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Effects of late Holocene climate variability and anthropogenic stressors on the vegetation of the Maya highlands

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ABSTRACT

Climate variability and human activities have shaped the vegetation communities of the Maya region of southern Mexico and Central America on centennial to millennial timescales. Most research efforts in the region have focused on the lowlands, with relatively little known about the environmental history of the regional highlands. Here we present data from two sediment sequences collected from lakes in the highlands of Chiapas, Mexico. Our aim was to disentangle the relative contributions of climate and human activities in the development of regional vegetation during the late Holocene. The records reveal a long-term trend towards drier conditions with superimposed centennial-scale droughts. A declining moisture trend from 3400 to 1500 cal yr BP is consistent with previously reported southward displacement of the Intertropical Convergence Zone, whereas periodic droughts were probably a consequence of drivers such as El Niño. These conditions, together with dense human occupation, converted the vegetation from forest to more open systems. According to the paleoecological records, cultural abandonment of the area occurred ca. 1500 cal yr BP, favoring forest recovery that was somewhat limited by low moisture availability. About 600 cal yr BP, wetter conditions promoted the establishment of modern montane cloud forests, which consist of a diverse mixture of temperate and tropical elements. The vegetation types that occupied the study area during the last few millennia have remained within the envelope defined by the modern vegetation mosaic. This finding highlights the importance of microhabitats in the maintenance biodiversity through time, even under scenarios of high climate variability and anthropogenic pressure.

1. Introduction

Given the confluence of diverse climates with a rich topography, southeastern Mexico harbors some of the greatest vegetation diversity found throughout Mexico and Central America (Ramirez-Marcial et al., 2001; Rzedowski, 2006). Thus, the region has been studied intensively with respect to patterns of modern vegetation diversity, and how its long history of climate variability and human occupation gave rise to the modern regional ecosystems (Curtis et al., 1998; Leyden, 2002; Domínguez-Vázquez et al., 2004 ; Bryant et al., 2005; Hodell et al., 2005; Correa-Metrio et al., 2012a, 2013). The intersection of the Neotropical and Nearctic biogeographic realms (Udvardy, 1975) produced a gradient characterized by tropical vegetation in the lowlands and temperate elements in the highlands. Effects of dense human occupation are evident through at least the last 4000 years in the lowlands (Leyden, 2002), and have certainly exerted an important influence on the evolution of vegetation composition and structure. Nevertheless, little is known about how natural and anthropogenic factors affected the vegetation of the highlands. Of special interest is the period of post-abandonment (ca. 1500 cal yr BP), when the montane cloud forests that occupy the area today developed.

The highlands of Chiapas are composed of valleys and ridges at elevations between 1500 and 2500 m above sea level (m asl) in the central part of the state of Chiapas, southeastern Mexico. Its

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geographic location and physiography give rise to conditions that promote high biodiversity given the intersection of two biogeographic realms across steep environmental gradients. Neotropical taxa from Central America and the Yucatan Peninsula intermingle with Nearctic elements from Central Mexico (Rzedowski, 2006). Tropical montane cloud forests (MCF) represent a prime example of how the mixture of floras can yield diverse vegetation (Hamilton et al., 1995). Study of the temporal dynamics of these vegetation types provides an opportunity to understand the effect of environmental stressors of different magnitude and intensity on biodiversity patterns, and shed light on the environmental dynamics of the Maya highlands.

Natural environmental variability over time caused rapid shifts in regional plant diversity. For example, following the Last Glacial Maximum, the average annual temperature in the Yucatan Peninsula was between 5 and 10 °C lower than present (Correa-Metrio et al., 2012a; Hodell et al., 2012), causing downslope migration of species. Additionally, there have been multiple episodes of late Holocene extreme droughts, associated with substantial changes in the composition and structure of vegetation and the patterns of human occupation (Curtis et al., 1998; Leyden, 2002; Correa-Metrio et al., 2012a). Much of this environmental variability was caused by abrupt climatic changes that, in turn, caused vegetation changes. Such rapid vegetation responses imply the persistence of small plant populations in areas with localized, favorable conditions, which facilitate the process of recolonization (Bush, 2002a; Correa-Metrio et al., 2016).

On the windward side and under the cloud line of mountainous regions, orographic precipitation and topography interact to create a broad range of microclimates. These microhabitats offset some of the effects of extreme regional climates and climatic variability on vegetation (Bush, 2002a). In these areas, moisture-laden air rises along the slopes, becoming cloudiness and rain. Thus, local humidity probably serves as a buffer to extreme droughts, preventing the loss of diversity throughout the late Quaternary. Extremely steep slopes are less likely to be occupied by people and therefore could have acted as biodiversity “reservoirs” that facilitated post-abandonment plant recolonization. Thus, vegetation responses to exogenic disturbances in these areas were likely buffered by higher moisture availability.

