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Ecology

Cloud forests on rock outcrop and volcanic soil differ in indicator tree species in Veracruz, Mexico

Los bosques mesófilos en afloramiento rocoso y suelo volcánico varían en especies arbóreas indicadoras en Veracruz, México

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Abstract

The tropical montane cloud forest (TMCF) of central Veracruz, Mexico, predominantly grows on volcanic substrate from the Quaternary (2–0.08 Mya), but in very small areas it grows on shallow soils over limestone rock outcrops from the Cretaceous (90 Mya). Our objective was to contrast the vegetation structure and tree species composition of forest communities growing on rock outcrops (FOR) with nearby forests on prevalent volcanic soil (FOV). Results show that species richness and vegetation structure were similar between FOR and FOV. However, a clear difference was revealed by indicator species analysis (ISA), and multinomial classification model (CLAM). ISA and CLAM, respectively, identified 14 indicators and 13 specialists in FOR, whereas, they identified 7 indicators and 14 specialists in FOV. Some FOR indicators were *Cercis canadensis*, *Clusia guatemalensis*, *Garrya laurifolia*, *Ostrya virginiana* and *Quercus pinnativenulosa*. Some FOV indicators were *Carpinus tropicalis*, *Clethra macrophylla*, *Liquidambar styraciflua* and *Quercus xalapensis*; these species are also common in several Mexican TMCF. Our study demonstrates that the tree community on rock outcrops differs from the surrounding forest on volcanic soils; this is of particular interest because of its different species assemblage and contribution to the high beta diversity of the region.

Keywords: Cloud forest; Limestone; Rare trees; Rock outcrops; Tree diversity; Vegetation structure; Volcanic soils

Resumen

El bosque mesófilo de montaña del centro de Veracruz, México, crece predominantemente en sustrato volcánico del Cuaternario (2-0.08 Ma), pero en áreas muy pequeñas crece en suelo poco profundo sobre afloramientos de roca caliza del Cretácico (90 Ma). El objetivo fue contrastar la estructura de la vegetación y la composición de especies arbóreas de comunidades en afloramientos rocosos (AR) con bosques cercanos en suelo volcánico (SV). Encontramos que la riqueza de especies y la estructura de la vegetación fueron similares entre AR y SV. Sin embargo, el análisis de especies indicadoras (ISA) y el modelo de clasificación multinomial (CLAM) revelaron una diferencia clara. ISA y CLAM, respectivamente, identificaron 14 especies indicadoras y 13 especialistas en AR, e identificaron 7 indicadoras y 14 especialistas en SV. Algunas especies indicadoras AR fueron: *Cercis canadensis*, *Clusia guatemalensis*, *Garrya laurifolia*, *Ostrya virginiana*, *Quercus pinnativenulosa*. Algunas especies indicadoras de SV fueron: *Carpinus tropicalis*, *Clethra macrophylla*, *Liquidambar styraciflua* y *Quercus xalapensis*; estas especies también son comunes en varios bosques mesófilos mexicanos. Se concluye que la comunidad de árboles en afloramientos rocosos difiere del bosque circundante en suelo volcánico. Estas diferencias en el ensamblaje de especies son de particular interés debido a que contribuyen a la alta diversidad beta regional.

Palabras clave: Bosque de niebla; Suelo calizo; Árboles raros; Afloramientos rocosos; Diversidad de árboles; Estructura de la vegetación; Suelos volcánicos

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Introduction

Forest communities on rock outcrops have a distinctive floristic composition and physiognomy with respect to that of the surrounding forests. Outcrops with different substrates have been recognized worldwide as providing important habitats for biodiversity conservation, particularly for endemic and rare species (Aukema, Carlo, & Collazo, 2007; Cantero et al., 2014; Gallardo-Hernández, Velázquez, & Asbjornsen, 2008; Pérez-García & Meave, 2004; Pérez-García, Sevilha, Meave, & Scariot, 2009; Rivera, Zimmerman, & Aide, 2000; Wiser & Buxton, 2009). Some differential trends have also been reported in vegetation structure and species composition on outcrops compared to those of nearby forests on deeper soils (Brewer, Rejmánek, Webb, & Fine, 2003; Gallardo-Hernández et al., 2008; Sawada et al., 2015; Tang, Lü, Yin, & Qi, 2011). In the tropics, in Mt. Kinabalu, Borneo, basal area and stem density differed among geological substrates but were similar among the topographical units of each substrate, indicating that the effects of geological substrate were generally stronger than those of topography (Sawada et al., 2015). In Xishuangbanna, China, the limestone forest had lower species diversity than other tropical forests in the area and differed in floristic composition and structure (Tang et al., 2011). In Chimalapas, Oaxaca, Mexico, the tropical montane cloud forest differed in woody plant composition but not in vegetation structure between communities growing on metamorphic rocks and sedimentary geological substrates forming a karst topography with rock outcrops (Gallardo-Hernández et al., 2008).

