Forest Ecosystems 9 (2022) 100016

Contents lists available at ScienceDirect

Forest Ecosystems

journal homepage: www.keaipublishing.com/cn/journals/forest-ecosystems

Carbon stocks in a highly fragmented landscape with seasonally dry tropical forest in the Neotropics

N. Mesa-Sierra [a,b,*], J. Laborde [c], R. Chaplin-Kramer [d,e], F. Escobar [f]

[a] *Instituto Tecnológico y de Estudios Superiores de Occidente, Centro Interdisciplinario para la Formación y Vinculación Social, Periférico Sur Manuel Gómez Morín 8585, 45604, Tlaquepaque, Jalisco, Mexico*
[b] *Gnosis - Naturaleza con ciencia, A.C., Lorenzo Barcelata 5101, 45239, Guadalajara, Jalisco, Mexico*
[c] *Instituto de Ecología, A. C., Ecología Funcional, Carretera Antigua a Coatepec 351, El Haya, 91073, Xalapa, Veracruz, Mexico*
[d] *Natural Capital Project, Woods Institute for the Environment, Stanford University, 327 Campus Drive, Stanford, CA, 94305, USA*
[e] *Institute on the Environment, University of Minnesota, 1954 Buford Ave, St. Paul, Minnesota, 55108, USA*
[f] *Instituto de Ecología, A.C., Ecoetología, Carretera Antigua a Coatepec 351, El Haya, 91073, Xalapa, Veracruz, Mexico*

ARTICLE INFO

Keywords:
Seasonally dry tropical region
Ecosystem services
Carbon sequestration
Human modified landscapes
Climate change mitigation

ABSTRACT

Background: Global modeling of carbon storage and sequestration often mischaracterizes unique ecosystems such as the seasonally dry tropical forest of the central region of the Gulf of Mexico, because species diversity is usually underestimated, as is their carbon content. In this study, aboveground and soil carbon stocks were estimated to determine the climate mitigation potential of this highly degraded landscape (<25% of forest cover).

Results: Tree species in the study area had carbon content values that were 30%–40% higher than the standard value proposed by the IPCC (i.e., 50%). Tropical oak forest in the region, despite its restricted distribution and low species richness, accounted for the highest mean carbon stocks per unit area. The main factors driving spatial variability in carbon stocks were: maximum precipitation, soil organic matter, clay and silt content. No strong relationship was found between aboveground carbon stocks and soil organic carbon in the study area. Quantification of carbon stocks is an important consideration in the assessment of the conservation value of remnants of native vegetation in human-modified landscapes.

Conclusions: This study demonstrates the importance of the highly fragmented tropical dry regions of the Neotropics in maintaining landscape functionality and providing key ecosystem services such as carbon sequestration. Our results also highlight how crucial field-based studies are for strengthening the accuracy of global models. Furthermore, this approach reveals the real contribution of ecosystems that are not commonly taken into account in the mitigation of climate change effects.

1. Background

Global trends in biodiversity conservation and ecosystem services in terrestrial ecosystems continue to be negative, caused in part by drastic climatic and environmental changes (e.g., greater frequency and impact of hurricanes, presence of novel viruses) that also threaten human well-being (Soto-Navarro et al., 2020). Recent commitments to avert climate change, made by governments and businesses at the local and international levels, have generated policy mechanisms and funding for nature-based climate solutions such as carbon sequestration payments. As the uptake of such strategies increases, information regarding the carbon sequestration potential of different landscapes is urgently needed, so their contribution can be accurately assessed and appropriate incentives set. There is a growing consensus regarding the need to generate national policies aimed at the local implementation of actions to achieve the global goals set forth in intergovernmental agendas. Given the current rates of emission and the fact that some of the greenhouse gases remain in the atmosphere for hundreds of years, it is necessary to design and implement corrective actions on suitable time scales to ensure successful mitigation (Anderegg et al., 2020). Terrestrial ecosystems, particularly forest, are among the most important contributors needed to meet the goals set in the global agreements (e.g., Paris Agreement, Bonn Challenge) recognized by several countries (Chazdon et al., 2016; Bastin et al., 2019; Soto-Navarro et al., 2020; Anderegg et al., 2020; Heilmayr

---

* Corresponding author. Instituto Tecnológico y de Estudios Superiores de Occidente, Centro Interdisciplinario para la Formación y Vinculación Social, Periférico Sur Manuel Gómez Morín 8585, 45604, Tlaquepaque, Jalisco, Mexico.

