtained.

From molecular analyses alone it could have been argued that Quaternary ice ages did not induce any ecological or evolutionary changes in abrocomids. Paleomiddens of *A. cinerea* from the central Atacama Desert, however, tell a different (and perhaps more interesting) story: past abrupt changes in precipitation likely drove rapid changes in body size. These changes were estimated from variations in fecal pellet size following previous studies in other rodents. Owing to difficulties in capturing living individuals however, this relationship could not be tested. If confirmed, these results could provide evidence of environmental drivers causing body size variations, a topic of major biological interest for its consequences on the ecology and evolution of organisms. Particularly, it could provide more importance to precipitation (a *proxy* for productivity) rather than temperature as a factor potentially promoting body size variations. Meanwhile, pellet size variations enabled reconstruction of the past 16,000 years of hydroclimatic variability in the central Atacama Desert and identifying inter-hemispheric forcings working at different times. These results are crucial for assessing and developing

accurate projections of rainfall variability for this century in the dry central Andes, a region where water availability is a critical resource. Increased fieldwork efforts could certainly allow testing the relationship between fecal pellet size and body mass in *A. cinerea*, yet accomplishing these efforts might involve considerable time. Using ancient DNA (aDNA) methods however could provide an indirect approach to address this issue and explore several other topics.

Over the last decade paleogenomic studies using paleomiddens collected in arid regions from northern Chile, the western US, South Africa and Australia have successfully addressed taxonomic identification, plant-pathogen interactions, and changes in plant diversity at multiple temporal scales. Similar approaches could then be employed to test, for instance, whether pellet size changes in *A. cinerea* could be explained alternatively by local replacement of either species or populations. If the same species and population lineages persisted in the area throughout multiple dry/wet phases then another important question to address is whether these changes resulted from rapid adaptation or phenotypic plasticity. Owing to submission deadlines but mostly due to funding limitations this topic could not be addressed in this doctoral thesis yet some data was still generated during a research stay at the McMaster Ancient DNA Centre directed by Professor Hendrik Poinar. Here DNA from 58 radiocarbon dated middens from the central Atacama Desert mostly spanning the past 16 ka BP was extracted and libraries were prepared for future amplification and sequencing. Additionally, the complete mitochondrial genomes of *A. bennettii* and *A. uspillata* (best available tissues) were sequenced and assembled.

Understanding how individual species responded to environmental change in the past is critical for the elaboration of conservation strategies seeking to protect biodiversity during present and future anthropogenic climate change. Perhaps the most important contribution of this doctoral thesis is then, beyond the aforementioned results, settling the basis for future studies on the effect of abrupt climate change on small mammals using chinchilla rats as a study model. These and other rodent species from

arid regions with similar features provide indeed a unique research system to better understand the impact of past environmental change on individual species. It is expected then that this work encourages future studies also integrating paleoclimatic, paleoecological, and evolutionary research.