Research Article

The timing and ecological consequences of Pleistocene megafaunal decline in the eastern Andes of Colombia

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Abstract

Examining the ecological consequences of the late Quaternary megafaunal extinctions within biodiversity hotspots is crucial for our understanding of the potential consequences of contemporary extinctions. We present the first multi-species record of spores of coprophilous fungi (SCF) from Monquentiva and the high-Andean forests of Colombia to reconstruct Late Pleistocene and Holocene megafaunal abundance. Fossilised pollen and charcoal are used to examine the consequences of megafaunal declines on the surrounding vegetation and fire activity. Our SCF record indicates the presence of Pleistocene megafauna at least since 30,290 BP, with two waves of megafaunal decline at ca. 22,900 BP and 10,990 BP. At Monquentiva, megafaunal decline in the Early Holocene resulted in transitional non-analogue vegetation, loss of some herbivore-dispersed plant taxa, an encroachment of palatable and woody flora, and a rise in fire activity. Differences with other published South-American records suggest that ecological consequences of megafaunal declines were habitat-specific. Overall, we show that ecosystems in the eastern Colombian Cordillera were highly sensitive to the decline of megafaunal populations. Under the current biodiversity crisis, management and conservation efforts must account for the effects of local herbivore declines on plant dispersal, on fire activity, and the potential loss of ecosystem services.

Keywords: Pleistocene-Holocene transition, Palaeoecology, Colombian Andes, Spores of coprophilous fungi (SCF), Megafaunal decline, *Sporormiella*, Multiproxy, Vegetation, Fire

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INTRODUCTION

Megafauna includes mammals that weigh >45 kg and can have an important ecological role in shaping habitats and entire ecosystems (Martin and Klein, 1984; Mills et al., 1993; Gill et al., 2009). Megafauna can modify vegetation composition (Gordon et al., 2021), influence seed dispersal (Peres et al., 2016), maintain grass versus woody cover (Sankaran et al., 2005), change soil carbon storage (Derner et al., 2006; Wigley et al., 2020) and suppress fire activity (Waldram et al., 2008). In modern savannas, antelope-induced grazing suppresses grass and tree growth (Staver and Bond, 2014) while rhinos can limit fire activity by feeding on grasses and controlling fuel build up (Waldram et al., 2008). Pleistocene megafauna likely played similar roles in the ecosystems they inhabited (Johnson, 2009).

A large proportion of megafauna species went extinct on all continents during the Pleistocene (Barnosky et al., 2004). Given their ecological importance, the consequences of these Pleistocene extinctions are thought to be significant (Johnson, 2009; Malhi et al., 2016). South America lost an estimated 80%

of its megafauna, including ground sloths (*Megatherium americanum*) and glyptodons (*Glyptodon clavipes*) (Barnosky et al., 2004; Wroe et al., 2004; Lima-Ribeiro and Diniz-Filho, 2013). Despite experiencing one of the most significant declines of megafauna species, information about South American megafaunal extinctions remains limited.

The timing of the Pleistocene megafaunal extinction in South America is yet to be determined because records are scarce (e.g., Elias and Schreve, 2007; Rozas-Dávila et al., 2016; Raczka et al., 2018, 2019). In North America, robust archaeological evidence suggests the timing of megafaunal extinction between 11,500–11,000 years ago (Barnosky et al., 2004). However, extinctions may have occurred earlier, between 14,000–12,700 cal yr BP (calibrated years before present, hereafter BP) (Robinson et al., 2005; Gill et al., 2009, 2012; Perrotti, 2018). In South America, the extinction window has been suggested to have occurred between 15,000–10,000 years ago (Barnosky et al., 2004). The limited records available suggest variability in megafaunal extinction timings. In the Peruvian Andes, researchers found the local extinction occurring as early as 15,800 BP (Rozas-Dávila et al., 2016), whereas in the Ecuadorian Andes extinction was recorded by 12,800 BP (Raczka et al., 2019). This timing is similar to the extinction recorded in the Brazilian cerrado, which was reached by 12,000 BP (Raczka et al., 2018). However, in Argentina and Brazil, fossilised megafauna bones have been dated to the

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Early Holocene and as late as 6555 ^{14}C yr BP (calibrated to ca. 7400 cal yr BP) (Borrero et al., 1998; Steadman et al., 2007), thus suggesting an Early Holocene survival of some megafauna (Neves and Piló, 2003). The available information in South America results in a broad range for the timing of Pleistocene megafaunal decline between 15,800–7400 BP.

Late Pleistocene megafaunal extinctions likely had significant ecological consequences on the ecosystems we know today. The extinction of the megafauna in North America possibly led to the formation of flora without modern analogues and increased fire activity (Gill et al., 2009, 2012). In the Peruvian Andes, the collapse of megafauna was followed by a rise in fire activity and species turnover (Rozas-Dávila et al., 2016). In the Brazilian cerrado, the ecosystem remained largely stable but showed an increase in some palatable species (Raczka et al., 2018). However, the ecological consequences of extinctions in other high-biodiversity regions in South America and whether these were habitat-specific remains unclear.

Fossilised bones of megafauna provide accurate dating; however, they are rare, isolated, and often geographically concentrated (Johnson et al., 2015; van Asperen et al., 2020). The use of spores of coprophilous fungi (SCF) to indicate megafaunal presence can circumvent these limitations because they preserve well in stratigraphic units where chronological frameworks can be built (van Geel et al., 2007, 2011; Lee et al., 2022). SCF grow and reproduce on herbivore feces, making them reliable indicators for the presence/absence and abundance of megafauna (Davis and Shafer, 2006; Wood and Wilmshurst, 2013; Johnson et al., 2015). Furthermore, SCF can be found in conjunction with other palaeoecological proxies, including pollen and charcoal, providing information on the consequences of megafaunal extinctions on vegetation and fire activity (Raczka et al., 2018; van Asperen et al., 2020). Since first proposed as a proxy for Pleistocene megafaunal abundance (Davis, 1987), *Sporormiella*-type spores have been the dominant source of information for reconstructing Pleistocene megafaunal extinction. However, other SCF can reflect the presence of megafauna (Perrotti and van Asperen, 2019). In fact, the sum of all SCF may provide the most reliable measure for megafaunal presence and enhance the interpretation of palaeoecological spore records (Conroy et al., 2020). Despite the information provided by SCF, just a handful of studies in South America have used SCF to reconstruct Pleistocene megafaunal presence (Rozas-Dávila et al., 2016; Raczka et al., 2018; Pino et al., 2019; Raczka et al., 2019). However, these studies have relied on *Sporormiella* as the only SCF indicative of megafaunal presence.

Here we present the first investigation of the timing and ecological consequences of megafaunal declines from Monquentiva—a diverse ecosystem in the eastern Colombian Cordillera. We analysed a well-dated sedimentary record for pollen and charcoal and used a multi-species SCF approach to investigate the timing and ecological consequences of megafaunal declines on the vegetation and fire activity of the eastern Andes of Colombia.

STUDY AREA

Pantano de Monquentiva (hereafter Monquentiva) is a peat bog that lies in the high Andean slopes of the eastern Colombian Cordillera within the Vista Hermosa Regional Natural Park (4°54′N, 73°45′W) (Fig. 1). The site is found in the jurisdiction of the Municipality of Guatavita, Cudinamarca, ~50 km northeast of the city of Bogotá. Monquentiva lies in an altitudinal strip between 2900–3500 m above sea level (m asl). Despite this elevation, the site is a relatively flat oval area, with slopes <5° (Espinoza et al., 2022). Small streams on the eastern side of the mountain range contribute to the site's hydrology, which feeds into the Orinoco River basin (Avella-M et al., 2014). During pre-Hispanic times, Monquentiva was prone to flooding and may have contained a water body (Avella-M et al., 2014; Espinoza et al., 2022). The contemporary peat bog underwent transformations through the establishment of colonial drainage systems for livestock (Gomez and Rubio, 2003; Avella-M et al., 2014). The shape and position of Monquentiva are controlled by the Río Blanco-Machetá Anticline fold and Machetá fault (Kammer et al., 2020; Espinoza et al., 2022) built upon sedimentary Cretaceous rocks (Kammer et al., 2020).

Monquentiva is characterised by a low 11°C mean annual temperature (CAR, 2007; Rojas et al., 2010). The mean annual precipitation is 1425 mm, with a unimodal regime of heaviest rainfall between April and November (CAR, 2007; Avella-M et al., 2014). The main climatic factors influencing Monquentiva are the annual migration of the Intertropical Convergence Zone (ITCZ) bringing moisture from the Amazon and the Atlantic Ocean, and the irregular variation in winds and sea surface temperatures associated with the El Niño-Southern Oscillation (ENSO) (Poveda et al., 2005, 2006). The topography of the Andean mountain range also plays an influential role. This orographic barrier interrupts the easterly airflows from the Amazon basin, forcing the airflows to rise and cover the slopes of the eastern Andean flank with fog (Poveda et al., 2005).

The climate, geographical location, and topography of Monquentiva favour a mosaic of vegetation and concentration of biodiversity along a narrow altitudinal gradient in which the High Andean Forest, Subpáramo, and Páramo are the most abundant vegetation types (Avella-M et al., 2014; Espinoza et al., 2022). High Andean forest is the most represented vegetation surrounding Monquentiva today (76%), where *Weinmannia* and *Clusia* dominate (Avella-M et al., 2014). Other abundant arboreal genera include *Brunellia*, *Clethra*, *Drimys*, *Hedyosmum*, *Ternstroemia*, and *Vallea* (Rangel-Ch, 2000; Avella-M et al., 2014). The Subpáramo is represented by shrubs including *Aragoa*, *Arcytophyllum*, *Diplostephium*, *Hypericum*, *Gaultheria*, *Paepalanthus*, and *Puya* (Avella-M et al., 2014). The Páramo vegetation represents >20% of the flora in Monquentiva and contains various vegetation types in which grasses and herbs dominate (Avella-M et al., 2014). Poaceae (primarily *Calamagrostis*) is the largest component of the Páramo (Rangel-Ch, 2000; Avella-M et al., 2014).

Monquentiva's ecological richness and the abundance of palatable plant species make the site an attractive habitat for extant megafauna. This includes species of megafauna that survived the Pleistocene extinction, such as the white-tailed deer (*Odocoileus virginianus*), Brocket deer (*Mazama pita*), and Andean bear (*Tremarctos ornatus*) (Cooke, 1998; García-Rangel, 2012; Martínez-Polanco, 2019). Known macrofaunal evidence for extinct Pleistocene megafauna in Colombia is concentrated in the Cundinamarca department (Barnosky and Lindsey, 2010). In Bogotá, skeletal records of Mastodons (*Haplomastondon*) have been dated between ca. 40,000–15,000 years BP (van der Hammen and Correal Urrego, 1978). Megafaunal remains have also been found in Tocaima, an archaeological site at 340 m asl (Correal Urrego, 1993; Correal Urrego et al., 2005; Alfonso-Rojas et al., 2021). Here, bones of gomphotheres (*Notiomastodon platensis*) and bone fragments of giant ground sloths (*Eremotherium*) have been recovered. These faunal
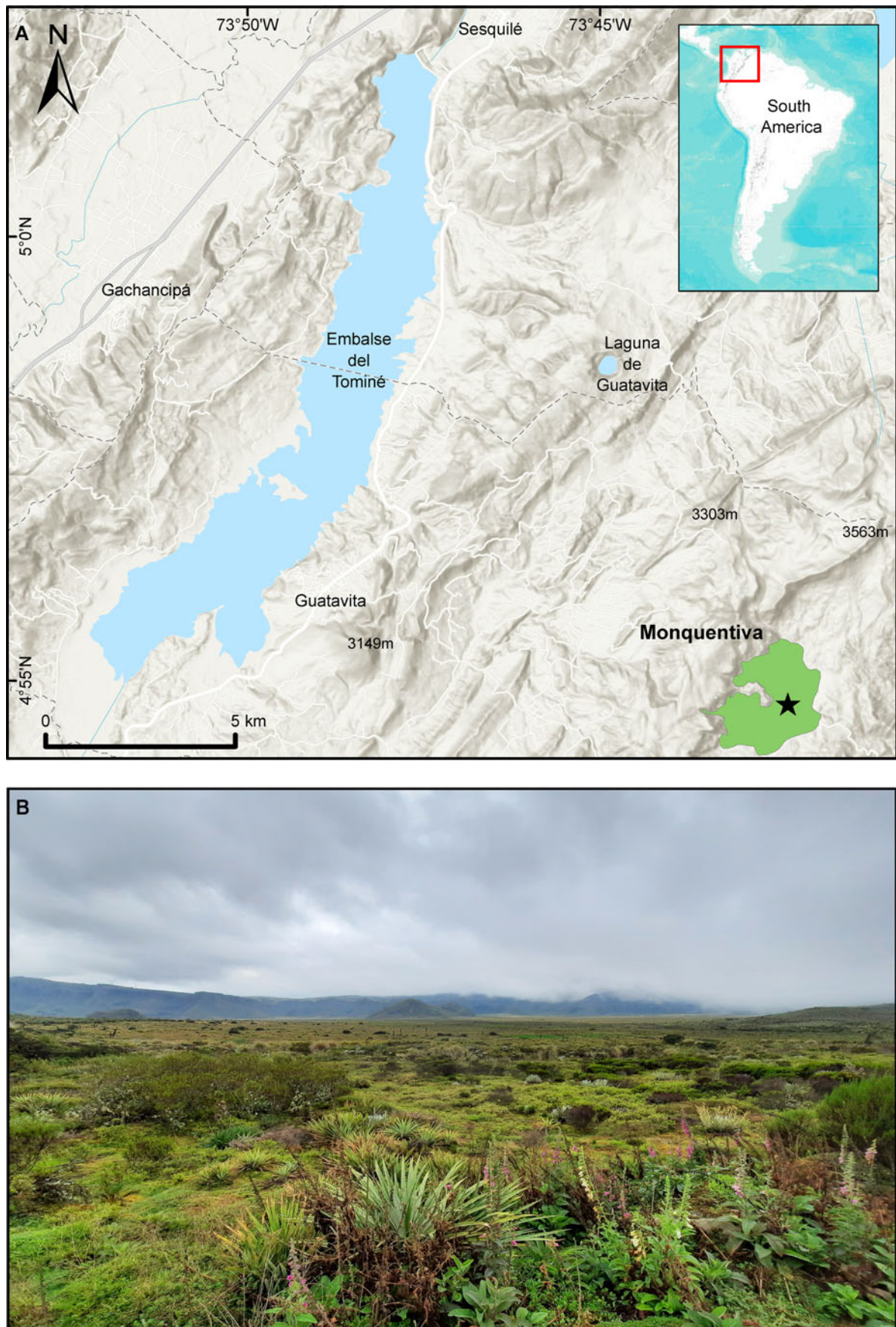
Figure 1. Location of the study site. (**A**) Map of Pantano de Monquentiva (green polygon), Colombia (red square). The black star shows the location of the coring site. (**B**) Field photograph of the Monquentiva peat bog; photo taken by Pym, 2022.

