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Forest diversity plays a key role in determining the stand carbon stocks of Mexican forests

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ABSTRACT

Defining the most important factors related with forest carbon (C) stocks in different forest types is still a controversial topic. In this study we used data from 10,500 plots from The National Forest Inventory of Mexico encompassing the six main forest types in Mexico (conifer, broadleaf, mixed, evergreen and semi-deciduous, dry and semiarid forests) in order to identify the main factors related to the spatial pattern of C stocks, including climate (temperature and rainfall), forest diversity (structural and species richness), topographic and soil characteristics (soil depth, slope and land tenure) and disturbance factors (fires, pests and tree felling). We built two different types of models, one taking all plots into account (global model, $R^2 = 0.54$, $P < 0.001$) and others for each forest type separately. Overall, structural richness was the most important variable related to C stock both in the global model and in each forest type model. Tree richness had a strong relationship in tropical forests (both dry and evergreen) but not in temperate forests (conifer, broadleaf and mixed forests), where slope and climate variables had greater effects on C stocks. C stock was strongly and positively correlated with precipitation in almost all forest types, while it was strongly and negatively correlated with temperature in broadleaf and mixed forests. Surprisingly, slope was the second most important factor positively correlated with C stock in broadleaf and mixed forests. Surprisingly, soil depth, land tenure and disturbance variables had a negligible effect in almost all models, partially due to the poor quality of disturbance and soil depth data available from INFyS. The results suggest that, in order to enhance C stock in Mexican forests, management techniques should encourage increases of the number of tree species and, especially, tree size inequality, since both these factors were shown to have a key role in C stock.

1. Introduction

Forests are one of the largest reservoirs of organic carbon (C) in the medium and long term (Houghton, 2005; Peichl and Arain, 2007; Canadell and Raupach, 2008). Therefore, a better knowledge of the distribution patterns and variability of both aboveground and belowground C stocks is of crucial importance for understanding how C stock changes through time (Houghton, 2005) and for increasing the efficiency and C stock of forest ecosystems (Zhao and Zhou, 2006). C sinks in forests are determined by processes that either allow C sequestration (photosynthesis, C accumulation in soils, tree growth) or induce C losses (disturbances, respiration, tree mortality, microbial decomposition of litter; Malhi et al., 1999). These processes are influenced by many climatic, biological, topographic, and site factors, and even small alterations in these processes can alter the whole C cycle (Malhi et al., 1999).

When considering large spatial scales, environmental factors are the main variables influencing C stocks and C dynamics (Keeling and Phillips, 2007; Vayreda et al., 2012). Specifically, temperature, precipitation and light availability are the most determinant variables for forest growth (Malhi et al., 1999). Temperature has been described as the most determinant factor for C stocks (Raich et al., 2006; Zhao and

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Zhou, 2006; Keeling and Phillips, 2007) but water availability can become the most important driver in dry ecosystems (Malhi et al., 1999; Keeling and Phillips, 2007; Vayreda et al., 2012), even in environments that are not usually considered as water-limited (Allen et al., 2010). When reducing the spatial scale to local sites, topographic and soil variables as well as forest disturbances become more important predictors of C stocks (Alves et al., 2010; McEwan et al., 2011; Xu et al., 2015). Topographic and soil characteristics influence tree growth by controlling nutrient distribution, soil water content, soil drainage, light availability and temperature regime (Alves et al., 2010; Sharma et al., 2010; McEwan et al., 2011; Sattler et al., 2014; Xu et al., 2015). For instance, a steep slope is correlated with a decrease in tree biomass (Sattler et al., 2014; Xu et al., 2015) whereas a deeper soil has positive effects on plant growth (Dimitrakopoulos and Schmid, 2004). Disturbance regimes also have large impacts on C stocks (Pregitzer and Euskirchen, 2004; McEwan et al., 2011; Schowalter, 2012). Silvicultural practices, although causing an initial decrease of C stocks, lead to increases several years after intervention (Canadell and Raupach, 2008). Natural disturbances such as fires, pests, droughts and heat can reduce C stocks by causing increased tree mortality (Allen et al., 2010; Crowley et al., 2016; Hurteau and Brooks, 2011).

C stock in forests can also be affected by biotic variables such as species richness and structural diversity. With regards to species richness, there is still controversy over the influence of stand species number on C stocks (Lei et al. 2009; Wang et al., 2011; Con et al., 2013). Although the vast majority of studies indicate a positive correlation between species richness and biomass production (e.g., Balvanera et al., 2006; Kirby and Potvin, 2007; Vayreda et al., 2012; Vilà et al., 2013; Poorter et al., 2015; Dayamba et al., 2016, among many others), Szwagrzyk and Gazda (2007) and An-ning et al. (2008) noted a negative correlation in temperate forests, whereas Vilà et al. (2003) found no relationship between productivity and species richness in coniferous forests. Sullivan et al. (2017) also failed to find a diversity-carbon positive relationship in old-growth tropical forests. Greater unanimity is found when examining the positive relationship between structural diversity (trees of different age, height or size) and C stock (Vayreda et al., 2012; Con et al., 2013; Zhang and Chen, 2015).