E-mail address: natalia.mesa@iteso.mx (N. Mesa-Sierra).

https://doi.org/10.1016/j.fecs.2022.100016

et al., 2020). It has been estimated that strategies based on the protection of forests can help to sequester approximately 7 Pg CO_2e per year by 2030 (Anderegg et al., 2020), however these estimates are usually based on temperate forest assessments or on satellite information at very coarse scales and are therefore limited. Information obtained at the local level from actual landscapes is essential to design plans tailored to each landscape's context and local anthropic pressures. This information could ultimately be incorporated into local and national policies and help build more accurate global models.

Today, most landscapes worldwide have been modified by anthropogenic activities such as urbanization, agriculture, tourism, infrastructure development, mining, and others that seriously threaten their dynamics and long-term function (Melo et al., 2013; Chazdon, 2014; IPBES et al., 2019; WWF, 2020). Understanding and quantifying the resulting changes in biogeochemical processes (e.g., nutrient flow in soil) are critical for the reliable assessment of all the consequences of land-use and land cover change to landscape functionality (i.e., the capacity of the landscape to provide services by maintaining ecosystem functions). It is known that environmental variables that are susceptible to climate change, such as temperature, precipitation, soil moisture, and pH, among others, may have a strong influence on the process of carbon sequestration and thus, should be incorporated into climate mitigation assessments (Jaramillo et al., 2003; Ibrahim et al., 2006; Corona-Núñez et al., 2018). Assessing and monitoring carbon stocks over time is critical to designing effective landscape management plans and conservation strategies to enhance carbon sequestration in human-modified landscapes.

Most research and policy development efforts in the tropics have focused on humid ecosystems such as tropical rain forests and mangroves, with less attention to other tropical vegetation types, such as tropical dry forest (Stoner and Sánchez-Azofeifa, 2009; Portillo-Quintero et al., 2015; Corona-Núñez et al., 2018). The latter, also known as seasonally dry tropical forest (SDTF, *sensu* Pennington et al., 2009), is the most widely distributed type of forest cover in the tropics, accounting for approximately 42% of tropical forest worldwide (Pennington et al., 2009; Dirzo, 2011; Banda et al., 2016). It is found in areas where the mean annual temperature is 17 to 26 °C and annual precipitation 250 to 2,000 mm. As its name implies, this type of tropical forest is highly seasonal. Its growing season only lasts five to seven months of the year (Jaramillo et al., 2003). Some traits (e.g., leaf area) of the dominant species in these forests allow the trees to have efficient systems for nutrient fixation, to exploit limited resources and to ensure the growth of their foliage and wood (Powers and Tiffin, 2010). In the Americas, this forest type is distributed from Mexico to northern Argentina, including the Caribbean islands, and it is regarded as one of the most threatened terrestrial ecosystems in the world due to the expansion of human activities (Dirzo, 2011). A greater proportion of SDTF has been degraded or transformed than that of tropical rain forest, with less than 10% of the original cover of Neotropical SDTF remaining (Jaramillo et al., 2003; Banda et al., 2016). The available information on current and potential carbon storage of SDTF is scarce when compared to that of humid tropical forests (Corona-Núñez et al., 2018).

Currently, Mexico retains 25% to 36% of its original SDTF—the vast majority of which is relatively young secondary vegetation—and this is a larger proportion of the original SDTF cover than remains in the rest of the Neotropics (Jaramillo et al., 2003; López-Barrera et al., 2014). Seasonally dry tropical regions in Mexico are located on the Pacific Slope, in the northwestern region of the Yucatan Peninsula and the central part of the Gulf of Mexico coast in the state of Veracruz. Assessments of the carbon stocks in Mexican SDTF have focused on the first two regions, while the carbon storage potential of the Gulf of Mexico remains largely unknown, though there is some information in government reports. In this region, less than 25% of the original cover of SDTF remains today (Mesa-Sierra, 2020), making its conservation and the assessment of its carbon stocks a crucial and urgent task. The latter is especially critical if climate mitigation policy and funding are to be used as leverage for securing the protection of the remaining SDTF in this region.

Here, we characterize the potential climate-mitigation value of SDTF in Veracruz, by: *i*) estimating the basal area of different types of old-growth and secondary forest present within the region, *ii*) estimating the carbon stored in each forest type, both aboveground (in the vegetation) and in the soils, and *iii*) evaluating which environmental variables are related to the spatial variation of the aboveground and soil organic carbon stocks. The aim is to provide solid quantitative information that is urgently needed for the reliable assessment of the carbon storage potential of the different types of SDTF still present in this highly transformed and populated region. This is crucial for designing management programs and policies aimed at maximizing carbon stocks, and therefore climate change mitigation in human-modified landscapes in the tropics, by incorporating spatial heterogeneity into the priorities for protecting the remaining well-preserved forest and the restoration or natural regeneration of secondary forest.

