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Forests of the tropical eastern Andean flank during the middle Pleistocene

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ABSTRACT

Inter-bedded volcanic and organic sediments from Erazo (Ecuador) indicate the presence of four different forest assemblages on the eastern Andean flank during the middle Pleistocene. Radiometric dates (^{40}Ar–^{39}Ar) obtained from the volcanic ash indicate that deposition occurred between 620,000 and 192,000 years ago. Examination of the organic sediment composition and the fossil pollen, wood and charcoal it contains provides insight into depositional environment, vegetation assemblage and fire history. The high organic content and abundance of macro fossils found throughout the sediment suggest that during the period of deposition the local environment was either a swamp or a shallow water body. The correlation of fire activity (peaks in charcoal abundance) with volcanic ash deposits through most of the record suggests that volcanoes were the main source of ignition. The low abundance of grass (typically <10%) throughout the sedimentary sequence along with the low abundance of other taxa indicative of open vegetation suggests the persistence of forest at Erazo. Four types of forest assemblage were identified (with the first taxa as the most dominant): i) *Alnus*-Arecaceae, ii) *Miconia*-Melastomataceae/Combretaceae-Moraceae/Urticaceae, iii) Arecaceae-*Alnus*, and iv) *Podocarpus* with *Oreopanax* sp. and Melastomataceae/Combretaceae. Changes in the forest floristic composition indicate high vegetation turnover and reassortment of taxa between upper and lower montane forests during the middle Pleistocene as well as the persistence of forest cover.

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1. Introduction

Global climate during the Quaternary (last 2.6 million years) has been driven by changes in the Earth's orbital pathway (Milankovitch, 1948). Evidence for an orbital 'pacemaker' of global climatic change during this time has been primarily obtained from oxygen isotope records contained within ice sheets and marine sediments (Shackleton, 1969). The oxygen isotope record indicates that the Quaternary was characterised by fluctuations between glacial and interglacial states. The consequences of climatic fluctuations and associated waxing and waning of ice sheets upon terrestrial vegetation have been investigated using fossil material from around the globe, e.g. Hanselman et al. (2011), Hooghiemstra (1984) and Tzedakis et al. (1997). Fossil pollen analyses from a wide range of study sites have helped to understand vegetation change across the last glacial–interglacial transition (c. 21–10 thousand years ago [ka]); however, earlier in the Pleistocene (>21 ka) a lack of suitable study sites and poor dating control has meant that only a few locations have provided information on associated vegetation and climate change (Chambers, 2011).

To date, the data obtained from high and mid-latitude fossil pollen records have demonstrated a close association between vegetation type and temperature/proximity of ice. In contrast, at low latitudes (tropics) the impact of glacial–interglacial cycles remains uncertain due to a paucity of study sites (Bush and Gosling, 2012). In the Neotropics research focusing on past environmental change was polarised for many years around the debate regarding the development, or otherwise, of extensive savannah formations within the Amazon basin during glacial periods (Haffer, 1969; van der Hammen and Hooghiemstra, 2000; Colinvaux et al., 2001; Haffer and Prance, 2001). Over the last decade, thanks to new sites and modelling studies, the research community has moved towards more of a consensus that suggests that global glacial climates reduced the area of evergreen forest within the Amazon basin, altered the forest structure and its floristic composition, but did not result in widespread fragmentation of forest vegetation (Cowling, 2004; Mayle et al., 2004; Urrego et al., 2010; Gosling and Holden, 2011). However, empirical evidence for the nature and

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variability of vegetation in Amazonia during other periods of the Quaternary remains scarce. The new data presented here builds upon initial findings from the Erazo sedimentary sequence (Ecuador) (Cárdenas et al., 2011a, 2011b). In previous publications Cárdenas et al. focused solely on the upper (youngest) Erazo sediments which were: i) described, and summary pollen data presented, ii) dated to the middle Pleistocene, iii) established to contain vegetation composition shifts, and iv) interpreted as most likely influenced by past temperature change. In this paper we present modern pollen-vegetation data from the eastern Andes collected to improve the overall interpretation of the fossil pollen records, and focus on the entire Erazo sedimentary profile (including new evidence from lower [older] sediments), specifically we: i) present detailed fossil pollen data for the entire Erazo section, ii) new ^{40}Ar–^{39}Ar ages placing the lower (oldest) Erazo sediments in the middle Pleistocene, and iii) provide further insight into the nature of forest composition change on the eastern Andean flank (western Amazonia) during the middle Pleistocene.

2. Eastern Andean flank (Ecuador)

2.1. Modern environmental setting

The eastern Andean flank is an ideal location for studying the impact of past climate change on vegetation because the sharp elevation gradient results in temperature changes occurring over relatively small horizontal distances, i.e. roughly 3.5 m of elevation change for every 10 m horizontal distance (Johnson, 1976). Moreover, the floral composition of the vegetation is known to be closely associated with climate (Olson et al., 2001). Furthermore, climate is thought to be the major driver of vegetation change in the Andes over multi-millennial timescales (Gosling et al., 2008; Torres et al., 2013).

2.1.1. Geological and climatic setting

The topography of the Andes is a product of tectonic uplift of pre-Quaternary rocks (>2.6 Ma) resulting from the collision between the Nazca and South American plates and the deposition of Quaternary age volcanic rocks and sedimentary materials (Montgomery et al., 2001). The diversity of the geological formations in the Ecuadorian Andes has in turn produced a large variety of soils (Jorgensen and León-Yáñez, 1999).