Table 1. Radiocarbon ages (^{14}C) from organic lake sediments and calibrated ages (cal yr BP, IntCal20, Reimer et al., 2020) for the Monquentiva core. Calibrated ranges are rounded to the nearest 10 years.

LabID	Depth (cm)	Age (BP)	Error (±)	Age (calibrated range, 2σ)
UBA-45475	3–4	2115	26	1990–2160
UBA-44495	8–9	2647	25	2720–2760
UBA-45476	14–15	3047	30	3110–3380
UBA-44496	24–25	3750	28	3890–4270
UBA-42144	38–39	5734	36	6300–6700
UBA-43589	54–55	7868	37	8480–9000
UBA-44497*	63–64	7499*	37	8990–10090
UBA-44498	72–73	9077	46	10000–10550
UBA-45477*	81.3–82.3	1786*	30	10520–12100
UBA-44499*	88.8–89.8	5068*	31	11120–13190
UBA-45478*	95.1–96.1	7367*	40	11600–13620
UBA-44500	106.4–107.4	11981	63	13300–14400
UBA-45479	117–118	15347	69	16990–18740
UBA-43590	128.7–129.7	20707	103	21090–25270
UBA-45480	141.5–142.5	36818	598	30710–41500
UBA-42145	161.7–162.7	42623	162.7	36310–48260

*Indicates ages identified as outliers using Oxcal analysis (Ramsey, 2009a, b).

remains and records of other gomphotheres (*Cuvieronius* and *Stegomastodon*) from Tibitó (∼2500 m asl) provide evidence for a diverse Late-Pleistocene megafaunal presence in Colombia (Correal Urrego, 1981; Prado et al., 2005; Borrero, 2009; Alfonso-Rojas et al., 2021). However, at higher elevations, such as Monquentiva, no macrofaunal remains have been reported in the literature.

MATERIAL AND METHODS

Core collection and sampling

A 3.65 m sediment core was recovered from Monquentiva using a modified Livingston piston corer (Colinvaux et al., 1999) in 2019. The core was transported in sealed aluminium tubes to the Tropical Palaeoecology Laboratory at the University of Exeter. Subsequently, the cores were open lengthwise and stored at 4°C. The Troels-Smith method (Kershaw, 1997) was used to describe stratigraphic units in the four 1-m sections. Sixteen bulk sediment samples were extracted and sent to the radiocarbon dating facility at the Queen's University Belfast for ^{14}C dating (Table 1). The intervals for ^{14}C dating were selected by visual analysis of stratigraphic changes and by distributing equally other dated intervals in the whole core. A general outlier model (Ramsey, 2009b) was used to detect outlying ages using Oxcal v.4.4 (Ramsey, 2009a). A chronological model was built using the Bacon package v.2.3.9.1 (Blaauw and Christen, 2013) within R (R Core Team, 2021) using acc.mean = 200 yr/cm and acc.shape = 1.5 as priors (Fig. 2). Radiocarbon dates were calibrated using the IntCal20 calibration curve (Reimer et al., 2020).

To cover the Late Pleistocene and Early Holocene this study focused on the upper two drives, Drive 1 (40–77 cm) and

Drive 2 (78.1–137.1 cm) of the Monquentiva-I sediment core. Volumetric samples of 1 cm^3 were extracted for fungal spore quantification between 40–137.1 cm at 1 cm intervals. Samples of 1 cm^3 for charcoal and 0.5 cm^3 for pollen were also extracted at 1 cm intervals between 40–137.1 cm core depth. Five samples at the top of drive 2 were restored to the top of drive 1 after ^{14}C ages revealed they represented Holocene sediment. Locked pistons generally do not slip when pushed through lake mud (Colinvaux et al., 1999) and sediment mixing is rare. However, maintaining an efficient core seal is complex and, in this case, pressure may have released the rubber seal of the piston (Colinvaux et al., 1999; Last and Smol, 2002) resulting in Holocene sediments being collected at the top of drive 2.

Laboratory analysis

Fungal spores were prepared following a modified version of Fægri et al. (1989). This modification removed acetolysis, which can cause spore deterioration (van Asperen et al., 2016). In each sample, a *Lycopodium* tablet with a known number of spores (Batch 1031; 20,848 ± 691 spores/tablet) was added for SCF and pollen analysis. The *Lycopodium* spike was used to calculate concentrations per volume (Stockmarr, 1971). Percentages were calculated based on the total pollen assemblage (hereafter %TPA). SCF treatment included 10% HCl and 10% KOH, warming in a 90°C ultrasonic bath, sieving at 180 μm, density separation using sodium metatungstate $Na_6(H_2W_{12}O_{40})$ at 1.9–2.0 grams/litre, and suspending in glycerol (van Asperen et al., 2016). Spores and pollen were identified using a Zeiss Axioskop light microscope at 400× and 1000× magnification. All fungal spores were quantified until 300 *Lycopodium* were counted per sample (Etienne and Jouffrey-Bapicot, 2014).

The fungal spore quantification included the commonly used *Sporormiella* taxon and other identifiable spores of coprophilous, semi-coprophilous, and non-coprophilous taxa. Spore identification was conducted using published descriptions, fungal keys, and published images (van Geel et al., 2003; Cugny et al., 2010; Guarro et al., 2012; Revelles et al., 2016; Loughlin et al., 2018). Where identification at a particular taxonomic level became difficult, spores were assigned to their closest morphotype (van Asperen et al., 2020). Spore morphotypes were assigned to their primary substrate following existing associations (Perrotti and van Asperen, 2019; van Asperen et al., 2020).

The pollen and charcoal records were used to assess vegetation changes and past fire activity. Pollen and charcoal were recorded in separate samples selected from the same stratigraphic levels as samples for SCF analysis. These samples were prepared following their respective standard protocols (Fægri et al., 1989; Whitlock and Larsen, 2002). Pollen sums of 300 pollen grains per sample were identified and described using keys and descriptions for Andean vegetation (Hooghiemstra, 1984; Colinvaux et al., 1999; Bush and Weng, 2006; Velásquez et al., 2022) and modern reference material archived in the tropical pollen reference collection at the University of Exeter. The ecological and habitat affinities of pollen taxa were extracted from the literature (e.g., van der Hammen and González, 1960; Hooghiemstra, 1984; Marchant et al., 2002; Bernal et al., 2019; Espinoza et al., 2022). Charcoal particles were sieved to retain fragments >180 μm (macroscopic) and 106–63 μm (microscopic). The size fractions were determined by sieve size availability and closely followed the size fraction standards in charcoal analysis (Whitlock and Larsen, 2002). The retained particles were manually separated and photographed using a Zeiss Stemi
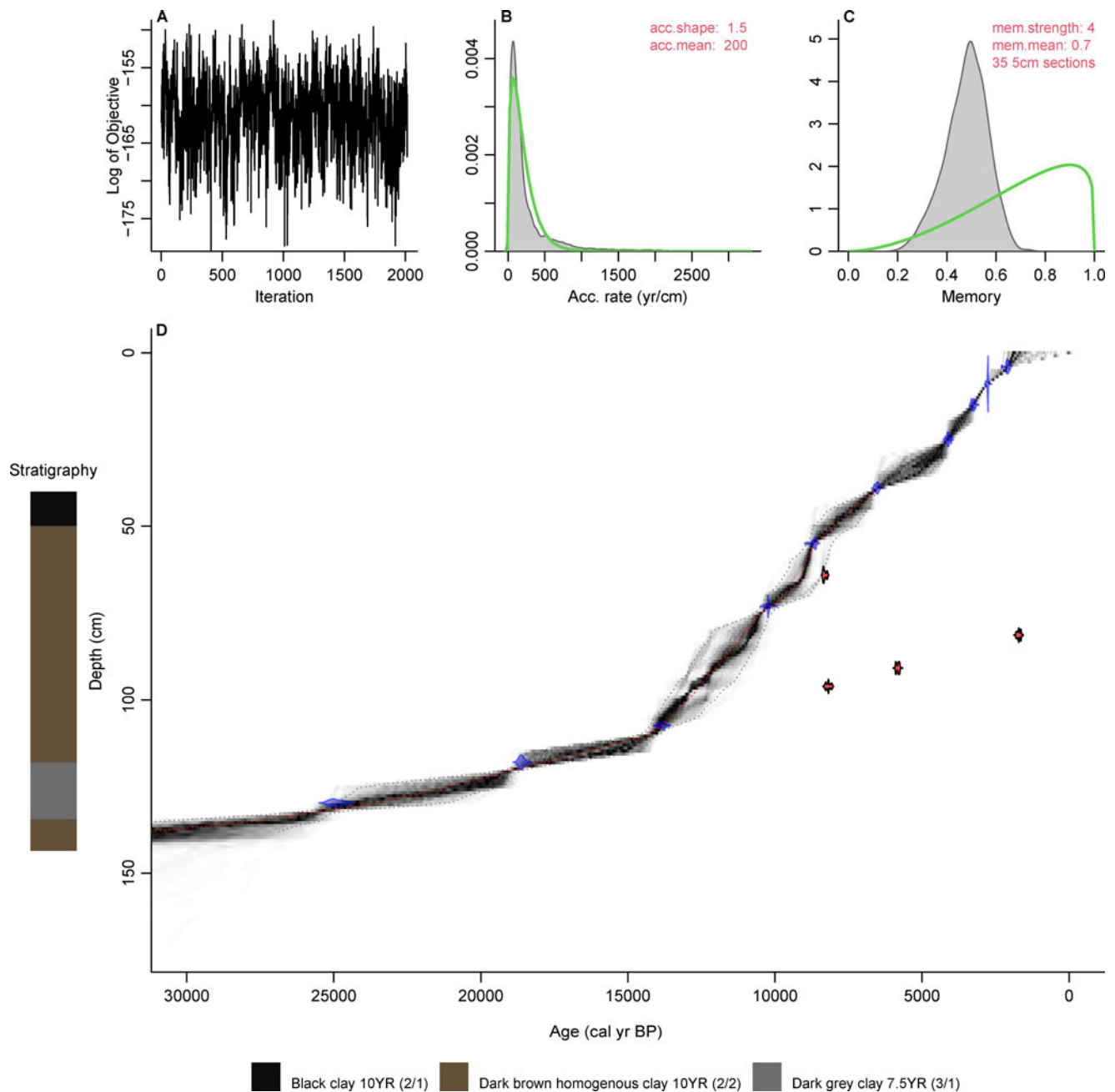
Figure 2. Bayesian age-depth model and stratigraphic descriptions for the Monquentiva core. The inset figures show the models: (**A**) Markov Chain Monte Carlo (MCMC) iterations; (**B**) distributions for the accumulation rate (Bacon MCMC iterations estimates the accumulation rate in years/cm; so more correctly, sedimentation times); (**C**) the memory of variability; and (**D**) the calibrated ^{14}C dates (transparent blue) and the age-depth model; red curve shows the 'best' model based on the weighted mean age for each depth. The filled red radiocarbon dates represent the outliers identified using Oxcal analysis (Ramsey, 2009a, b). Stratigraphic descriptions include Munsell colour notations (Munsell Color, 1992).

stereo microscope at 50× magnification. Subsequently, charcoal area and raw counts (Clark and Patterson, 1997; Halsall et al., 2018) were extracted using image analysis in ImageJ software (Abràmoff et al., 2004). Stratigraphic diagrams of SCF, selected pollen taxa, and charcoal were plotted using C2 v.1.7.7 (Juggins, 2007).

Quantitative analysis

Pearson correlation coefficients were calculated among all identifiable SCF at the 0.01 and 0.05 levels of significance

(Supplementary Table 2) using SPSS (IBM Corp, 2020). SCF that showed positive and significant correlations were grouped to create a multi-species group of key SCF associated with megafaunal presence (Dix and Webster, 1995; Johnson et al., 2015; Perrotti and van Asperen, 2019). Confidence limits were calculated for the key SCF concentrations to assess uncertainty linked to sampling effort (Maher, 1981, p. 179). A sequential t-test analysis of regime shifts (STARS) (Rodionov, 2004) was performed using key SCF concentrations to identify statistically significant deviations in megafaunal abundance. The analysis utilised a

regime shift index (hereafter RSI) to quantify the size of the regime shift (Rodionov and Overland, 2005) and was calculated using a cut-off length $l = 4$ and probability level $p = 0.05$. STARS analysis was deployed using the R package *rshift* (Room et al., 2022). Canonical correspondence analysis (CCA) (Oksanen, 2009) was performed to test the influence of constraining variables (key SCF and charcoal concentration) on the pollen assemblages. CCA analysis was performed on key SCF concentrations, macroscopic and microscopic charcoal counts, and pollen percentages. The CCA was performed using the R package *vegan* (Oksanen et al., 2007), and included every pollen taxon quantified with an abundance over 1% TPA to reduce the weighting of rare taxa (Urrego et al., 2009, 2013). Both STARS and CCA were performed within R (R Core Team, 2021).

To reconstruct local fire history and identify significant fire events near Monquentiva (Clark et al., 1996; Higuera et al., 2009), raw charcoal counts were converted into interpolated charcoal concentration (particles/cm^3) and separated into peak magnitude and peak frequency using CharAnalysis v.1.1 at the 0.99 level of significance within Matlab (Higuera, 2009; MathWorks, 2019). Zone division for charcoal in CharAnalysis used the entire record of samples with depth data from the youngest to oldest age (6700–32,290 BP). Charcoal concentrations were interpolated into 200-year intervals based on the median sample resolution (Espinoza et al., 2022). Charcoal frequency (C$_{back}$) was estimated using a LOWESS smoother method with a 1000-year smoothing record (Higuera, 2009; Espinoza et al., 2022).