2. Materials and methods

2.1. Study area

The seasonally dry tropical region of the Gulf of Mexico is located in the central part of the state of Veracruz. It is distributed from the lowlands of the Manuel Díaz mountain range that extends down to and is perpendicular to the Atlantic coast and extends southwards along the coastal plain ending between the city of Cardel and the Puente Nacional zone, from 19°16′55″ to 19°48′16″ N and from 96°19′13″ to 96°48′48″ W (Fig. 1). The region's weather is classified as AW_2, characterized by marked seasonality in its rainfall regime. During five to eight months of the year, precipitation is very low compared to that of other regions in the tropics that are more humid and less seasonal (García, 2004). Mean annual temperature is 22–26 °C, and mean annual rainfall is 1,200 to 1,500 mm (Travieso-Bello and Campos, 2006). Ten different types of soils have been found in the region (Travieso-Bello and Campos, 2006), including: obrist histosols, cambid aridisols and mollic gleysols (FAO/UNESCO classification).

2.2. Vegetation types and aboveground carbon

Based on a previous analysis of land cover using SPOT5 images from 2014 and intense field verification (Mesa-Sierra et al., 2020a, 2020b), ten sampling sites with forest cover that were at least 1 km apart were selected for sampling across the study area (approximately 1,100 km^2). In each of these 10 sites an area of 600 by 600 m (36 ha) with forest patches inside was delimited. All forest patches >1 ha present within these ten sites, were sampled, totaling 29 forested patches (Fig. 1). All forest patches sampled had a stand-age equal to or greater than five years.

Three 50 m × 20 m parallel belt-transects were set up (at least 20 m apart) within each of the 29 patches (87 transects in total). All woody plants with a DBH ≥5 cm and rooted within the transects were identified to the species or genus level and their DBH was measured during January and September 2016. Along the central line of each transect, the height of the canopy was measured every 5 m in order to generate a vertical profile of the canopy. Following Mesa-Sierra et al. (2020a), six types of forested vegetation were distinguished based on species composition and physiognomy: three old-growth forest types, tropical oak forest (TOF), low-statured deciduous forest (LWF), semi-deciduous forest (SDF), and three secondary forest types (with SDF cover before disturbance), late secondary forest (LSF; > 20 years old), intermediate secondary forest (ISF; 10–20 years old) and early secondary forest (ESF; 5–10 years old).

For this study 29 tree species were selected to extract woody samples and assess their carbon content (Table S1). The species selected included those with the highest importance value index (IVI) in each vegetation type (i.e., dominant species per type), and were a subset of the 157 species recorded in vegetation sampling (Mesa-Sierra et al., 2020a). This index allowed us to select species based on their relative frequency, relative density, and relative dominance and ensure that they were a