The prevailing climate in Ecuador is predominantly controlled by the interplay between the Andes and two major climate systems: i) the Inter Tropical Convergence Zone (ITCZ), and ii) the South Atlantic Convergence Zone (SACZ) (Waliser and Gautier, 1993; Cook, 2009). On the eastern Andean flank the mean annual temperature (MAT) ranges from 18 to 20 °C at altitudes of 1000–2400 m above sea level (asl) down to <10 °C above 3000 m asl (Webster, 1995). Precipitation along the eastern Andean flank is more complex with mean annual precipitation (MAP) at mid and low elevations (i.e. <3000 m asl) varying from c. 2000 to 4000 mm dependent on orography, whilst in the highland areas (>3000 m asl) precipitation is typically below <1000 mm per year (Montgomery et al., 2001).

2.1.2. Vegetation

Topography, temperature and precipitation are the principal factors which determine the distribution of modern vegetation in the eastern Ecuadorian Andes (Harling, 1979). At the largest scale two biomes are present 'woodland' and 'grassland'. Within the two biomes Harling (1979) describes five major modern vegetation associations: i) lowland evergreen rainforest, ii) lower montane cloud forest (LMF), iii) upper montane cloud forest (UMF), and iv) 'Paramo' grassland, which contains v) high Andean woodland.

Lowland evergreen rainforest at the base of the Ecuadorian Andes (<1000 m asl) has high MAT (23–26 °C) and MAP (>2000 mm) with little seasonal variation in rainfall (Harling, 1979). The forest canopy is high (40 m) and well developed with straight stems (Patzelt, 2008). Due to the limitation of light, trees, epiphytes and lianas are constantly reaching upwards for the light (Patzelt, 2008). The most diverse tree families within the lowland evergreen rainforest are: Melastomataceae, Mimosaceae, Euphorbiaceae, Rubiaceae, Lauraceae, Clusiaceae and Moraceae; diverse shrub families also include Piperaceae, Solanaceae and Arecaceae (palms) (Webster, 1995; Jorgensen and León-Yáñez, 1999; Pitman et al., 2001). Epiphytes and large woody climbers are also abundant (Harling, 1979).

The LMF occurs between c. 1000 and 2400 m asl where MAT is c. 18–20 °C, MAP is high (up to 4000 mm), cloud cover is permanent throughout the year and seasonality is low (Harling, 1979). The tree canopy height is between 15 and 33 m and plants are typically large leafed (182–1640 cm^2). Diverse families present in LMF include: Melastomataceae, Ericaceae and Rubiaceae (Jorgensen and León-Yáñez, 1999); common epiphytes include orchids, bromeliads, ferns and mosses. Families present in LMF that have less relative abundance at higher elevation include Myristicaceae, Lecythidaceae and Vochysiaceae (Harling, 1979).

The UMF grows roughly between 2400 and 3400 m asl under a MAT of c. 10 °C and MAP ranging from c. 2800 to 4000 mm which is distributed evenly throughout the year; cloud cover is present for most of the year (Harling, 1979). This forest is structurally distinct because of its dense low canopy (c. 1.5–18.0 m), plants typically have small leaf sizes (2–20 cm^2), and abundant mosses, filmy ferns and lycopods can be found on trees, and tree ferns are common (Webster, 1995). Important UMF families that also occur at lower elevations, albeit at generally lower relative abundance include: Actinidiaceae, Betulaceae (*Alnus* sp.), Aquifoliaceae, Chloranthaceae (*Hedyosmum* spp.), Buddleiaceae, Caprifoliaceae, Clethraceae, Campanulaceae, Chloranthaceae, Cunoniaceae, Ericaceae, Magnoliaceae, Podocarpaceae and Winteraceae (Harling, 1979).

At high elevation (>3400–3800 m asl), above the zone of permanent cloud cover, where MAT (c. 6–8 °C) and MAP (1000–2000 mm) are relatively low, the vegetation is characterised by a depleted assemblage of UMF with taxa adapted to low temperatures. Plant species common to both UMF and higher elevation vegetation include: *Gaultheria* spp., *Drimys* spp., *Podocarpus* spp., *Ilex* spp., *Clusia* spp. and *Weinmannia* spp. (Harling, 1979). The vegetation of the highland is dominated by grass (Poaceae) and is known as 'Páramo' (Webster, 1995). The most prominent woody genus found within the Páramo is *Polylepis* spp. (Rosaceae), which grows in isolated patches and is the highest occurring woody taxa in Ecuador (Webster, 1995).

2.2. Past climate and vegetation change

Evidence for past vegetation change on the eastern flank of the Ecuadorian Andes is limited due to the small number of sites studied (Fig. 1). Evidence from fossil pollen and wood samples obtained at Mera (900 m asl) and San Juan de Bosco (1100 m asl) (Fig. 1) indicate that forests were present in the region during the last glacial period (33,000–26,000 year BP) (Liu and Colinvaux, 1985; Bush et al., 1990; Colinvaux et al., 1997). However, the glacial age forests were shown to be compositionally distinct from the modern forests on the eastern Andean flank; containing *Podocarpus* spp., *Drimys* spp., *Hedyosmum* spp., *Weinmannia* spp. and *Alnus* sp. The presence of a fossil pollen assemblage comprised of taxa found today predominantly at higher (cooler) elevations has been interpreted to suggest that during the last glacial period temperature on the lower portion of the eastern Ecuadorean flank of the Andes was 6–8 °C cooler than today (Bush et al., 1990). Fossil pollen and wood samples from the Erazo study site revealed a comparable reorganization of the vegetation earlier in the Pleistocene that suggests that a similar magnitude of cooling (c. 5 °C) probably occurred during the preceding glacial period (equivalent to Marine Isotope Stage 6) (Cárdenas et al., 2011b).

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