RESULTS

Chronology and stratigraphy

The 97.5-cm sediment section analysed provided a record of sediment accumulation from ca. 30,290–6700 BP (Table 1, Fig. 2). Four radiocarbon ages detected as outliers (Supplementary Table 1) were excluded from the age-depth model because they likely represented age reversals (Trachsel and Telford, 2017). Between 137.1–135 cm depth (ca. 30,290–27,740 BP) the sediment is characterised by dark-brown homogenous clay (Munsell Color, 1992, 10YR 2/1) (Fig. 2). A sharp boundary from 135 cm is followed by a 17 cm layer of very dark-grey clay (7.5YR 3/1) sediment up to 118 cm (ca. 17,900 BP). From 118–92.5 cm depth (17,900–12,350 BP) the sediments returned to a dark-brown homogenous clay (10YR 2/2). This section is overlain at the top of drive 2 with a layer of black homogenous clays (10YR 2/1) that extends to 40 cm depth (ca. 6700 BP) in drive 1.

Spores of coprophilous fungi (SCF) pollen and charcoal records

The SCF record was composed of 28 identifiable taxa, including eight key SCF (Supplementary Figure 1). SCF were found in 36 of the 52 samples analysed. Confidence intervals calculated for key SCF concentrations showed that the uncertainties attributable to count size were minimal (Fig. 3). This suggested the sampling effort was sufficient to provide statistical validity to the key SCF data (Maher et al., 2012). The SCF and pollen records were divided into five palynological zones based on sedimentological changes, key SCF regime shifts, and prominent changes in SCF and pollen assemblages (Fig. 3, Supplementary Figure 2). This includes zone M5, dating between ca. 2150–1170 BP. Charcoal counts and area showed no observable differences in the Late Holocene (Supplementary Figure 3). Charcoal concentration

and peak magnitude and frequency of fires in Monquentiva were greater in the Early and Middle Holocene samples (Fig. 4). CHAR analysis could not be run on the charcoal data from zone M5 due to the low number of samples.

Zone M1 (ca. 30,300–22,900 BP)

The highest abundance of SCF was observed in Zone M1 (Fig. 3). *Sporormiella* peaked at 417 spores/cm^3 (<1%), *Sordaria* at 1737 spores/cm^3 (3%), and *Podospora* at 139 spores/cm^3 (<1%). The record of key SCF also included: *Arnium imitans* (1946 spores/cm^3; 3%), *Coniochaeta* (695 spores/cm^3; 1%), *Delitschia* (208 spores/cm^3; <1%), and *Cercophora* (139 spores/cm^3; <1%). The most abundant pollen taxa were Poaceae (49%), Asteraceae (16%), and *Alnus* (15%) (Fig. 3). Other prominent tree and shrub taxa occurring at <5% are *Hedyosmum*, *Hypericum*, Melastomataceae, *Podocarpus*, and *Weinmannia*. Before 25,000 BP, macroscopic and microscopic charcoal concentrations were low (<20 particles/cm^3), but increased to 91 and 157 particles/cm^3, respectively at ca. 24,240 BP (Fig. 4). Peak frequency for both charcoal fractions remained at <2 fires per 1000 yr. The STARS analysis identified a key SCF regime shift at 24,240 BP, reaching 2.3 RSI (Fig. 3).

Zone M2 (ca. 22,900–17,890 BP)

Zone M2 is characterised by the near absence of SCF (Fig. 3). OU-100 and UAB-2 were the only fungal spores recovered at ca. 19,900 and 17,890 BP (69 spores/cm^3) (Supplementary Figure 4). Asteraceae (36%) and *Alnus* (25%) were the most abundant pollen taxa, while Poaceae remained relatively low (20%) (Fig. 3). *Hedyosmum* (4%), *Podocarpus* (4%), *Valeriana* (2%), and *Weinmannia* (1%) were all present. Arboreal taxa such as *Morella* and *Myrsine* increased slightly (1–2%). Macroscopic (<2 particles/cm^3) and microscopic (0–29 particles/cm^3) charcoal remained low (Fig. 4). Peak frequency for both charcoal fractions increased in this zone (between 0–2.5 fires per 1000 yr). One key SCF regime shift was detected in the zone, reaching 1.23 RSI at 17,890 BP (Fig.4).

Zone M3 (ca. 17,890–10,990 BP)

SCF rebounded in zone M3 to levels comparable to those recorded in zone M1 (Fig. 3). Key SCF concentration fluctuated between 0–2154 spores/cm^3 (0–3%). *Sporormiella* increased within this zone (278 spores/cm^3; <1%), along with *Arnium imitans* (3336 spores/cm^3; 2%), *Delitschia* (416 spores/cm^3; <1%), and *Sordaria* (695 spores/cm^3; < 1%). *Podospora* (139 spores/cm^3; <1%), *Coniochaeta* (208 spores/cm^3; <1%), and *Trichodelitshia* (208 spores/cm^3; <1%) were also present. Herbaceous taxa such as Asteraceae (20%) and Poaceae (27%) dominated in this zone (Fig. 3). Acanthaceae (1–5%), *Ambrosia* (0–3%), Apiaceae (0–4%), Cyperaceae (0–4%), *Draba* (0–2%), *Ranunculus* (0–8%), and *Valeriana* (0–24%) all increased in abundance. *Alnus* (29%) and *Podocarpus* (4%) increased again up to ca. 14,150 BP before declining to 2% and 0%, respectively, by 10,990 BP. *Hedyosmum* (4%) and Melastomataceae (1%) were present while Ericaceae (0–2%) and *Morella* (1–4%) increased. Macroscopic charcoal was absent at 17,890 BP, but increased to 59 particles/cm^3 by 11,200 BP, alongside the largest macroscopic charcoal peak recorded ([25 particles/cm^2]/peak) (Fig. 4). Peak frequency steadily increased (from 2 to 3 fires per 1000 yr). Microscopic charcoal increased from 0 to 65 particles/cm^3 across the zone. By 14,200 BP, microscopic peak frequency decreased to <1 fire per 1000 yr, before rising to >3 fires per 1000 yr by 12,000
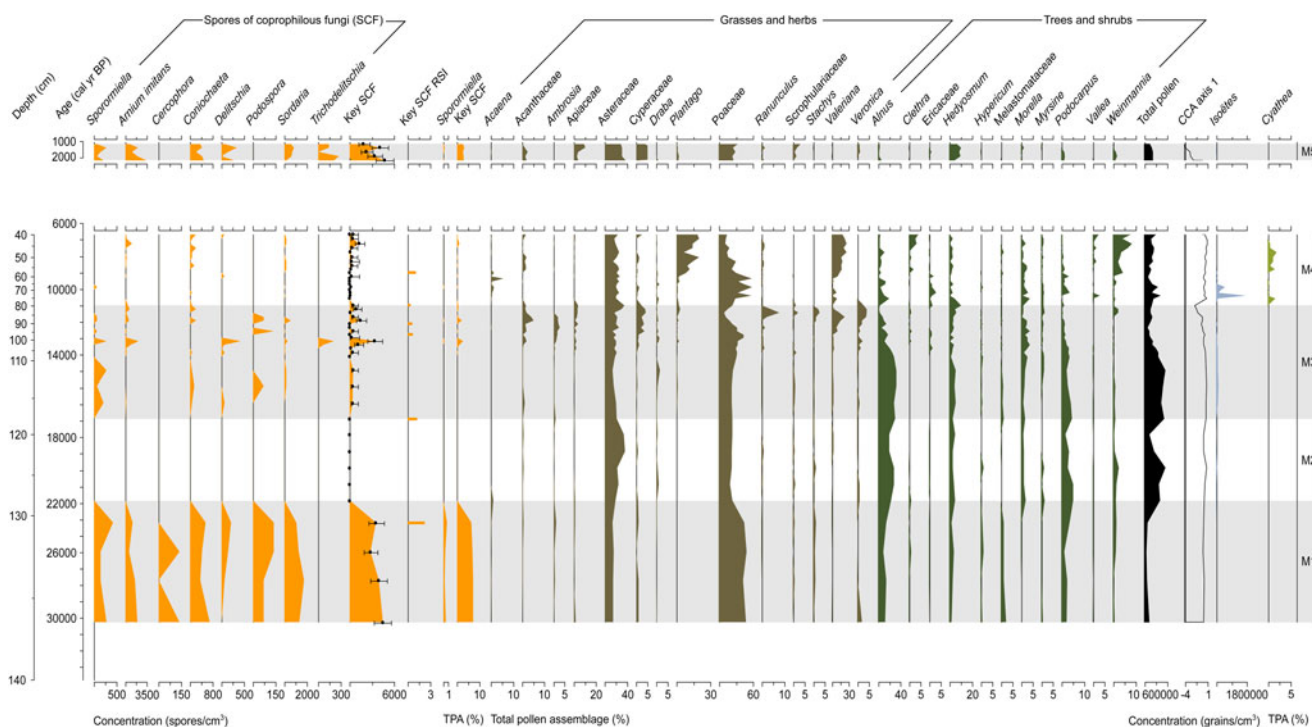
Figure 3. Summary diagram of the most abundant spore and pollen taxa recorded from the sediments of Monquentiva. All spores are expressed as a concentration per cubic centimeter (spores/cm^3). Key SCF concentration shows the 0.95 confidence interval as whiskers (Maher, 1981). The key SCF RSI shows the regime shift analysis and plots the statistically significant shifts in key SCF concentration (p-value < 0.05). *Sporormiella* and the key SCF (%) are also expressed as a percentage of the total pollen assemblage (%TPA) (see Supplementary Figure 4 for all spores quantified as %TPA). Canonical correspondence analysis (CCA) plots Axis 1 scores from the site. *Cyathea*, a pteridophyte, is not grouped.

BP. The regime shift analysis recorded two key SCF changes at 12,770 and 12,140 BP (0.681 and 0.621 RSI) (Fig. 3).

Zone M4 (ca. 10,990–6700 BP)

Zone M4 showed a reduction of all SCF (Fig. 3). Between 11,915–9720 BP, key SCF declined from 1459 to 0 spores/cm^3 (2–0%). *Sporormiella* was found in only one sample at 9890 BP while *Cercophora*, *Podospora*, and *Trichodeltischia* were absent. At ca. 7220 BP, *Arnium imitans* (1112 spores/cm^3; 1%) and *Sordaria* (139 spores/cm^3; <1%) increased, aligning with a rise in key SCF to 1251 spores/cm^3 (>1%). Most grasses and herbs, including Cyperaceae (2–0%), Acanthaceae (2–0%), *Ambrosia* (2–0%), Apiaceae (4–0%), *Ranunculus* (8–0%), *Stachys* (3–0%), and *Veronica* (3–0%), declined at the onset of this zone (Fig. 3). Poaceae increased up to 59% and then decreased to 15% by 6700 BP. Asteraceae remained abundant (22%) while *Acaena* (0–6%), *Plantago* (1–20%), and *Valeriana* (9–27%) increased. Tree taxa such as *Alnus* (20–0%), *Hedyosmum* (5–0%), and *Podocarpus* (4–0%) decreased in the zone, while *Clethra* (0–4%), Ericaceae (1–3%), *Vallea* (0–3%), and *Weinmannia* (1–8%) increased. *Cyathea* (2%) was recorded for the first time at ca. 10,600 BP. Zone M4 displayed the highest macroscopic charcoal concentration (123 particles/cm^3) in the record ca. 10,990 BP (Fig. 4). Macroscopic charcoal peak frequency continued to increase across the zone (2.5–3.5 fires per 1000 yr). Microscopic charcoal and peak magnitude were highest in abundance, reaching 190 particles/cm^3 and (123 particles/cm^2)/peak (ca. 10,990 BP). Between 9600–6700 BP, microscopic charcoal frequency increased then decreased from 3.5 to 1.4 fires per 1000 yr.

The interval recorded two final key SCF regime shifts at 10,990 BP and 9018 BP, reaching 0.41 RSI and 1.1 RSI, respectively.

Zone M5 (ca. 2150–1150 BP)

Key SCF peaked at 4726 spores/cm^3 (3%) ca. 2150 BP in zone M5 (Fig. 3). *Sporormiella* (278 spores/cm^3; <1%), *Arnium imitans* (3405 spores/cm^3; 2%), *Coniochaeta* (487 spores/cm^3; <1%), *Delitshia* (347 spores/cm^3; <1%), *Sordaria* (695 spores/cm^3; <1%), and *Trichodelitschia* (278 spores/cm^3; <1%) were all present. Herbaceous taxa including Apiaceae (10%), Asteraceae (36%), Cyperaceae (6%), and Poaceae (34%) dominated the zone and were accompanied by Acanthaceae (<3%), Scrophulariaceae (<4%), and *Veronica* (<2%) (Fig. 3). From the arboreal record, *Alnus* (3%) and *Hedyosmum* (8%) were the most representative. In this zone, *Rumex* appeared for the first time (1%) (Supplementary Figure 2). Concentrations of both macroscopic (624–1308 particles/cm^3) and microscopic (1484–3574 particles/cm^3) charcoal were the highest in the record (Supplementary Figure 3).

