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CORRESPONDENCE

Ecological stability in a changing world? Reassessment of the palaeoenvironmental history of Cuatrociénegas, Mexico

ABSTRACT

Previous work on the palaeoenvironmental history of Cuatrociénegas, Coahuila, Mexico, suggests that the local environments of the basin have been relatively stable since the last glacial period. Reassessment of the palaeoenvironmental record from Cuatrociénegas, combined with the analysis of a glacial-age packrat midden (~ 16,900 cal-yr BP), shows that this region has experienced substantial climatic and ecological changes during the Late Quaternary. Woodlands occurred near the valley floor until ca. 11,000 years ago, migrating upslope as climate warmed. The apparent lack of change in the flora of the basin floor may be attributable to high soil salinity. This edaphic control led to earlier interpretations that the region was environmentally stable.

Keywords: Biodiversity, Chihuahuan Desert, conservation, endemism, Mexico, palaeoecology

The highest level of local endemism anywhere in North America occurs in the desert spring ecosystems of the Cuatrociénegas Basin, Coahuila, Mexico (Abell *et al.*, 2000). Endemic species include eight fishes (Minckley, 1984), ten molluscs (Hershler, 1985; Hershler *et al.*, 2007) and four reptiles (McCoy, 1984), as well as numerous invertebrates, plants (Pinkava, 1984) and a diverse microbial assemblage (Souza *et al.*, 2006). Many of these endemics indicate long isolation and divergence of the order of millions of years based on morphological and molecular data (Taylor, 1966; Hulsey *et al.*, 2004; Echelle *et al.*, 2005; Johnson, 2005; Souza *et al.*, 2006). Because of the concentration of so many unique taxa, Cuatrociénegas has been designated a high-priority conservation region (Abell *et al.*, 2000). The system faces numerous threats, most recently groundwater mining in the basin (Souza *et al.*, 2006) amplified by recent drought.

The biodiversity hotspot at Cuatrociénegas poses significant conservation, biogeographical, ecological and evolutionary questions spanning multiple disciplines. Given the apparent duration of biogeographical isolation in the Cuatrociénegas Basin, the impact of repeated glacial/interglacial cycles over the past *c.* 2 Myr on the extent, abundance and interconnectedness of its endemic populations is of obvious importance. The basin is widely perceived as an island of stability in a sea of change, which raises questions that are relevant not only to the Cuatrociénegas Basin but more broadly to the origin, history and fate of biodiversity hotspots throughout the world (Bush, 2005). What was the extent of environmental variability at local and regional