Here we present a paleoecological reconstruction based on two sedimentary records collected from two lakes in the highlands of Chiapas, southeastern Mexico. The two neighboring sites, about 6 km from one another, represent contrasting topographic and physiographic environments that enabled us to evaluate the spatial and temporal consistency of the environmental history of the area. Our study provides insights into the response of plant communities to changes in climate and land use through a multi-site, multi-proxy approach. Our aim was to investigate the impacts of environmental stressors (e.g. droughts, fires, land-use changes, etc.) on tropical mountain vegetation during the late Holocene. We used pollen, charcoal, and geochemical analyses to address three basic questions: (1) what is the relationship between modern and fossil vegetation diversity, as revealed by the comparison of modern and fossil pollen spectra?, (2) do late Holocene climate patterns in the area reflect trends reported elsewhere in the northern Neotropics?, and (3) Was the 9th-century cultural collapse in the lowlands evident in the highlands?

2. Regional background

Lagunas de Montebello National Park is a ~6022-ha protected area in the central highlands of Chiapas, southern Mexico (Fig. 1). The area lies on Lower Cretaceous karstic limestones, which favored the development of a lake district that includes more than 50 water bodies, including dolines, uvalas, and poljes (Padilla y Sánchez, 2007).

The region is characterized by a mean annual temperature of 18 °C and mean annual precipitation of ~2500 mm. Temperature shows an annual range of ~4 °C, with the coldest and warmest periods from December to February and April to September, respectively (climate data from Tziscao Meteorological station, Servicio Meteorológico Nacional, 2017). The rainy season is centered from May to October (Fig. 1C) with rainfall associated with the northern position of the Intertropical Convergence Zone (ITCZ), during the boreal summer (Mestas-Nuñez et al., 2007). During the boreal winter, the southern migration of the ITCZ is associated with dry condition in the region, whereas polar air masses bring light sporadic rains into the area. El Niño Southern Oscillation (ENSO) plays an important control upon interannual rainfall variability over southern Mexico (Magaña et al., 2003). ENSO produces spatially variable effects in the precipitation across Mexico, although the general pattern can be summarized as a reduction of rainfall, especially in regions characterized by strong convection (Bhattacharya and Chiang, 2014). In the region of Montebello, meteorological data covering from February 1961 to December 2015 (Servicio Meteorológico Nacional, 2017) suggest that El Niño years are associated with a longer and more intense dry season and a drier wet season (Fig. S1). Additionally, during El Niño years minimum and maximum temperature from February to May increase between 1 and 2 °C, causing higher evapotranspiration, and therefore more stressful conditions for biological communities. During La Niña years, the most evident change in the precipitation regime is a drier wet season, whereas minima and maxima monthly temperatures decrease slightly (Fig. S1).

The climate, geographic location, and diverse topography of the area have favored the establishment of forests composed of a mixture of coniferous and broadleaf species (Ramirez-Marcial et al., 2001). Although the mosaic of regional vegetation types is highly diverse, it can be described generally by three main vegetation types: pine forest, *Pinus-Quercus -Liquidambar* forest, and MCF (Breedlove, 1981; Rzedowski, 2006). Pine forests are common in disturbed areas or areas subjected to extreme temperatures, intense solar radiation, and/or low soil moisture (Ramírez-Marcial, 2003). *Pinus-Quercus-Liquidambar* forests are a mixture of pine and broadleaf elements, dominated by these genera, together with *Clethra macrophylla* (Carlson, 1954). MCF remnants are dominated by broadleaf species and are located in the northeastern extreme of the National Park. Their distribution is driven largely by soil moisture availability and human impact. These factors restrict MCF to areas with steep topography and slopes that receive little direct sunlight and are subject to minimal human disturbance. These forests are rich in understory broad-leaved trees species, with dominance of *Podocarpus matudai*, *Turpina tricomuta* and *Prunus brachybotria* (Ramirez-Marcial et al., 2010). All these vegetation types have been influenced by the long history of human activities in the region, which created substantial patches of open vegetation and regrowth.

2.1. Settlement history

Maya communities from the lowlands seem to have colonized the highlands of Chiapas between the Late Preclassic and the Early Classic (from 2200 to 1500 cal yr BP, see Maya chronostratigraphy in Fig. 7), reflecting a settlement pattern characterized by an almost total abandonment of valleys and colonization of the mountains (Adams, 1961). Nevertheless, there is evidence of Preclassic settlements along the neighboring Grijalva River (Adams, 1961; Bryant and Clark, 1983; Bryant et al., 2005) that probably excerted early influence in the region of Montebello. The landscape heterogeneity