SCF correlations

Sporormiella concentration in the Monquentiva record correlates positively with *Arnium imitans*, *Delitschia*, *Podospora*, *Sordaria*, and *Trichodelitschia* (p-value < 0.01) and with *Cercophora* and *Coniochaeta* (p-value < 0.05) (Table 2). This includes a high positive correlation between *Sporormiella* spores with *Sordaria* (R^2 = 0.633, p < 0.01), *Arnium imitans* (R^2 = 0.644, p < 0.01), and *Delitschia* (R^2 = 0.691, p < 0.01). Twenty other spores were recorded at Monquentiva and included 13 spores described
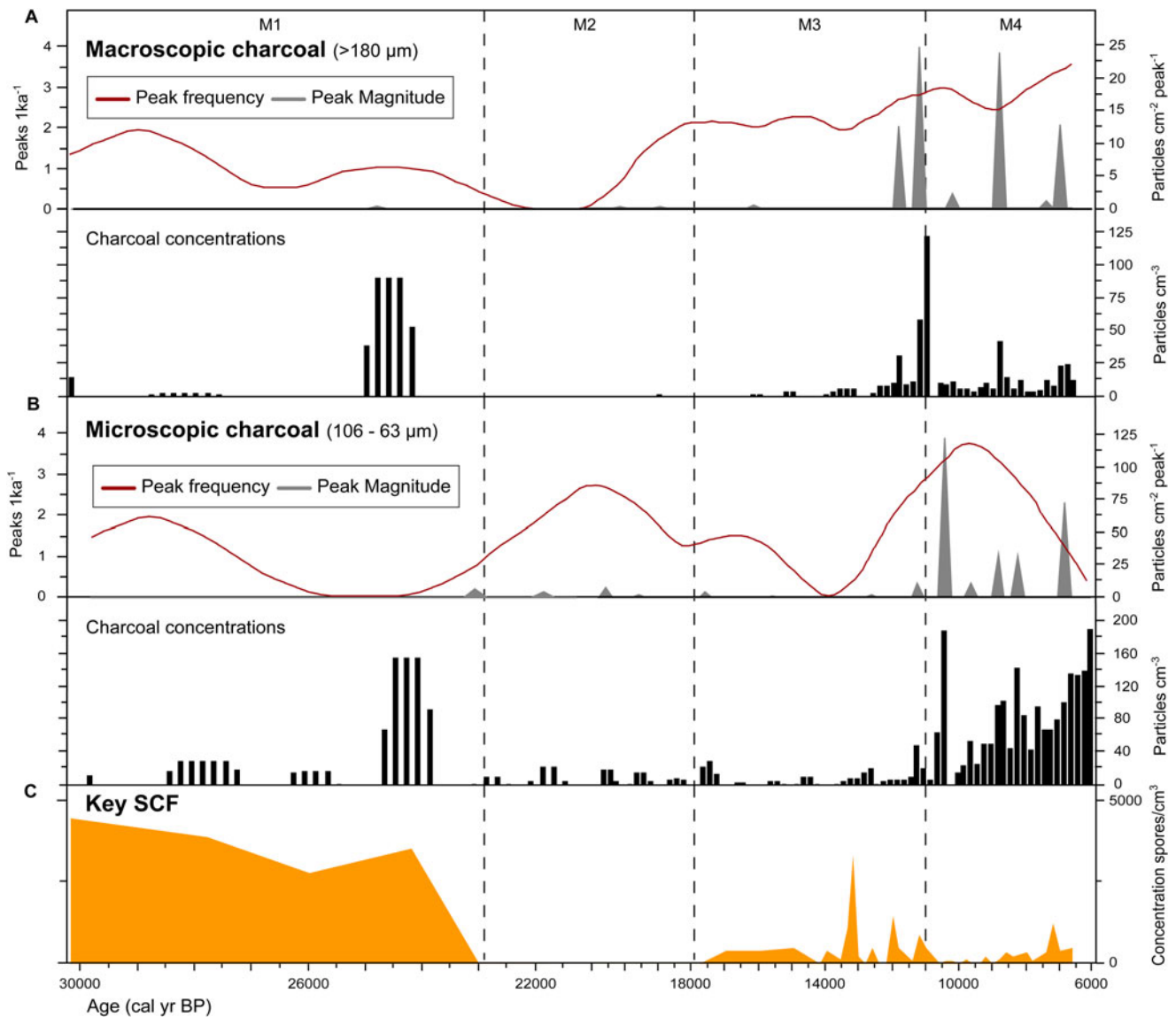
Figure 4. Monquentiva charcoal record and concentration of key SCF. (**A**) Macroscopic charcoal; (**B**) microscopic charcoal; and (**C**) key SCF record. Charcoal concentration (black bars; particles/cm^3), peak frequency (red line, left hand axis; peaks/ka), and peak magnitude (grey silhouettes, right hand axis; particles/cm^2/peak) for charcoal data analysed in CharAnalysis using a LOWESS smoother model (Higuera et al., 2009). Vertical dashed lines show the four palynological zones (M1–M4) based on sedimentological changes in the core stratigraphy, key SCF regime shifts, and prominent changes in SCF and pollen assemblages as in Figure 3.

Table 2. Pearson correlation coefficients calculated among SCF concentrations from the Monquentiva record. Statistical significance of correlations are highlighted at p-value < 0.01 (**) and < 0.05 (*) levels.

| Monquentiva	Key spores of coprophilous fungi (key SCF)						
	Sporormiella	*Arnium imitans*	*Cercophora*	*Coniochaeta*	*Delitschia*	*Podospora*	*Sordaria*
Arnium imitans	0.644**						
Cercophora	0.312*	0.225					
Coniochaeta	0.672*	0.714**	0.530**				
Delitschia	0.691**	0.722**	0.069	0.435**			
Podospora	0.468**	0.176	0.485**	0.462**	0.138		
Sordaria	0.633**	0.574**	0.562**	0.797**	0.392**	0.586**	
Trichodelitschia	0.364**	0.749**	−0.067	0.402**	0.605**	−0.133	0.206
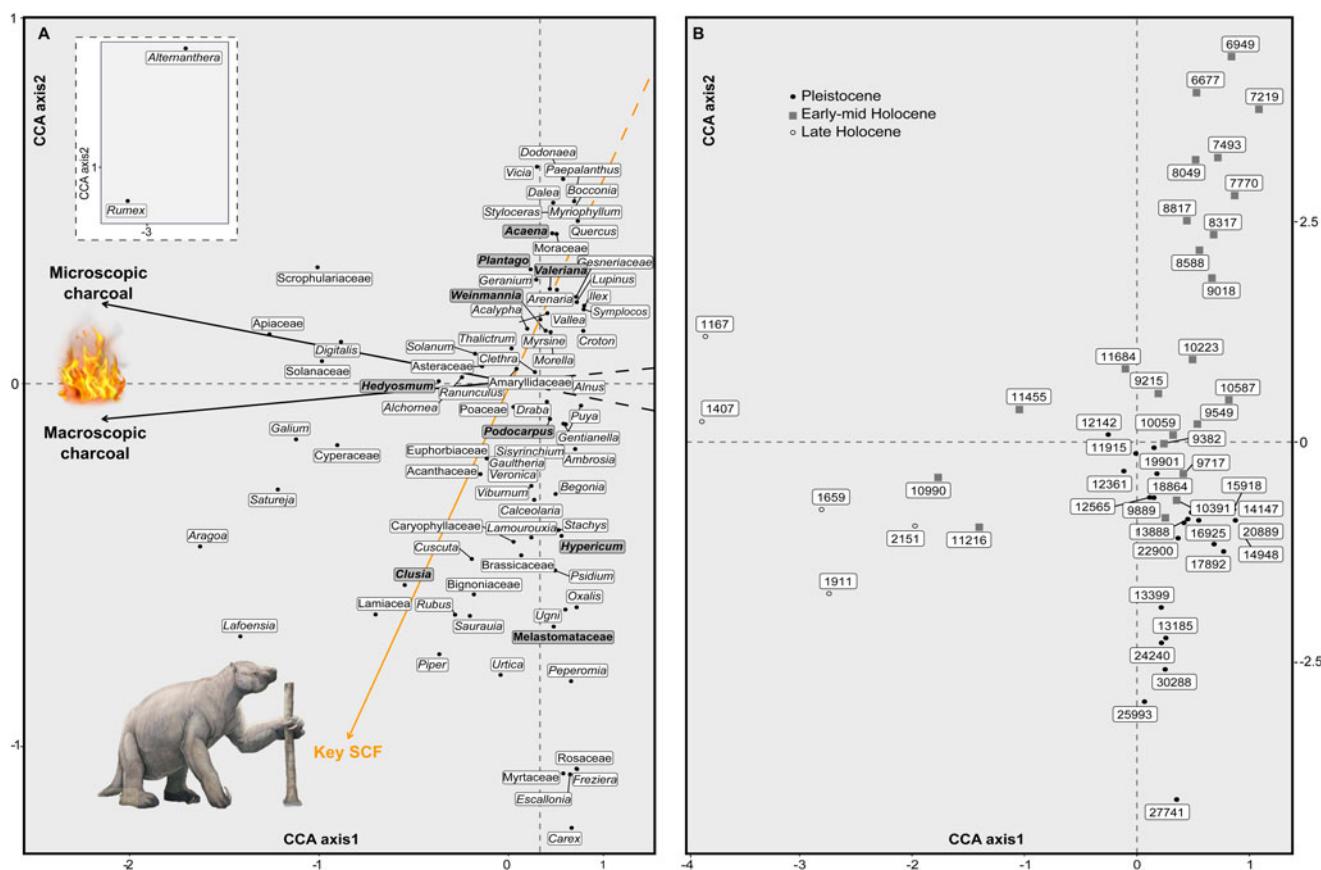
Figure 5. Canonical correspondence analysis (CCA) results for the pollen, charcoal, and spore records from Monquentiva. (**A**) Species scores for the pollen record of taxa >1% the total pollen sum, using key SCF and macroscopic and microscopic charcoal as constraining variables. Bold taxa in grey boxes are discussed in detail in the text. The inset shows pollen species with high CCA Axis 1 and Axis 2 scores. The giant ground sloth (*Eremotherium*) concept art sourced from Ugueto (2020). (**B**) Sample scores labelled with their corresponding ages in calibrated years before present (BP).

relatively recently in the literature (Supplementary Figure 1) (Revelles et al., 2016; Loughlin et al., 2018). *Sporormiella* concentration was positively correlated with four of these newly described fungal spores: OU-5 ($R^2 = 0.624$, $p < 0.01$), OU-100 ($R^2 = 0.770$, $p < 0.01$), OU-108 ($R^2 = 0.549$, $p < 0.01$) and UAB-50 ($R^2 = 0.412$, $p < 0.01$), but showed no significant correlation with OU-18, UAB-1, UAB-2, UAB-7, UAB-15, UAB-30A, UAB-32, UAB-40, UAB-48, or UAB-49 at the 0.01 level of significance (Supplementary Table 2). The significant correlations between *Sporormiella* and the other SCF were used to create the key SCF sum to represent megafaunal abundance changes over time (Fig. 3).

Multivariate ordinations

CCA analysis of the fossil pollen record grouped taxa along two axes, which explained a cumulative 87% of the total variance in the dataset (Fig. 5). CCA Axis 1 explained 63% of the variance (eigenvalue: 0.0879) of the pollen data, and CCA Axis 2 explained 24% of the variance (eigenvalue: 0.0337). CCA Axis 1 ordinated taxa including *Ilex*, *Croton*, Gesneriaceae, and *Oxalis* at the positive end, and *Rumex*, *Alternanthera*, *Aragoa*, and Apiaceae at the negative end (Fig. 5a). The pollen taxa with the highest scores in Axis 2 were *Alternanthera*, *Rumex*, *Vicia*, and *Dodonaea* at the positive extreme of the axis, whereas *Carex*, *Escallonia*, Myrtaceae, and Rosaceae were distributed at the negative end. The CCA ordination displayed a clear separation between samples from the

Holocene at the positive extreme and the Pleistocene at the negative end of Axis 2 (Fig. 5b). Taxa in the centre of the ordination, such as Asteraceae, Poaceae, *Alnus*, *Hedyosmum*, and *Podocarpus*, are more constant throughout the record, thus they are not strongly grouped to any of the environmental variables. The CCA also showed that the key SCF variable covaried with the negative end of Axis 2 and explained 74% of the variance along this axis. Macroscopic and microscopic charcoal covaried with the negative end of Axis 1 and both explained 98% of the variance along this axis.

DISCUSSION

The timing of megafaunal decline in the northern tropical Andes

We found robust evidence for megafaunal presence and decline at Monquentiva (Table 2, Fig. 3). In our record, *Sporormiella* remained below the 2% functional megafaunal extinction threshold proposed from arid sites in western North America (Davis and Shafer, 2006). However, that threshold may be inappropriate for other environments (Perrotti and van Asperen, 2019). *Sporormiella* percentages below 2% are not uncommon in the literature (e.g., Burney et al., 2003; Perrotti, 2018). The use of *Sporormiella* concentrations (Perrotti, 2018; Chepstow-Lusty et al., 2019; Conroy et al., 2020) instead of percentages has been

shown to be effective to infer megafaunal extinctions (Johnson et al., 2015; Raczka et al., 2018, 2019). In southeastern Brazil, *Sporormiella* concentrations between 0–339 spores/cm^3 have been interpreted to indicate low to medium numbers of cattle that were present around lakes (Raczka et al., 2016). We recovered *Sporormiella* at concentrations between 0–417 spores/cm^3, suggesting Pleistocene megafaunal presence. We also found statistically significant positive correlations (p-value < 0.01 and p-value < 0.05) between *Sporormiella* concentrations and the concentrations of all of the other SCF (Table 2). These correlations allowed us to create a multi-species key SCF group to estimate megafaunal presence and track megafaunal declines in Monquentiva (Fig. 3).

The recovery of SCF can also be influenced by biotic and abiotic conditions related to fungal spore germination and growth. Dung fungi face interspecific competition (Kuthubutheen and Webster, 1986; Dix and Webster, 1995) and have genus- or species-specific responses to microenvironmental factors, including temperature and limnological conditions (Dickinson and Underhay, 1977; Krug et al., 2004). Our understanding of the role of environmental conditions on fungal spore germination is focused on temperature zones (Lee et al., 2022). However, fluctuating water levels have been shown to skew *Sporormiella* (Raper and Bush, 2009; Raczka et al., 2016) and other spore records (Ponel et al., 2011). This can increase or decrease the transportation and accumulation of spores in lakes (Raper and Bush, 2009; Etienne et al., 2013; Lee et al., 2022). At Monquentiva, we used the multi-species key SCF concentration record to minimise the effects of environmental conditions on individual SCF germination and growth.

The key SCF record indicates the presence of megafauna in Monquentiva and the eastern Colombian Cordillera at least since 30,290 BP (Fig. 3). Megafaunal bone remains are scarce in northern South America (Barnosky and Lindsey, 2010), but have been dated in Venezuela back to 41,000 ^{14}C age BP (calibrated to 42,060 BP) (Jull et al., 2004), in Ecuador back to 20,980 ^{14}C age BP (calibrated to 23,240 BP) (Coltorti et al., 1998), in Peru back to 14,150 ^{14}C age BP (calibrated to 15,270 BP) (MacNeish et al., 1970), and in Brazil back to 20,060 BP (Neves and Piló, 2003). The limited spore records produced to date provide evidence for megafaunal presence in Ecuador back to 16,280 BP (Raczka et al., 2019), in Peru back to 25,000 BP (Rozas-Dávila et al., 2016), and in Brazil back to 23,000 BP (Raczka et al., 2018). In Colombia, macrofaunal remains are limited (Barnosky and Lindsey, 2010) but have been dated back to 40,000 ^{14}C age BP (van der Hammen and Correal Urrego, 1978). Faunal remains have been found in Tocaima (Correal Urrego, 1993; Correal Urrego et al., 2005; Alfonso-Rojas et al., 2021) and at Tibitó (Correal Urrego, 1981; Borrero, 2009). Megafaunal presence has also been inferred from rock shelter cave paintings from Serranía de la Lindosa (~500 km from Monquentiva) that date back to ca. 12,600 years ago (Bischler and Pinto, 1959; Correal et al., 1990). However, this evidence has been highly criticised because cave art does not contain organic material that can be directly dated and heavily relies on artist representation (Hedges et al., 1997). Our key SCF record reveals that megafauna also roamed the higher altitudes of Colombia during the Pleistocene and were present at Monquentiva and the Colombian Andes dating back to at least 30,290 BP.