Many researchers have studied the factors that influence C stocks in tropical and subtropical regions, but there is still high uncertainty about how these variables affect C stock, mainly because most studies have been conducted at small spatial scales and/or include a small number of plots (de Castilho et al., 2006; Urquiza-Haas et al., 2007; Cavanaugh et al., 2014). Mexico, due to its location and the variety and extent of its tropical and subtropical forests, is an excellent place to conduct a large-scale study, one which can provide considerable accuracy in C stock predictions for this region: Mexico is located at a point of confluence of the Nearctic and Neotropic ecozonal regions, and presents a large latitudinal and longitudinal gradient (Llorente-Bousquets and Ocegueda, 2008). These features, combined with one of the most heterogeneous topographies in the world, its particular dominant wind direction, and the characteristic pressure oscillation of the region (Murray-Tortarolo et al., 2016), permit the hosting of a wide variety of biomes in a relatively small area. In fact, Mexico contains four of the five major Köppen's climate types (Espinosa and Ocegueda, 2008) and the main natural terrestrial land biomes (CONAFOR, 2012).

In recent years, information on the composition of Mexican ecosystems has increased considerably, but there have been few studies focusing on their structure and functioning (INECC, 2009). Here, we aim to identify the main factors related with the spatial pattern of C stocks across the main forests types of Mexico. Specifically, we attempt to (1) quantify and compare the mean C stocks of the different forest types; (2) determine the main factors related to C stocks of these main forest types and (3) quantify the relative contribution of abiotic (climate, topographic and soil characteristics), diversity (species richness and structural diversity) and disturbance factors explaining the variability of C stocks. For this, we used an extensive dataset from the latest National Forest Inventory of Mexico (INFyS 2009–2014), a network of 26,000 plots including all forest types in Mexico.

2. Materials and methods

2.1. Study area

The study encompasses forests from throughout Mexico (south of North America, situated between 86° 42′W and 118° 27′W and 14° 32′N and 32° 43′N), extending through a large variety of climates and reliefs. The northern and central plateaus are governed by a dry and warm climate, while in the southern and southeastern regions the dominant climate ranges from warm sub-humid to very humid. In the northern regions of the country the climate is temperate and even cold in the highest mountain areas (Murray-Tortarolo et al., 2016).

2.2. The main forest types of Mexico

Mexico has 648,000 km^2 of forestland extending over approximately one third of the national territory (FRA, 2010). Six main forest types can be identified in the region; temperate forests are the most widespread forest ecosystem, occupying 16.3% of the country's surface. These forests extend from south to north in the high and relatively cold regions of the country and can be clearly differentiated into three distinct forests types: broadleaf forests (BRO), conifer forests (CON) and mixed forests (MIX). BRO forests occupy 5.7% of the territory and can be found from sea level (Sonora) to more than 3000 m (Mexico State). This forest type is dominated by the *Quercus* genus which, with more than 200 species, includes forests adapted to a wide range of mean annual temperatures (MAT, ranging from 9.5 to 26.8 °C) and rainfall regimes (from 300 to 4000 mm; Challenger and Soberon, 2008). CON forests cover 4% of the territory and are represented by *Pinus* (predominantly), *Abies, Pseudotsuga, Picea* and *Cupressus* species. CON forests are located at the highest altitudes (4000 m in the Transvolcanic Belt), but can also be found in lower regions such as the Coahuila forests (300 m). Due to these wide altitudinal differences, mean annual temperatures can vary from 6.8 to 25.3 °C and annual rainfall ranges from 270 to 2500 mm. MIX forests of pine and oak (6.6%) are also present along a broad gradient of altitudes (from sea level in Chihuahua to more than 3100 m in Mexico state) with a wide range in MAT (9 to 27.8 °C) and rainfall (350–3600 mm, CONAFOR, 2012).

The second most extensive ecosystem in Mexico is tropical forest, which covers more than 15% of the nation. This ecosystem can be divided into two main forest types: evergreen and semi-deciduous tropical forests (EVE, 7.2%) and dry forests (DRY, 8.2%). Evergreen tropical forests are found in warm and very humid places, mainly in the Atlantic zone: the plains of the Gulf of Mexico, southeast of the Yucatan Peninsula, and the easterly side of Chiapas and surrounding areas (Challenger and Soberon, 2008). This forest type is the most diverse of Mexico, hosting 5000 species of plants (17% of all those found in Mexico) but it is also the most threatened (Challenger and Soberon, 2008; CONAFOR, 2012). The physiognomy and structure of semi-deciduous tropical forests are very similar to evergreen tropical forests, but they differ in phenology, since at least half of the trees of this forest type lose their leaves during the dry season (Rzedowski, 2006). Their distribution is irregular, forming discontinuous patches across the warm and sub-humid areas across Mexico (Rzedowski, 2006). EVE forests can be found from sea level (Yucatan) to 2000 m (Oaxaca), and have a MAT of 15.4–28.1 °C and an annual rainfall of 800–4700 mm. DRY forests are heavily influenced by the dry season, which can last 7–8 months (Challenger and Soberon, 2008); such severe conditions cause most trees in these forests to lose their leaves during the dry season (Rzedowski, 2006). This forest type is typical of the Pacific zone, extending over a large area from southern Sonora to Chiapas, from sea level to more than 2700 m altitude, and includes a significant part of the northern Yucatan Peninsula (Challenger and Soberon, 2008).