Tropical montane cloud forest (TMCF) is very heterogeneous and exhibits remarkable turnover in tree species assemblages across the landscape, with great natural diversity in its vegetation structure due to the variety of microhabitats and the elevation gradient over which it grows. Climate, topography, geology and substrate all contribute to the enormous biodiversity of this forest type (Bruijnzeel, Kappelle, Mulligan, & Scatena, 2010; Churchill, Balslev, Forero, & Luteyn, 1995; Williams-Linera, 2002; Williams-Linera, Toledo-Garibaldi, & Gallardo-Hernández, 2013). In Mexico, TMCF is the most diverse vegetation type per unit area and although it covers less than 1% of the national territory, it accounts for 10% of plant diversity. One reason for the high diversity of TMCF is the mixing of Holartic and Neotropical biogeographic elements, and a high degree (30–35%) of endemism (Rzedowski, 1996; Sánchez-Ramos & Dirzo, 2014). Forest canopy trees primarily belong to Holartic taxa also common in the eastern deciduous forests of the United States, while subcanopy and understory vegetation are dominated by tropical genera, taxa common in the Andean forests of South America, and even a high number of taxa shared with eastern Asia (Rzedowski, 1996).

In central Veracruz, Mexico, the TMCF region is characterized by irregular topography, formed by hills and plateaus that are dissected by deep gorges. The morphology and prominent slopes in the region are mostly controlled by the volcanic chain formed by the Cofre de Perote Volcano. The Quaternary volcanic deposits are 0.08 to 2 million years old (Rodríguez, Morales-Barrera, Layer, & González-Mercado, 2010). Isolated rock outcrops are uncommon in this region, and are part of a pre-volcanic floor from the Late Mesozoic (Cretaceous, ca. 90 Ma BP). In a few places on the cloud forest belt, these rock outcrops are quite exposed and form small, elongated mountain ranges oriented in a NW–SE direction; this carbonate sedimentary substrate is dominated by limestone with minor shale intercalations (Rodríguez et al., 2010).

Most of our current knowledge of Mexican TMCF comes from studies carried out on plant communities growing on soils of volcanic origin (Muñoz-Villers et al., 2012; Rossignol, 1987; Williams-Linera, 2002). For the present study, within the TMCF region, forest remnants on limestone outcrops were identified, and we asked whether forest on isolated limestone rock outcrops differed in its tree species composition and vegetation structure from the nearby forests growing on the most common geological substrate (volcanic soils). Our working hypothesis was that forest fragments growing on limestone rock outcrops would differ in their tree species composition and structure from forest remnants on volcanic soils. We based this hypothesis on the expectation that the tree species assemblage encountered in a particular habitat will reflect geological substrate and topography. We further expect that, if this is the case, there will be a subset of tree species that differed from the tree species pool of the TMCF developed on volcanic soils in central Veracruz.

Materials and methods

This study was conducted in central Veracruz, Mexico (19°30′13.12″–19°29′35.56″ N; 96°57′28.14″–96°58′28.65″ W; elevation 1,250–1,550 m asl) within the Trans-Mexican Volcanic Belt on the eastern slopes of the Cofre de Perote Volcano. The climate is mild and humid throughout the year with 3 seasons: a cool season from November to March, a short dry-warm season in April–May, and a wet warm season from June to October. At lower and higher elevation sites, mean annual precipitation values are 1,500 and 2,000 mm, and mean annual temperature decreases from 19 °C to 17 °C (Williams-Linera, 2002; Williams-Linera et al., 2013). The main vegetation type is tropical montane cloud forest (Williams-Linera et al., 2013). The soils are predominantly on volcanic substrate across >95% of the region (Inegi, 2010; Rossignol, 1987).

In this area, some sites are located on limestone rock prominences with abrupt slopes. The rock outcrops are in a small area ca. 5 km long between the towns of Xalapa and Coatepec (Fig. 1). Volcanic soils are deep (ca. 2.5 m) (Muñoz-Villers et al., 2012), well drained and with abundant organic matter, and the soil on the outcrops is shallow and rocky.

The study sites on rock outcrops were selected by examining geological maps from INEGI (2010; E14-B27 and E14-B37), images in Google Earth to locate hilltops with forest remnants, and ground verification of the entire surface on pre-volcanic limestone. With the help of a local guide, we visited all of the sites that still had forest on the hilltop. We found 8 and selected 4 sites based on the following criteria: (1) the forest was on a limestone rock outcrop, (2) cover >1 ha of forest at the relatively