Our SCF data indicated the first wave of megafaunal decline in Monquentiva at ca. 22,900 BP, followed by a recovery ca. 16,900 BP and a second decline by ca. 10,990 BP (Fig. 3). Such SCF fluctuations could result from differential preservation due to water-level changes (Wood and Wilmshurst, 2013; Raczka et al., 2019) and water-body size (Raper and Bush, 2009; Lee et al., 2022). However, the pollen record shows that *Isoëtes* was low during the onset of both megafaunal declines and did not coincide with changes in SCF (Fig. 3). *Isoëtes* is an aquatic taxon, common in lake bottoms, marshes, and bogs in the high Páramo (van der Hammen and González, 1960). *Isoëtes* did increase in the Monquentiva record, suggesting the formation of a small water body, but ca. 600 years after the second SCF decline. Consistently low water levels and independence of the SCF and *Isoëtes* records at Monquentiva suggest that the SCF concentration decreases represent megafaunal declines and are not due to water-level fluctuations.

The first megafaunal decline at ca. 22,900 BP was identified as a statistically significant regime shift in Monquentiva (Fig. 3). Three further key SCF regime shifts were identified at ca. 12,770, 12,140, and 10,990 BP. The shifts at 12,140 BP and 10,990 BP are linked to reductions in key SCF concentrations from 1459 to 0 spores/cm^3. We interpret these shifts as the extinction of Pleistocene megafauna at Monquentiva. This record is consistent with a two-wave megafaunal decline reported from Lake Pacucha in the high Andes of Peru (Rozas-Dávila et al., 2016). However, the first megafaunal decline at Pacucha started at 21,000 BP and resulted in an extinction by 15,800 BP (Rozas-Dávila et al., 2016). We have little evidence to explore the causes of extinction, but it is notable that megafaunal extinctions were recorded ca. 3,000 years before early records of human occupation at Pacucha (Rozas-Dávila et al., 2016), while at Monquentiva the second wave of megafaunal decline coincides with early archaeological records (see discussion in next section). In Ecuador, the extinction of Pleistocene megafauna is recorded at 12,800 BP (Raczka et al., 2019), while in Lagoa Santa, Brazil, extinction was reached by 12,000 BP and showed no evidence of megafaunal recovery (Raczka et al., 2018). At Monquentiva and the Colombian Andes, the second megafaunal decline (ca. 10,990 BP) was recorded later than at other diverse South American sites, suggesting that Monquentiva provided a suitable habitat for megafauna. Additionally, macrofaunal remains from species such as *Doedicurus* sp. have been dated as late 7400 BP (Steadman et al., 2007). Because ecosystems are complex and highly diverse across South America, this heterogeneity could be linked to variability in megafaunal extinction timings (Gill et al., 2009, 2012; Rozas-Dávila et al., 2016), with sites like Monquentiva probably providing a temporary refuge until the final extinction.

Climate, vegetation, and human occupation during megafaunal declines

Páramo vegetation dominated Monquentiva between 30,000–22,900 BP (Fig. 6). The dominance of Poaceae up to ca. 24,240 BP, the low abundance of arboreal elements, and low total pollen concentration indicate a cool and dry climate. The tree line, defined as the upper altitudinal boundary of continuous forests (Urrego et al., 2011a), was lowered and open vegetation was found not just at Monquentiva but also across the high elevations in the eastern Colombian Andes (van Geel and van der Hammen, 1973). This period corresponded with the coldest phase of the last glacial period (van der Hammen, 1974, Bogotá-A et al., 2011). High concentrations of key SCF during the last glacial period at Monquentiva indicate that open vegetation was favourable for megafaunal presence. Between 25,000–24,200 BP, charcoal concentration increased, indicating fire activity surges at
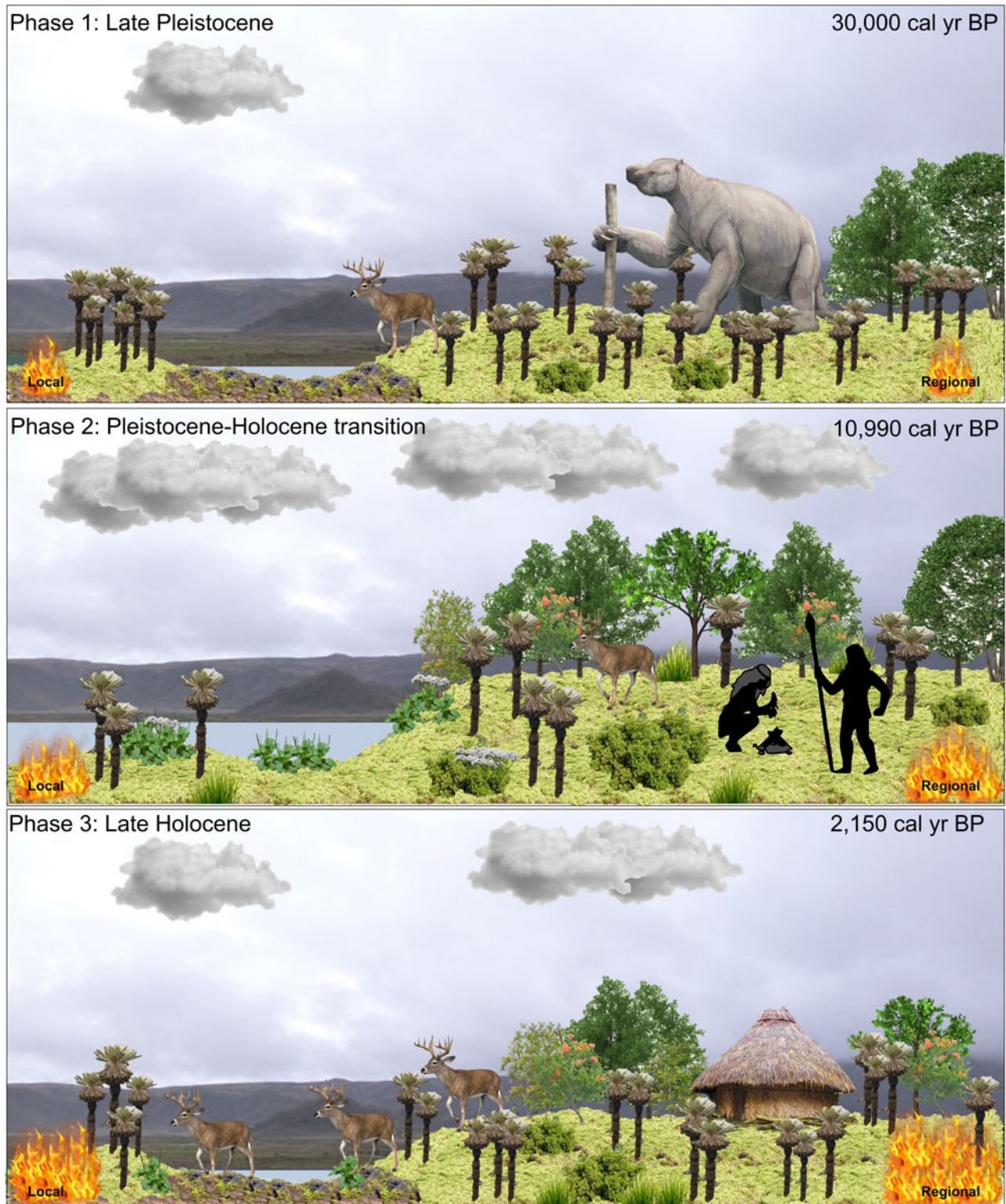
Figure 6. A conceptual landscape drawing of the changes in megafaunal presence, vegetation and fire activity reconstructed for Monquentiva during the Late Pleistocene and Holocene. Produced using Inkscape (Inkscape Project, 2022). Megafauna are depicted by the giant ground sloth (*Eremotherium*; concept art sourced from Ugueto, 2020) and a white-tailed deer representation (*Odocoileus virginianus*) (https://www.allwhitebackground.com/?p=4845; viewed 04 January 2022). The flora clipart not cited are sourced from Microsoft clipart 2016. Trees and shrubs include representations of *Alnus* (https://www.turbosquid.com/Search/Index.cfm?keyword=Alnus+glutinosa&media_typeid=2; viewed 10 January 2022) and *Morella* (https://globalpollenproject.org/Taxon/Myricaceae/Morella/cerifera; viewed 10 January 2022). Herbaceous taxa include *Espeletia* (Asteraceae), *Stachys* (Mergili, 2007; Zwerver, n.d.), and *Valeriana* (https://vancouverislandgrows.wordpress.com/2018/01/23/valeriana officinalis/; viewed 12 January 2022). Local and regional fire activity represented by relative size of flame. Silhouettes indicate hunter-gatherer groups (Vlasiuk, 2020). Kogi hut represents occupation by the pre-Hispanic indigenous group Muiscas (Benedek, 2015). Clouds and lake (blue polygon) represent humidity and lake level at the site (Garcia, 2022). Photographic backdrop of Monquentiva taken by J.W. Oughton in 2019.

Monquentiva, however, charcoal peak magnitude and frequency remained low, suggesting the fires were of low intensity and low frequency (Fig. 4). Increased fire activity could have resulted from relatively dry conditions, as indicated by the low abundance of aquatic and wetland taxa including *Isoëtes* and Cyperaceae (Fig. 3). However, fire activity was not sustained, particularly during the first wave of megafaunal decline ca. 22,900 BP. This could have resulted from the cold and dry conditions in the Andes at the end of the late glacial period (Bogotá-A et al., 2011; Urrego et al., 2011b) and from a reduction in fuel-load by the decrease of Poaceae from 24,240 BP (Fig. 3).

The first wave of megafaunal decline at 22,900 BP took place during a short period of a slightly warm and humid climate at Monquentiva, as evidenced by displacements of Páramo by SubPáramo vegetation and increases in arboreal elements (Figs. 3, 7). The increase of Andean forest taxa including *Alnus* and *Podocarpus* indicated a relative increase in temperatures, whereas the absence of *Isoëtes* indicated low water levels. *Alnus* and *Podocarpus* are cold-tolerant and generous wind-pollinated pollen producers, and their high abundance could imply over-representation from lower altitudes (van der Hammen and González, 1960; Colinvaux et al., 1999). However, we suggest an upslope tree line migration, because *Weinmannia* and *Podocarpus*, two taxa associated with upper montane forest in the tropical Andes, also increased (Gómez et al., 2007; Hagemans et al., 2019). This relative warming was short-lived, and temperatures decreased, as indicated by a further rise in Subpáramo taxa such as Asteraceae and a decline of arboreal elements at ca. 20,890 BP. Fluctuations of the upper forest line are consistent with changes from lower altitudes of Colombia (van Geel and van der Hammen, 1973; Bogotá-A et al., 2011) and suggest temperature changes as megafaunal populations declined during the Late Pleistocene. By ca. 16,930 BP, environmental conditions once again provided a favourable habitat for megafauna at Monquentiva.

The second wave of megafaunal decline occurred at ca. 10,990 BP, during the El Abra stadial (Fig. 6) (Hooghiemstra and van der Hammen, 1993). This period coincided with an increase of high Andean forest and Páramo vegetation, suggesting novel and transitional vegetation (see ecological consequences discussion). Nearby vegetation records from Lake Fuquene (2580 m asl; Bogotá-A et al., 2011) and Cienaga del Visitador (3300 m asl; van der Hammen and González, 1965) also show rises in *Alnus* and a vegetation mosaic composed by Andean forest, Subpáramo, and Páramo. The decline of megafauna at Monquentiva during the cool El Abra stadial contrasts with the literature, which suggests extinctions during warm interstadials (Cooper et al., 2015; Rozas-Dávila et al., 2016), but converge with declines occurring during periods of climate instability.

The decline of megafauna at ca. 10,990 BP also coincided with the earliest evidence of hunter-gatherers in Colombia (Fig. 6). Hunter-gatherer groups are reported since the Guantiva intersta-dial ca. 12,500 BP in the Bogotá highlands (2600 m asl) and downslope from Monquentiva at 340 m asl since 11,740 BP (van der Hammen and Correal Urrego, 1978; Correal Urrego, 1993; Triana-Vega et al., 2019; Alfonso-Rojas et al., 2021). Megafaunal extinctions have been linked to overhunting by humans worldwide (Martin and Klein, 1984; MacPhee and Sues, 1999) and suggested as a major driver of extinction in North America and Australia (Martin and Klein, 1984; Stuart, 1999; Rule et al., 2012). In South America, our understanding of the role of overhunting in the decline of Pleistocene megafauna

is less clear due to the paucity of records. Records from coastal Ecuador suggest a stratigraphic correlation between megafaunal remains and stone tools of suspected Holocene age (Ficcarelli et al., 1997). However, megafauna hunting by humans is not thought to be the cause of extinction at this site (Ficcarelli et al., 1997). The Pleistocene collapse of megafauna in Brazil occurred during a window of human occupation (Raczka et al., 2018), but megafauna populations in Peru collapsed before the first records of human presence (Rozas-Dávila et al., 2016). At Monquentiva, megafauna populations were unable to recover after 10,990 BP, suggesting that both humans and climate could have contributed to their decline. Overall, our record allows us to infer the timing of megafaunal decline and ecological conse-quences, but we have little evidence to explore the cause of extinctions.

Ecological consequences of megafaunal collapse

We found that some tree and shrub species became absent from the record during both waves of megafaunal decline, increasing in abundance during the partial recovery of megafauna ca. 16,930– 10,990 BP (Fig. 3). Melastomataceae and *Hypericum* increased at Monquentiva when megafaunal abundance recovered. These pollen taxa can be dispersed by herbivores (Grabandt, 1980), sug-gesting a close link that is corroborated by the CCA analysis (Fig. 5a). Similarly, we found that several herbaceous taxa, includ-ing Acanthaceae, Apiaceae, *Ranunculus*, and *Veronica*, became absent from the record during the second wave of megafaunal decline ca. 10,990 BP (Fig. 3). This suggests that the decline of these taxa are likely a result of reduced seed dispersal by mega-fauna, rather than climate alone. Such relations between seed dis-persal and the loss of megafauna have been found in the Neotropics today, where the loss of primates has led to dispersal limitation in plant species (Peres et al., 2016). As Pleistocene megafauna declined in the high Andes of Peru, the abundance of grasses and forbs also decreased (Rozas-Dávila et al., 2016). In the Brazilian lowlands, vegetation remained largely unchanged, with only a few taxa declining in abundance (Raczka et al., 2018). These contrasting records probably relate to differences in the original vegetation and suggest the ecological consequences of megafaunal declines were habitat-specific. In the Colombian Andes however, our palaeoecological record suggests an impor-tant role of the megafauna in the reproduction and dispersion of tree, grass, and herb taxa.