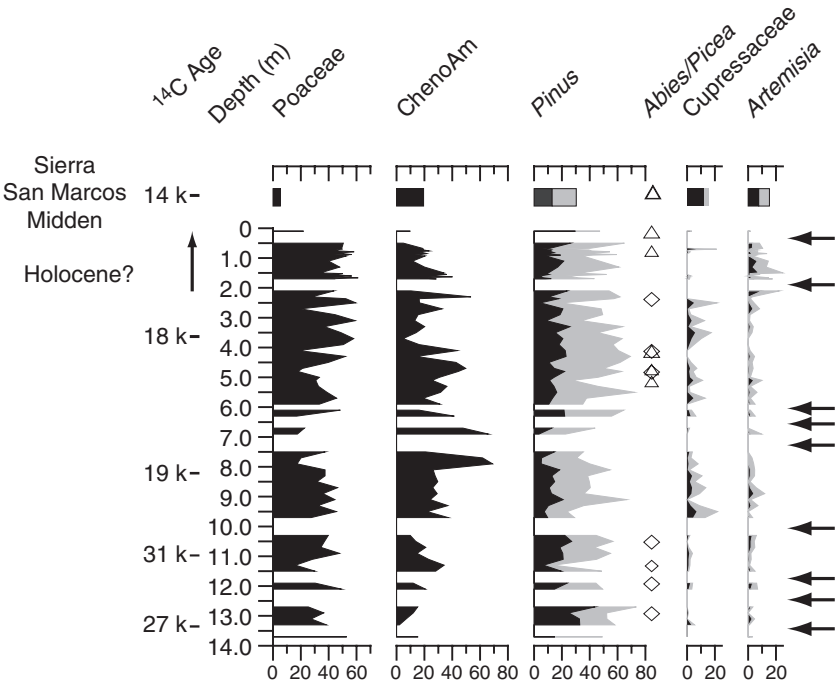

Figure 1 Pollen spectra from the packrat midden collected on Sierra San Marcos (funded by 2002–03 UC MEXUS to F. T. Ledig) is compared with the salient aspects of Meyer's record. Shown are the ^{14}C dates rounded to the nearest 1000 years (k), pollen-free zones (arrows) and important pollen types. The pollen spectra from the midden are considered to be contemporaneous with spectra from *c.* 2 m depth of the sediment core. Poaceae and Chenopodiaceae/Amaranthaceae (ChenoAm) pollen types dominate the pollen percentage calculations (black), suppressing even *Pinus*. Cupressaceae does appear during the glacial period, but was not interpreted as significant. Recalculated pollen percentages are based on sums < 100 grains (grey). Excluding Poaceae and ChenoAm pollen from the sum shows that *Pinus* is dominant. The presence/absence of *Abies* (△) and *Picea* (◇) show these pollen types mostly restricted to the glacial period. Cupressaceae pollen is also indicative of glacial pollen spectra.

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scales during the Quaternary? How were high endemism and biodiversity maintained in the face of environmental change? Do hydrological changes, whether from global climate change or local groundwater pumping, constitute threats to the Cuatrociénegas ecosystems and biota?

A pollen record from the Cuatrociénegas valley floor (Meyer, 1973) has been construed as indicating long-term environmental stability for the region. Meyer's record was based on two cores taken from spring deposits consisting of intercalated peats, clays and precipitates. The cores span the last 30,000+ years, based on four Late Pleistocene radiocarbon dates (Fig. 1). Chenopodiaceae/Amaranthaceae (ChenoAm) and Poaceae dominate the record (55–83% of total pollen), similar to modern basin-floor pollen spectra (Fig. 1) (Meyer, 1973). Based on this evidence, together with the high endemism in the basin and the lack of evidence for local pluvial lakes, Meyer concluded that the 'aquatic and terrestrial environments of the valley lowlands had remained environmentally stable' over the length of this record. Concurrent with the lowland stability were changes in the uplands that were obscured by the inclusion of ChenoAm and Poaceae in the pollen diagrams. Using the ratio of tree pollen to Asteraceae pollen, Meyer inferred that pine woodlands expanded into the uplands of the surrounding mountains, and that oak–piñon–acacia woodlands may have covered the lower slopes during the glacial period. These taxa presumably did not occupy the valley floor because of poorly drained salt- and clay-rich soils.

The Cuatrociénegas record presents a regional paradox that has grown with subsequent palaeoecological research in North American deserts. While Meyer's data suggest long-term stasis of the aquatic system, valley floor vegetation and regional vegetation, other records from the Chihuahuan Desert (Van Devender, 1990; Metcalfe *et al.*, 2002; Holmgren *et al.*, 2003, 2006; Metcalfe, 2006) and other North American deserts (see Betancourt *et al.*, 1990) indicate extensive vegetational changes since the last glacial period. These records, mainly from fossil packrat (*Neotoma*) middens, show widespread piñon–juniper woodlands in desert basins from 21,000 to *c.* 13,000 yr BP. Late glacial temperature estimates are 7–11°C cooler than present across the North American deserts (Van Devender *et al.*, 1987), and pluvial lakes occupied many valley floors. In the Chihuahuan Desert, midden data suggest a mix of modern desert flora with piñon–juniper woodlands (Van Devender, 1990). These changes contrast with the apparent stability of the Cuatrociénegas Basin (see Metcalfe, 2006).

Re-examination of Meyer's published record, together with new packrat midden data, indicates that the region experienced substantial environmental and ecological change in the Late Quaternary. To assess regional upland vegetation, we recalculated Meyer's pollen percentages using the original pollen count data from Core F. For our analysis, ChenoAm and Poaceae were considered riparian taxa and were excluded from the pollen sum resulting in an amplification of upland vegetation abundances (Fig. 1). In this reanalysis, regional pollen spectra are dominated by *Pinus*, varying between 14% and 73% (average 45%), and stratigraphic patterns of other arboreal taxa indicate significant ecological changes (Fig. 1). *Picea* pollen occurs in trace amounts in the glacial period. Cupressaceae (probably *Juniperus*) is abundant (> 5%) during the glacial period but sparse during the Holocene. *Artemisia* pollen has low percentages during the glacial period and increases (> 5%) during the Holocene. These data suggest conifer woodlands of glacial age in the uplands adjacent to the Cuatrociénegas Basin.