The pollen record also showed palatable and woody taxa increasing at Monquentiva following the second decline of mega-fauna ca. 10,990 BP (Fig. 3). *Plantago* and *Valeriana*, which are palatable SubPáramo and Páramo herbs (Kutschker and Morrone, 2012; Rozas-Dávila et al., 2016; Hooghiemstra and Flantua, 2019), increased after the second megafaunal decline. The CCA analysis shows that these taxa ordinate on the opposite extreme of key SCF, indicating their sensitivity to megafaunal presence (Fig. 5a). Therefore, the Early Holocene *Plantago* and *Valeriana* abundance increases likely suggest their release from megafaunal grazing rather than warming. At Monquentiva, Ericaceae increases after the second megafaunal decline (Fig. 3) and plots on the opposite ecological extreme of key SCF in the CCA (Fig. 5a). Some Ericaceae species are woody shrubs in Andean sites (Bush et al., 2015; Rozas-Dávila et al., 2016), so this increase suggests woody species overgrowth following mega-faunal declines. Such woody overgrowth is also recorded in other palaeoecological records from Andean and North American sites

(Gill et al., 2009, 2012; Rozas-Dávila et al., 2016; Raczka et al., 2018). The lack of herbivory after the second megafaunal decline probably contributed to the encroachment of palatable and woody species at the higher altitudes of the eastern Colombian Cordillera.

At Monquentiva, a turnover in arboreal taxa and reduction of an open Poaceae-dominated grassland is recorded after the second wave of megafaunal decline ca. 10,990 BP (Fig. 6). The prominent Andean taxa were Ericaceae, *Hedyosmum*, *Podocarpus*, and *Weinmannia*, surrounded by shrubby Subpáramo herbs including *Acaena*, Asteraceae, and *Valeriana*. The presence of *Cyathea*, a tree fern that typically inhabits gaps in closed forests, suggests increases in forest cover (Crystal-Arens, 2001). This ecosystem transformation at Monquentiva suggests the replacement of open vegetation with a closed formation of non-analogue vegetation following the second megafaunal decline. This finding coincides with the consequences of defaunation reported for the Peruvian Andes (Rozas-Dávila et al., 2016) and other Neotropical (Dantas and Pausas, 2022) and North American sites (Gill et al., 2009, 2012). The flora turnover at Monquentiva occurred during the warmer Guantiva interstadial and cooler El Abra stadial 12,000–10,200 BP (Hooghiemstra and van der Hammen, 1993), thus climate oscillations could have played a role in vegetation changes observed. However, the CCA analysis showed that the abundance of some of these novel taxa including *Acaena*, *Valeriana*, and *Weinmannia* ordinate on the opposite end of the constraining variable for megafauna (Fig. 5a). This suggests the transitional non-analogue vegetation was closely linked to megafaunal declines and their role in determining vegetation composition and structure at Monquentiva.

Andean megafauna likely acted as fuel-load suppressors in the tropical Andes. The charcoal record from Monquentiva represents a transition to increased local and regional fire activity during the Early Holocene megafaunal decline (Fig. 4). The reduction of herbivory during the Early Holocene probably led to fuel build-up of woody and grass biomass and increased fire activity. Megafaunal presence and fire activity on our CCA show an opposite relationship (Fig. 5a), highlighting the link between rising fire activity and megafaunal absence. For instance, white-tailed deer are browsers, thus trample on vegetation and feed on palatable flora (Martínez-Polanco, 2019). Our record is consistent with increased fire activity after megafaunal collapse, as has been reported in other systems (Burney et al., 2003; Gill et al., 2009, 2012; Rule et al., 2012; Rozas-Dávila et al., 2016). However, the record of Monquentiva contrasts with the record from the Brazilian Cerrado where the collapse of megafauna populations did not coincide with increased fire activity (Raczka et al., 2018). We suggest that the complexity and diversity of South American ecosystems led to heterogeneity and habitat specificity regarding the relationship between Pleistocene megafaunal declines and increasing fire activity.

Extant Holocene megafauna, climate, and human activity

Monquentiva witnessed a recovery in key SCF concentrations from ca. 8800 BP (Figs. 3, 6) that could represent the presence of extant megafauna (Perrotti, 2018; Conroy et al., 2020). This probably included those that inhabit Colombian ecosystems today, such as the Brocket and white-tailed deer (Cooke, 1998; Martínez-Polanco, 2019) and the Andean spectacled bear (García-Rangel, 2012). This is consistent with surveys of white-tailed deer bone remains dated back to 2320 ± 50 ^{14}C age BP

(Becerra, 1995). The recovery of megafauna during human occupation could relate to a change from hunter-gatherer societies to sedentism (Triana-Vega et al., 2019; Archila et al., 2021). In the Late Holocene, Poaceae and Asteraceae were dominant, suggesting an increase in open vegetation at Monquentiva. Increases in *Hedyosmum*, *Weinmannia* and *Podocarpus* indicated an expansion of forest on the surrounding slopes (Bogotá-A et al., 2011). *Rumex* appeared in the record at low but consistent percentages (Supplementary Figure 2) and has been linked to degraded soils in Monquentiva (Espinoza et al., 2022). The increase in *Hedyosmum* also could be linked to disturbed areas (Gentry, 1993). These vegetation changes could reflect disturbance by pre-Hispanic Muisca groups (Langebaek, 1985, 2001). Increased humidity could have resulted in the formation of a shallow water body from a peat bog, as suggested by the rise in Cyperaceae and low abundance of *Isoëtes* (Hooghiemstra and van der Hammen, 1993). The Late Holocene vegetation cover and environmental conditions at Monquentiva likely provided habitat, water, and food for extant megafauna, allowing some species to persist in this part of the Colombian Andes until today.

During the late Holocene, fire activity escalated at Monquentiva (Espinoza et al., 2022) (Supplementary Figure 3, Fig. 6). High charcoal concentrations likely reflected increased fires linked to agriculture (Gómez et al., 2007) and other anthropogenic activities (Espinoza et al., 2022). Thus, the escalated fire record during Late Holocene megafaunal presence is likely to have been induced by human activities and facilitated by climate, which coupled to override the suppressive effect of megafauna on the vegetation.

CONCLUSIONS

This study is the first in the eastern Andes of Colombia, and probably across the South American continent, to use a multi-species SCF record to investigate the decline of Late Pleistocene megafauna. We showed that the combined spore record of coprophilous and semi-coprophilous fungi provided more robust evidence than using *Sporormiella* spores alone to infer megafaunal presence and declines. The multi-species SCF record from Monquentiva indicated the presence of Pleistocene megafauna in the eastern Colombian Cordillera since at least ca. 30,290 BP. At Monquentiva, megafauna populations declined in two waves. The first decline was reached by ca. 22,900 BP during a short period of a slightly warm and humid climate. The second megafaunal decline was reached by 10,990 BP, in a period coeval with the El Abra stadial and the presence of hunter-gatherer groups. The extinction of some megafauna at Monquentiva also points to declines occurring during periods of climate instability. However, our data do not allow us to infer the direct causes of megafaunal extinctions or the potential role of overhunting.

One ecological consequence of the megafaunal declines at Monquentiva was the formation of novel vegetation assemblages. The abundance of some plant species decreased while other palatable and woody taxa increased. This highlighted the role of megafauna in seed dispersal and herbivory. Another ecological consequence was the increase in fire activity after megafauna declined. Pleistocene megafauna likely acted as fuel-load suppressors in the tropical Andes as they trampled on vegetation and fed on palatable flora.

Overall, we show that ecosystems in the high eastern Andes of Colombia were highly sensitive to the decline of megafauna populations. Under the current biodiversity crisis, our understanding of the ecological consequences of megafaunal declines suggests

that current and future extinctions could have devastating consequences for biodiversity. This knowledge is fundamental for contemporary management and conservation efforts. To effectively manage biodiversity, these efforts must account for the effect of local herbivore declines on the dispersal of certain plant species, on fire activity, and the potential loss of ecosystem services.

Supplementary material. The supplementary material for this article can be found at https://doi.org/10.1017/qua.2022.66

REFERENCES

Abràmoff, M.D., Magalhães, P.J., Ram, S.J., 2004. Image processing with ImageJ. *Biophotonics International* 11, 36–42.

Alfonso-Rojas, A., Herrera-Gutierrez, L.M., Suárez, C. M., Ciancio, M.R., Pelegrin, J.S., Cadena, E-A., 2021. Late Pleistocene biota from Pubenza, Colombia; turtles, mammals, birds, invertebrates and plant remains. *Journal of Quaternary Science* 36, 450–466.

Archila, S., Groot, A.M. Ospina, J.P., Mejía, M., Zorro, C., 2021. Dwelling the hill: traces of increasing sedentism in hunter-gatherers societies at Checua site, Colombia (9500–5052 cal BP). *Quaternary International* 578, 102–119.

Avella-M, A., Torres, S.R., Gómez, W.A., Pardo, M.P., 2014. The paramos and high Andean forests of the Monquentiva swamp or Martos swamp (Guatavita, Cundinamarca, Colombia): ecological characterization and conservation status. *Biota Colombiana* 15, 3–39.

Barnosky, A.D., Koch, P.L., Feranec, R.S., Wing, S.L., Shabel, A.B., 2004. Assessing the causes of Late Pleistocene extinctions on the continents. *Science* 306, 70–75.

Barnosky, A.D., Lindsey, E.L., 2010. Timing of Quaternary megafaunal extinction in South America in relation to human arrival and climate change. *Quaternary International* 217, 10–29.

Becerra, M., 1995. *Études Morphologiques et Traceologiques des Micro Pointes de Quartz de 'Duitama-Tocogua', Haut Plateau de Boyacá en Colombia*. Université de Paris-I, Panthéon Sorbonne, Crap, Paris.

Benedek, 2015. *Traditional Kogi Hut in Colombia, South America*. Benedek, Canada, https://www.istockphoto.com/photo/traditional-kogi hut in-sierra-nevada-desanta-marta-colombia-gm501625816-81436861. [viewed 14 January 2022]

Bernal, R., Gradstein, S.R, Celis, M. (Eds.), 2019. *Catálogo de Plantas Y Líquenes de Colombia*. Institute of Natural Sciences, Universidad Nacional de Colombia, Bogotá. http://catalogoplantasdecolombia.unal.edu.co/en/. [viewed 17 May 2021]

Bischler, H., Pinto, P., 1959. Cave paintings and engravings in the Serranía de la Macarena. *Lamp Magazine, International Petroleum Company, Bogota* 6, 1415.

Blaauw, M., Christen, J.A., 2013. *Bacon Manual—v2.3.9.1*. https://chrono.qub.ac.uk/blaauw/manualBacon_2.3.pdf.

Bogotá-A, R.G., Groot, M.H.M., Hooghiemstra, H., Lourens, L.J., Van der Linden, M., Berrio, J.C., 2011. Rapid climate change from north Andean Lake Fúquene pollen records driven by obliquity: implications for a basin-wide biostratigraphic zonation for the last 284 ka. *Quaternary Science Reviews* 30, 3321–3337.

Borrero, L.A., 2009. The elusive evidence: the archaeological record of the South American extinct megafauna. In: Haynes, G. (Ed.), *American Megafaunal Extinctions at the End of the Pleistocene*. Springer, Dordrecht, pp. 145–168.

Borrero, L.A., Zarate, M., Miotti, L., Massone, M., 1998. The Pleistocene-Holocene transition and human occupations in the southern cone of South America. *Quaternary International* 49–50, 191–199.

Burney, D.A., Robinson, G.S., Burney, L.P., 2003. Sporormiella and the Late Holocene extinctions in Madagascar. *Proceedings of the National Academy of Sciences* 100, 10800–10805.

Bush, M.B., Alfonso-Reynolds, A.M., Urrego, D.H., Valencia, B.G., Correa-Metrio, Y.A., Zimmermann, M., Silman, M.R., 2015. Fire and climate: contrasting pressures on tropical Andean timberline species. *Journal of Biogeography* 42, 938–950.

Bush, M.B., Weng, M.B., 2006. Introducing a new (freeware) tool for palynology. *Journal of Biogeography* 34, 377–380.

CAR, 2007. *Elaboración del Diagnostico, Prospectiva y Formulación Cuenca Hidrográfica del Río Gacheta Subcuenca Río Monquentiva*. Bogotá.

Chepstow-Lusty, A.J., Frogley, M.R., Baker, A.S., 2019. Comparison of *Sporormiella* dung fungal spores and oribatid mites as indicators of large herbivore presence: evidence from the Cuzco region of Peru. *Journal of Archaeological Science* 102, 61–70.

Clark, J.S., Patterson, W.A., 1997. Background and local charcoal in sediments: scales of fire in the paleorecord. In: Clark, J.S., Cachier, H., Goldammer, J.G., Stocks, B. (Eds.), *Sediment Records of Biomass Burning and Global Change*. Springer, Berlin, pp. 23–48.

Clark, J.S., Royall, D.P., Chumbley, C., 1996. The Role of Fire During Climate Change in an Eastern Deciduous Forest at Devil's Bathtub, New York. *Ecology* 77, 2148–2166.

Colinvaux, P.A., De Oliveira, P.E., Moreno, J.E., 1999. *Amazon Pollen Manual and Atlas*. Harwood Academic Press, New York.

Coltorti, M., Ficcarelli, G., Jahren, H., Espinosa, M.M., Rook, L., Torre, D., 1998. The last occurrence of Pleistocene megafauna in the Ecuadorian Andes. *Journal of South American Earth Sciences* 11, 581–586.

Conroy, K.J., Baker, A.G., Jones, V.J., van Hardenbroek, M., Hopla, E.J., Collier, R., Lister, A.M., Edwards, M.E., 2020. Tracking late-Quaternary extinctions in interior Alaska using megaherbivore bone remains and dung fungal spores. *Quaternary Research* 97, 99–110.

Cooke, R., 1998. Human settlement of Central America and northernmost South America (14,000–8000 BP). *Quaternary International*. 49–50, 177–190.

Cooper, A., Turney, C., Hughen, K.A., Brook, B.W., McDonald, H.G., Bradshaw, C.J.A., 2015. Abrupt warming events drove Late Pleistocene Holarctic megafaunal turnover. *Science*. 349, 602–606.

Correal, G., Piñeros, F., Van Der Hammen, T., 1990. Guayabero I: un sitio precerámico de la localidad Angostura II, San José del Guaviare. *Caldasia* 16, 245–254.

Correal Urrego, G., 1981. *Evidencias Culturales y Megafauna Pleistocénica en Colombia*. Fundación de Investigaciones Arqueológicas Nacionales, Bogotá.

Correal Urrego, G., 1993. New Pleistocene cultural evidences and megafauna in Colombia. *Archeology Bulletin* 8, 3–12.

Correal Urrego, G., Olano, J.G., Calderón, K.J., Cardozo, D.C.V., 2005. Archaeological evidence and extinct megafauna in a salt flat from the Upper Tardiaglacial. *Archeology Bulletin* 20, 3–58.

Crystal-Arens, N., 2001. Variation in performance of the tree fern *Cyathea caracasana* (Cyatheaceae) across a successional mosaic in the Andean cloud forest. *American Journal of Botany* 88, 545–551.

Cugny, C., Mazier, F., Galop, D., 2010. Modern and fossil non-pollen paly-nomorphs from the Basque Mountains (Western Pyrenees, France): the use of coprophilous fungi to reconstruct pastoral activity. *Vegetation History and Archaeobotany* **19**, 391–408.

Dantas, V.L., Pausas, J.G., 2022. The legacy of the extinct Neotropical mega-fauna on plants and biomes. *Nature Communications.* **13**, 129. https://doi.org/10.1038/s41467-021-27749-9.

Davis, O.K., 1987. Spores of the dung fungus *Sporormiella*: increased abun-dance in historic sediments and before Pleistocene megafaunal extinction. *Quaternary Research* **28**, 290–294.

Davis, O.K., Shafer, D.S., 2006. *Sporormiella* fungal spores, a palynological means of detecting herbivore density. *Paleogeography, Palaeoclimatology, Palaeoecology* **237**, 40–50.

Derner, J.D., Boutton, T.W., Briske, D.D., 2006. Grazing and ecosystem carbon storage in the North American Great Plains. *Plant and Soil* **280**, 77–90.

Dickinson, C.H., Underhay, V.H.S., 1977. Growth of fungi in cattle dung. *Transactions of the British Mycological Society* **69**, 473–477.

Dix, N.J., Webster, J., 1995. *Fungal Ecology*. Chapman and Hall. London.

Elias, S.A., Schreve, D., 2007. Late Pleistocene megafaunal extinctions. In: Elias, S.A. (Ed.), *Encyclopedia of Quaternary Science. Vol. 4*. Amsterdam: Elsevier Science Publishers B.V., North-Holland, pp. 3202–3217.

Espinoza, I.G., Franco-Gaviria, F., Castañeda, I., Robinson, C., Room, A., Berrío, J.C., Armenteras, D., Urrego, D.H., 2022. Holocene fires and eco-logical novelty in the high Colombian Cordillera Oriental. *Frontiers in Ecology and Evolution* **10**. https://www.frontiersin.org/articles/10.3389/fevo.2022.895152.

Etienne, D., Jouffroy-Bapicot, I., 2014. Optimal counting limit for fungal spore abundance estimation using *Sporormiella* as a case study. *Vegetation History and Archaeobotany* **23**, 743–749.

Etienne, D., Wilhelm, B., Sabatier, P., Reyss, J.L., Arnaud, F., 2013. Influence of sample location and livestock numbers on *Sporormiella* con-centrations and accumulation rates in surface sediments of Lake Allos, French Alps. *Journal of Paleolimnology* **49**, 117–127.

Fægri, K., Kaland, P.E., Krzywinski, K., 1989. *Textbook of Pollen Analysis*. John Wiley & Sons Ltd., Chichester, UK.

Ficcarelli, G., Azzaroli, A., Bertini, A., Coltorti, M., Mazza, P., Mezzabotta, C., Espinosa, M.M., Rook, L., Torre, D., 1997. Hypothesis on the cause of extinction of the South American mastodonts. *Journal of South American Earth Sciences* **10**, 29–38.

García-Rangel, S., 2012. Andean bear *Tremarctos ornatus* natural history and conservation, *Mammal Review* **42**, 85–110.

Garcia, M., 2022. *Cloud PNG*. 123PNGDownload. https://123pngdownload.com/cloud-png-images/. [viewed 15 January 2022]

Gentry, A.H., 1993. *A Field Guide to the Families and Genera of Woody Plants of Northwest South America (Colombia, Ecuador, Peru), with Supplementary Notes on Herbaceous Taxa*. Conservation International and University of Chicago Press, Chicago.

Gill, J.L., Williams, J.W., Jackson, S.T., Donnelly, J.P., Schellinger, G.C., 2012. Climatic and megaherbivory controls on late-glacial vegetation dynamics: a new, high resolution, multi proxy record from Silver Lake, Ohio. *Quaternary Science Reviews* **34**, 66–80.

Gill, J.L., Williams, J.W., Jackson, S.T., Lininger, K.B., Robinson, G.S., 2009. Pleistocene megafaunal collapse, novel plant communities, and enhanced fire regimes in North America. *Science* **326**, 1100–1103.

Gómez, A., Berrío, J.C., Hooghiemstra, H., Becerra, M., Marchant, R., 2007. A Holocene pollen record of vegetation change and human impact from Pantano de Vargas, an intra-Andean basin of Duitama, Colombia. *Review of Palaeobotany and Palynology* **145**, 143–157.

Gomez, C.L., Rubio, D., 2003. *The Martos Reservoir: Historical, Cultural And Geographical Study*. Academy of History of Cundinamarca and Secretary of the Environment of the Department of Cundinamarca, Colombia.

Gordon, C.E., Rion E.L., Allin, P., Greve, M., Svenning, J.-S., 2021. Elephant rewilding indirectly affects the abundance of an arboreal but not generalist Savanna Lizard. *Biodiversity and Conservation* **30**, 1277–1291.

Grabandt, R.A.J., 1980. Pollen rain in relation to arboreal vegetation in the Colombian Cordillera Oriental. *Review of Palaeobotany and Palynology* **29**, 65–147.

Guarro, J., Gené, J., Stchigel, A.M., Figueras, M.J., 2012. *Atlas of Soil Ascomycetes*. CBS-KNAW Fungal Biodiversity Centre, Utrecht, The Netherlands.

Hagemans, K., Tóth, C.D., Ormaza, M., Gosling, W.D., Urrego, D.H., León-Yánez, S., Wagner-Cremer, F., Donders, T.H., 2019. Modern pollen-vegetation relationships along a steep temperature gradient in the tropical Andes of Ecuador. *Quaternary Research* **92**, 1–13.

Halsall, K.M., Ellingsen, V.M., Asplund, J., Bradshaw, R.H.W., Ohlson, M., 2018. Fossil charcoal quantification using manual and image analysis approaches. *The Holocene* **28**, 1345–1353.

Hedges, R.E., Ramsey, C.B., Van Klinken, G.J., Pettitt, P.B., Nielsen-Marsh, C., Etchegoyen, A., Niello, J.F., Boschin, M., Llamazares, A.M., 1997. Methodological issues in the ^{14}C dating of rock paintings. *Radiocarbon* **40**, 35–44.

Higuera, P., 2009. *CharAnalysis 0.9: Diagnostic and Analytical Tools for Sediment Charcoal Analysis*. User's Guide, Montana State University, Missoula, USA. http://phiguera.github.io/CharAnalysis/.

Higuera, P.E., Brubaker, L.B., Anderson, P.M., Hu, F.S., Brown, T.A., 2009. Vegetation mediated the impacts of postglacial climatic change on fire regimes in the south central Brooks Range, Alaska. *Ecological Monographs.* **79**, 201–219.

Hooghiemstra, H., 1984. *Vegetational and Climatic History of the High Plain of Bogotá, Colombia: A Continuous Record of the Last 3.5 Million Years*. Lubrecht & Cramer Ltd., Cramer, Germany.

Hooghiemstra, H., Flantua, S.G.A., 2019. Colombia in the Quaternary: an overview of environmental and climatic change. In: Gómez, J., Pinilla-Pachon, A.O. (Eds.), *The Geology of Colombia*. Servicio Geológico Colombiano, Publicaciones Geológicas Especiales, Bogotá **38**, 43–95.

Hooghiemstra, H., van der Hammen, T., 1993. Late Quaternary vegetation his-tory and paleoecology of Laguna Pedro Palo (Subandean forest belt, Eastern Cordillera, Colombia). *Review of Palaeobotany and Palynology* **77**, 235–262.

IBM Corp., 2020. *IBM SPSS Statistics for Windows*, Version 26.0. IBM Corp., Armonk, New York.

Inkscape Project, 2022. *Inkscape v.1.1.2*. Inkscape's Contributors (vendor), annual updating.

Johnson, C.N., 2009. Ecological consequence of late Quaternary extinctions of megafauna. *Proceedings of The Royal Society B.* **276**, 2509–2519.

Johnson, C.N., Rule, S., Haberle, S.G., Turney, C.S.M., Kershaw, A.P., Brook, B.W., 2015. Using dung fungi to interpret decline and extinction of megaher-bivores: problems and solutions. *Quaternary Science Reviews* **110**, 107–113.

Juggins, S., 2007. *C2: Software for Ecological and Palaeoecological Data Analysis and Visualisation (User Guide Version 1.5)*. Newcastle, Newcastle University, 73 pp.

Jull, A.J.T., Iturralde-Vinent, M., O'Malley, J.M., MacPhee, R.D.E., McDonald, H.G., Martin, P.S., Moody, J., Rincón, A., 2004. Radiocarbon dating of extinct fauna in the Americas recovered from tar pits. *Nuclear Instruments and Methods in Physics Research Section B: Beam Interactions with Materials and Atoms.* **223**, 668–671.

Kammer, A., Piraquive, A., Gómez, C., Mora, A., Velásquez, A., 2020. Structural styles of the Eastern Cordillera of Colombia. In: Gómez, J., Mateus-Zabala, D. (Eds.), *The Geology of Colombia, Volume 3 Paleogene–Neogene*. Servicio Geológico Colombiano, Publicaciones Geológicas Especiales **37**, 143–183.

Kershaw, A.P., 1997. A modification of the Troels-Smith system of sediment description and portrayal. *Quaternary Australasia* **15**, 63–68.

Krug, J.C., Benny, G.L., Keller, H.W., 2004. Coprophilous fungi. In: Mueller, G.M., Bills, G.F., Foster, M.S. (Eds.), *Biodiversity of Fungi, Inventory and Monitoring Methods*. Elsevier, Boston, pp. 467–499.

Kuthubutheen, A.J., Webster, J., 1986. Water availability and the coprophi-lous fungus succession. *Transactions of the British Mycological Society* **86**, 63–76.

Kutschker, A., Morrone, J.J., 2012. Distributional patterns of the species of *Valeriana* (Valerianaceae) in southern South America. *Plant Systematics and Evolution* **298**, 535–547.

Langebaek, C.H., 1985. Cuando los Muiscas diversificaron la agricultura y crearon el intercambio. *Boletín Cultural Y Bibliográfico* **22**, 3–10.

Langebaek, C.H., 2001. *Arqueologia Regional en el Valle de Leiva: Procesos de Ocupacion Humana en una Region de los Andes Orientales de Colombia*. Colombiano de Antropologia e Historia, Bogota, Colombia.

Last, W.M., Smol, J.P. (Eds.), 2002. *Tracking Environmental Change Using Lake Sediments: Volume 1: Basin Analysis, Coring and Chronological Techniques*. Springer, Science & Business Media, Dordrecht, The Netherlands.

Lee, C.M., van Geel, B., Gosling, W.D., 2022. On the use of spores of coprophilous fungi preserved in sediments to indicate past herbivore presence. *Quaternary* 5, 30. https://doi.org/10.3390/quat5030030.

Lima-Ribeiro, M.S., Diniz-Filho, J.A.F., 2013. American megafaunal extinctions and human arrival: Improved evaluation using a meta-analytical approach. *Quaternary International* 299, 38–52.

Loughlin, N.J.D., Gosling, W.D., Montoya, E., 2018. Identifying environmental drivers of fungal non-pollen palynomorphs in the montane forest of the eastern Andean flank, Ecuador. *Quaternary Research* 89, 119–133.

MacNeish, RS, Berger, R., Protscha, R., 1970. Megafauna and man from Ayacucho, highland Peru. *Science* 168, 975–977.

MacPhee, R.D., Sues, H.D. (Eds.), 1999. *Extinctions in Near Time (Vol. 2)*. Springer Science & Business Media, Dordrecht, The Netherlands.

Maher, L.J., Jr., 1981. Statistics for microfossil concentration measurements employing samples spiked with marker grains. *Review of Palaeobotany and Palynology* 32, 153–191.

Maher, L.J., Jr., Heiri, O., Lotter, A.F., 2012. Assessment of uncertainties associated with palaeolimnological laboratory methods and microfossil analysis. In: Birks, H., Lotter, A., Juggins, S., Smol, J. (Eds.), *Tracking Environmental Change Using Lake Sediments. Developments in Paleoenvironmental Research, vol 5*. Springer, Dordrecht, pp. 143–166.

Malhi, Y., Doughty, C.E., Galetti, M., Smith, F.A., Svenning, J-C., Terborgh, J.W., 2016. Megafauna and ecosystem function from the Pleistocene to the Anthropocene. *Proceedings of the National Academy of Sciences* 113, 838–846.

Marchant, R., Almeida, L., Behling, H., Berrio, J.C., Bush, M., Cleef, A., Duivenvoorden, J., *et al.*, 2002. Distribution and ecology of parent taxa of pollen lodged within the Latin American pollen database. *Review of Palaeobotany and Palynology* 121, 1–75.

Martin, P.S., Klein, R.G., 1984. Prehistoric overkill: the global model. In: Martin, P.S., Klein, R.G. (Eds.), *Quaternary Extinctions: A Prehistoric Revolution*. The University of Arizona Press, Tucson, Arizona, pp. 354–403.

Martínez-Polanco, M.F., 2019. Beyond white-tailed deer hunting in Aguazuque: Archaeofaunal data from an archaic site at Sabana de Bogotá, Colombia. *International Journal of Osteoarchaeology* 29, 108–116.

MathWorks, 2019. *Matlab Software version R2019a*. MathsWorks, Natick, Massachusetts, USA.

Mergili, M., 2007. *Páramo El Ángel with frailejones*. The world in images, Piwigo. https://www.mergili.at/worldimages/picture.php?/8835. [viewed 11 January 2022]

Mills, S., Soulé, M.E., Doak, D.F., 1993. The keystone-species concept in ecology and conservation. *BioScience* 43, 219–224.