Woodland expansion is confirmed by macrofossil analysis of a fossil packrat midden collected from the lowermost slopes of Sierra San Marcos, a bedrock massif that nearly bisects the Cuatrociénegas Basin from the south-east. This midden, collected *c.* 30 m above the valley floor, and < 5 km south of Meyer's coring site, is dated between 16,400 and 17,350 cal yr BP (14,150 + 100 ^{14}C yr BP (Beta 184402)) (Fig. 1). Macrofossils from the midden include *Juniperus coahuilensis* (foliage, seeds), *Pinus remota* (needles, seeds, cone scales), *Quercus* sp. (leaves), *Yucca* sp. (leaf tips) and *Celtis reticulata* (seeds, leaves) (see Table S1 in Supplementary Material). Modern vegetation at the site today consists of Chihuahuan Desert scrub, with the nearest piñon–juniper–oak woodland some 700 m upslope. These data support Van Devender's (1990) proposal that woodlands occurred near the Cuatrociénegas Basin during the late glacial period, retreating upward during the Holocene transition.

Meyer's pollen record, together with the sediment lithology, suggests that the Cuatrociénegas Basin has been dominated by a mosaic of wetlands and halophytic scrub since the last glacial period. The paradox of local stability in the midst of global environmental change has arisen from a focus on the basin floor rather than the larger context of ecological change during the Late Quaternary. The dominant pollen types, ChenoAm and Poaceae, comprising numerous genera and species, represent an extraordinarily broad range of environmental tolerances, and are dominant across hot and cold desert regions in North America. Haline soils in desert regions are associated with seasonal extremes in temperature and precipitation, and seasonal to multidecadal droughts. Many genera and species characteristic of haline soils within the ChenoAm and Poaceae groups are widely distributed in desert basins from Mexico to Canada and from the Great Plains and Gulf of Mexico to the Pacific (e.g. *Atriplex canescens*, *Sarcobatus* sp., *Allenrolfea* sp.). Haline soils with salt-tolerant grasses (e.g. *Distichlis*) and chenopods (e.g. *Allenrolfea*) dominate the floor of the Cuatrociénegas Basin today. Given their broad climatic tolerances, these species may have persisted as dominants through the last glacial/interglacial cycle. And if temperature changes were sufficiently large to displace them during the Last Glacial Maximum, they were likely to have been replaced by other halophytic chenopods and/or grasses. Any such changes would go undetected in the pollen record owing to our inability to discriminate between genera within these families on a palynological basis.

In summary, the regional climate of the Cuatrociénegas Basin underwent substantial change during the last glacial/interglacial cycle, accompanied by large-scale vegetation shifts in the adjacent uplands. These regional changes may have been accompanied by changes in vegetation composition on the valley floor. The high level of endemism, together with Meyer's sediment stratigraphy, indicates that wetland habitats persisted throughout this period, and probably during the entire Quaternary. However, Meyer's record includes episodes of poor pollen preservation, suggesting either regional drought or local hydrological shifts in the spring complex. Wetland and aquatic habitats may have been buffered by persistent groundwater supply. Many of the extant springs are geothermally controlled (Minckley, 1984), and thus could have remained environmentally constant despite dramatic changes in regional climate. Specific locations and densities of aquatic and wetland habitats may have shifted, but they were always present somewhere. Thus, the paradox of ecological stability is resolved by nesting environmentally constant (but per-

haps spatially shifting) aquatic and wetland habitats within the relatively stable haline soils of the valley floor, in turn embedded within the ever-changing regional climate.

Teasing apart local and regional ecological and biogeographical responses to climate change represents a challenge for palaeoecology, requiring multiple proxies and sensors spanning a range of spatial scales. Palaeoecological records of the response of ecosystems to climate change can be used to inform management and conservation efforts, even in arid regions (e.g. Minckley & Brunelle, 2007). However, spatial and temporal scales of ecological and biogeographical changes need to be considered carefully in such applications (Bush, 2005). Effective management and conservation requires baseline information on environmental changes that allows for defined but flexible targets for the protection of species and habitats. Given the biotic uniqueness of Cuatrociénegas and ongoing conservation initiatives (http://www.desertfishes.org/cuatroc/), integrated studies of the environmental, ecological and evolutionary history of this system are clearly needed. The basin contains sediments and woodrat middens spanning at least the last glacial/interglacial cycle. Conceivably, valley floor sediments could provide records extending far deeper in time, possibly comprising the entire evolution of the desert spring system.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article online:

Table S1 Results of preliminary macrofossil analysis of a *Neotoma* (woodrat) midden from Sierra San Marcos.

This material is available as part of the online article from: http://www.blackwell-synergy.com/doi/abs/10.1111/j.1365-2699.2007.01829.x

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