Munsell Color, 1992. *Munsell Soil Color Charts*. Baltimore, Maryland.

Neves, W.A., Piló, L.B., 2003. Solving Lund's dilemma: new AMS dates confirm that humans and megafauna coexisted at Lagoa Santa. *Current Research in the Pleistocene* 20, 57–60.

Oksanen, J., 2009. *Multivariate Analysis of Ecological Communities in R: Vegan Tutorial*. University of Oulu, Oulu, Finland.

Oksanen, J., Kindt, R., Legendre, P., O'Hara, B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Wagner, H., 2007. *The vegan Package: Community Ecology Package*. R Foundation for Statistical Computing, Vienna.

Peres, C.A., Emilio, T., Schietti, J., Desmoulière, S.J., Levi, T., 2016. Dispersal limitation induces long-term biomass collapse in overhunted Amazonian forests. *Proceedings of the National Academy of Sciences* 113, 892–897.

Perrotti, A.G., 2018. Pollen and *Sporormiella* evidence for terminal Pleistocene vegetation change and megafaunal extinction at Page-Ladson, Florida. *Quaternary International* 466, 256–268.

Perrotti, A.G., van Asperen, E., 2019. Dung fungi as a proxy for megaherbivores: opportunities and limitations for archaeological applications. *Vegetation History and Archaeobotany* 28, 93–104.

Pino, M., Abarzúa, A.M., Astorga, G., Martel-Cea, A., Cossio-Montecinos, N., Navarro, R.X., Lira, M.P., *et al.*, 2019. Sedimentary record from Patagonia, southern Chile supports cosmic impact triggering of biomass burning, climate change, and megafaunal extinctions at 12.8 ka. *Scientific Reports* 9, 4413. https://doi.org/10.1038/s41598-018-38089-y.

Ponel, P., Court-Picon, M., Badura, M., Guiter, F., de Beaulieu, J.L., Andrieu-Ponel, V., Djamali, M., Leydet, M., Gandouin, E., Buttler, A., 2011. Holocene history of Lac des Lauzons (2180 m asl), reconstructed from multiproxy analyses of Coleoptera, plant macroremains and pollen (Hautes-Alpes, France). *The Holocene* 21, 565–582.

Poveda, G., Mesa, O.J., Salazar, L.F., Arias, P.A., Moreno, H.A., Vieira, S.C., Agudelo, P.A., Toro, V.G., Alvarez, J.F., 2005. The diurnal cycle of precipitation in the tropical Andes of Colombia. *Monthly Weather Review* 133, 228–240.

Poveda, G., Waylen, P.R., Pulwarty, R.S., 2006. Annual and inter-annual variability of the present climate in northern South America and southern Mesoamerica. *Palaeogeography, Palaeoclimatology, Palaeoecology* 234, 3–27.

Prado, J. L., Alberdi, M.T., Azanza, B., Sánchez, B., Frassinetti, D., 2005. The Pleistocene Gomphotheriidae (Proboscidea) from South America. *Quaternary International* 126–128, 21–30.

Raczka, M.F., Bush, M.B., De Oliveira, P.D., 2018. The collapse of megafaunal populations in southeastern Brazil. *Quaternary Research* 89, 103–118.

Raczka, M.F., Bush, M.B., Folcik, A.M., McMichael, C.H., 2016. *Sporormiella* as a tool for detecting the presence of large herbivores in the Neotropics. *Biota Neotropica* 16, e20150090. https://doi.org/10.1590/1676-0611-BN-2015-0090.

Raczka, M.F., Mosblech, N.A., Giosan, L., Valencia, B.G., Folcik, A.M., Kingston, M., Baskin, S., Bush, M.B., 2019. A human role in Andean megafaunal extinction? *Quaternary Science Reviews* 205, 154–165.

Ramsey, C.B., 2009a. Bayesian analysis for radiocarbon dates. *Radiocarbon* 51, 337–360.

Ramsey, C.B., 2009b. Dealing with outliers and offsets in radiocarbon dating. *Radiocarbon* 51, 1023–1045.

Rangel-Ch, J.O., 2000. La Región Paramuna y franja Aledaña en Colombia. In: Churio, R., Orlando, J. (Eds.), *Colombia Biotic Diversity III. La Región De Vida Paramuna*. Universidad Nacional de Colombia, Bogotá, pp. 1–23.

Raper, D., Bush, M., 2009. A test of *Sporormiella* representation as a predictor of megaherbivore presence and abundance. *Quaternary Research* 71, 490–496.

R Core Team, 2021. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. https://www.Rproject.org/.

Reimer, P.J., Austin, W.E., Bard, E., Bayliss, A., Blackwell, P.G., Ramsey, C.B., Butzin, M., *et al.*, 2020. The IntCal20 Northern Hemisphere radiocarbon age calibration curve (0–55 cal kBP). *Radiocarbon* 62, 725–757.

Revelles, J., Burjachs, F., van Geel, B., 2016. Pollen and non-pollen palynomorphs from the Early Neolithic settlement of La Draga (Girona, Spain). *Review of Palaeobotany and Palynology* 225, 1–20.

Robinson, G.S., Pigott Burney, L., Burney, D.A., 2005. Landscape paleoecology and megafaunal extinction in southeastern New York State. *Ecological Monographs* 75, 295–315.

Rodionov, S.N., 2004. A sequential algorithm for testing climate regime shifts. *Geophysical Research Letters* 31, L09204. https://doi.org/10.1029/2004GL019448.

Rodionov, S.N., Overland, J.E., 2005. Application of a sequential regime shift detection method to the Bering Sea ecosystem. *ICES Journal of Marine Science* 62, 328–332.

Rojas, E., Arce, B., Peña, A., Boshell, F., Ayarza, M., 2010. Quantification and interpolation of local trends in temperature and precipitation in the high Andean areas of Cundinamarca and Boyacá (Colombia). *Revista Corpoica-Ciencia y Tecnologia Agropecuarias* 11, 173–182.

Room, A., Franco-Gaviria, F., Urrego, D.H., 2022. *Package rshift: Paleoecology and Regime Shift Analysis*. R package version 2.1.1. https://CRAN.Rproject.org/package=rshift.

Rozas-Dávila, A., Valencia, B.G., Bush, M., 2016. The functional extinction of Andean megafauna. *Ecology* 97, 2533–2539.

Rule, S., Brook, B.W., Haberle, S.G., Turnery, C.S.M., Kershaw, A.P., Johnson, C.N., 2012. The aftermath of megafaunal extinction: ecosystem transformation in Pleistocene Australia, *Science*, 335: 1483–1486. doi.org/10.1126/science.1214261.

Sankaran, M., Hanan, N.P., Scholes, R.J., Ratnam, J., Augustine, D.J., Cade, B.S., Gignoux, J., *et al.*, 2005. Determinants of woody cover in African savannas. *Nature* **438**, 846–849.

Staver, A.C., Bond, W.J., 2014. Is there a "Browse Trap"? Dynamics of herbivore impacts on trees and grasses in an African Savanna. *Journal of Ecology* **102**, 595–602.

Steadman, D.W., Martin, P.S., MacPhee, R.D.E., Jull, A.J.T., McDonald, H.G., Woods, C.A., Iturralde-Vinent, M., Hodgins, G.W.L., 2007. Early Holocene survival of megafauna in South America. *Journal of Biogeography* **34**, 1642–1646.

Stockmarr, J.A., 1971. Tablets with spores used in absolute pollen analysis. *Pollen et Spores* **13**, 615–621.

Stuart, A.J., 1999. Late Pleistocene megafaunal extinctions. In: MacPhee, R.D.E. (Ed.), *Extinctions in Near Time. Advances in Vertebrate Paleobiology, vol. 2*. Springer, Boston, MA, pp. 257–269.

Trachsel, M., Telford, R.J., 2017. All age-depth models are wrong, but are getting better. *The Holocene* **27**, 860–869.

Triana-Vega, A.V., Sedov, S., Salinas-Acero, J., Carvajal-Contreras, D., Moreano, C., Tovar-Reyes, M., Solleiro-Rebolledo, E., Díaz-Ortega, J., 2019. Environmental reconstruction spanning the transition from hunter/gatherers to early farmers in Colombia: paleopedological and archaeological indicators from the pre-ceramic sites Tequendama and Aguazuque. *Quaternary International* **516**, 175–189.

Ugueto, G.N., 2020. *Morning Warmup Sketch, a concept sketch of the Giant Ground Sloth* Eremotherium laurillardi. Twitter for iPad. https://twitter.com/serpenillus/status/1297894174377877505. [viewed 04 January 2022]

Urrego, D.H., Bush, M.B., Silman, M.R., Correa-Metrio, A.Y., Ledru, M.P., Mayle, F.E., Paduano, G., Valencia, B.G., 2009. Millennial-scale ecological changes in tropical South America since the last glacial maximum. In: Vimeux, F., Sylvestre, F., Khodri, M. (Eds.), *Past Climate Variability in South America and Surrounding Regions. Developments in Paleoenvironmental Research, vol. 14*. Springer, Dordrecht, The Netherlands, pp. 283–300.

Urrego, D.H., Bush, M.B., Silman, M.R., Niccum, B.A., De La Rosa, P., McMichael, C.H., Hagen, S., Palace, M., 2013. Holocene fires, forest stability and human occupation in south-western Amazonia. *Journal of Biogeography* **40**, 521–533.

Urrego, D.H., Niccum, B.A., La Drew, C.F., Silman, M.R., Bush. M.B., 2011a. Fire and drought as drivers of Early Holocene tree line changes in the Peruvian Andes. *Journal of Quaternary Science* **26**, 28–36.

Urrego, D.H., Silman, M.R., Correa-Metrio, A., Bush, M.B., 2011b. Pollen vegetation relationships along steep climatic gradients in western Amazonia. *Journal of Vegetation Science* **22**, 795–806.

van Asperen, E.N., Kirby, J.R., Hunt, C.O., 2016. The effect of preparation methods on dung fungal spores: implications for recognition of megafaunal populations. *Review of Palaeobotany and Palynology* **229**, 1–8.

van Asperen, E.N., Perrotti, A., Baker, A., 2020. Coprophilous fungal spores: NPPs for the study of past megaherbivores. In: Marret, F., O'Keefe, J., Osterloff, P., Pound, M., Shumilovskikh, L. (Eds.), *Applications of Non-Pollen Palynomorphs: from Palaeoenvironmental Reconstructions to Biostratigraphy*. Geological Society of London, Special Publications **511**, 245–267.

van der Hammen, T., 1974. The Pleistocene changes of vegetation and climate in tropical South America. *Journal of Biogeography* **1**, 3–26.

van der Hammen, T., Correal Urrego, G., 1978. Prehistoric man of the Sabana de Bogotá: data for an ecological prehistory. *Palaeogeography, Palaeoclimatology, Palaeoecology* **25**, 179–190.

van der Hammen, T., González, E., 1960. Upper Pleistocene and Holocene climate and vegetation of the "Sabana de Bogota" (Colombia, South America). *Leidse Geologische Mededelingen* **25**, 261–315.

van der Hammen, T., González, E., 1965. A late-glacial and Holocene pollen diagram from Cienaga del Visitador (Dept. Boyaca, Colombia). *Leidse Geologische Mededelingen* **32**, 193–201.

van Geel, B., Buurman, J., Brinkkemper, O., Schelvis, J., Aptroot, A., van Reenen, G., Hakbijl, T., 2003. Environmental reconstruction of a Roman Period settlement site in Uitgeest (The Netherlands), with special reference to coprophilous fungi. *Journal of Archaeological Science* **30**, 873–883.

van Geel, B., Guthrie, R.D., Altmann, J.G., Broekens, P., Bull, I.D., Gill, F.L., Jansen, B., Nieman, A.M., Gravendeel, B., 2011. Mycological evidence of coprophagy from the feces of an Alaskan late glacial mammoth. *Quaternary Science Reviews* **30**, 2289–2303.

van Geel, B., van der Hammen, T., 1973. Upper Quaternary vegetational and climatic sequence of the Fuquene area (Eastern Cordillera, Colombia). *Palaeogeography, Palaeoclimatology, Palaeoecology* **14**, 9–92.

van Geel, B., Zazula, G.D., Schweger, C.E., 2007. Spores of coprophilous fungi from under the Dawson tephra (25,300 ^{14}C years BP), Yukon Territory, northwestern Canada. *Paleogeography, Palaeoclimatology, Palaeoecology* **252**, 481–485.

Velásquez, C., Jojoa, L., Restrepo, A., Vergara D., Samboni, V., Castañeda, I., 2022. *Polynic Catalogue of the Colombian Andes*, unpublished.

Vlasiuk, S., 2020. *Tribal people, gatherers and hunters, prehistoric civilizations vector*. https://www.alamy.com/tribal-people-gatherers-and-hunters-prehistoric-civilizations-vector-image364756722.html. [accessed 02 July 2022]

Waldram, M.S., Bond, W.J., Stock, W.D., 2008. Ecological engineering by a mega grazer: white rhino impacts on a South African savanna. *Ecosystems* **11**, 101–112.

Whitlock, C., Larsen, C., 2002. Charcoal as a Fire Proxy. In: Smol, J.P., Birks, H.J.B., Last, W.M., Bradley, R.S., Alverson, K. (Eds.), *Tracking Environmental Change Using Lake Sediments*. Developments in Paleoenvironmental Research **3**, pp. 75–97.

Wigley, B.J., Augustine, D.J., Coetsee, C., Ratnam, J., Sankaran, M., 2020. Grasses continue to trump trees at soil carbon sequestration following herbivore exclusion in a semiarid African savanna. *Ecology* **101**, e03008. https://doi.org/10.1002/ecy.3008.

Wood, J.R., Wilmshurst, J.M., 2013. Accumulation rates or percentages? How to quantify *Sporormiella* and other coprophilous fungal spores to detect late Quaternary megafaunal extinction events. *Quaternary Science Reviews* **77**, 1–3.

Wroe, S., Field, J., Fullagar, R., Jermin, L.S., 2004. Megafaunal extinction in the late Quaternary and the global overkill hypothesis. *Alcheringa* **28**, 291–331.

Zwerver, S.-R., n.d. Grote weegbree *(*Plantago*)* major *ssp* major 5. Saxifraga—Free Nature Images, http://www.freenatureimages.eu/Plants/Flora%20OR/Plantago%20major%2C%20Greater%20Plantain/index.html. [viewed 11 January 2022]