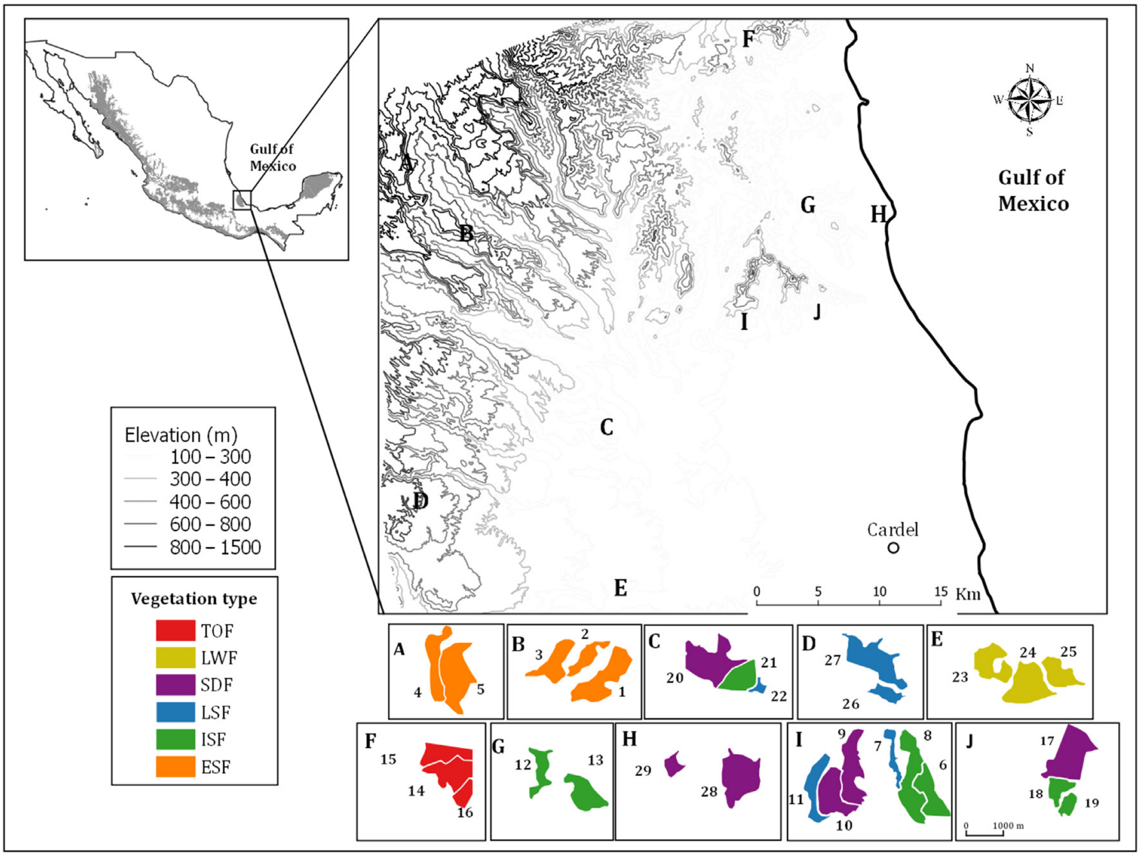

Fig. 1. Study area location in the seasonally dry tropical region of the Gulf of Mexico, Veracruz, Mexico. The distribution of tropical dry forest ecosystems in Mexico is shown (gray), in the upper left inset. The locations of the ten sampling sites (A–J) are shown and for each site all of the forest patches sampled are drawn, numbered from 1 to 29 (bottom right). Vegetation types (defined in Mesa-Sierra et al., 2020a) include: three old-growth forest types: Tropical Oak Forest (TOF); Low-statured Deciduous Forest (LWF) and Semi-Deciduous Forest (SDF); and three secondary forest (SF) types: Late SF (LSF); Intermediate SF (ISF) and Early SF (ESF).

representative sample of the trees recorded. Wood samples of the dominant species were extracted from the trunk of three individuals with DBH >10 cm in each sampled patch, using a Haglöf borer with a 10” penetration depth. Samples were only taken from stem wood; the other parts of the trees were not sampled (e.g., branches). The samples were dried at a constant temperature of 37 °C for at least 24 h and then a standardized sub-sample of one cubic centimeter was obtained from each field sample. Next, these 1 cm^3 samples were burned for 4 h in a high-temperature oven at 550 °C. After the temperature had decreased to below 100 °C, the samples were weighed again to determine the weight loss in grams after drying, which represents the organic carbon content (%) in the sample (*sensu* SARE, 2012). For wood density, different databases (Brown, 1997; Zanne et al., 2009; Harja et al., 2010; Ordóñez Díaz et al., 2015) were reviewed to obtain information for each of the 29 species. For those species that did not have specific information, the densities reported specifically in tropical areas for the genus were averaged. This information was used to estimate the aboveground biomass (AGB) for each of the species by forest patch, which was calculated using the model proposed by Chave et al. (2005) for dry forest:

$$AGB = 0.112 \times (\rho D^2 H)^{0.916}$$

where ρ is wood density ($t{\cdot}m^{-3}$), D is the diameter at breast height (cm) and H is mean canopy height (m). Finally, to assess the aboveground carbon content per species (AGCs) of the dominant species in each forest patch, biomass was multiplied by percent carbon for each one (FAO, 2011; Petrokofsky et al., 2012). Therefore, the aboveground carbon content per sampled patch (AGCp) was assessed by adding the AGCs values of the selected species that were present within the patch, and this was extrapolated to express the value per hectare. These values were, in turn, summed to obtain a value for the aboveground carbon content by vegetation type (AGCvt).

2.3. Soil organic carbon

Along each of the vegetation transects, soil samples were collected every 15 m. Each sample consisted of 300 g of soil extracted from an area of 100 cm^2 from the top 10 cm of mineral soil (excluding the litter layer), and were subsequently mixed to obtain a single combined soil sample per transect (3 samples per forest patch). These samples were dried at room temperature for approximately 24 h, ground and processed in the Soil Laboratory at the Instituto de Ecología, A.C. to determine: bulk density ($t{\cdot}m^{-3}$), organic carbon (OC), organic matter (OM), pH, and sand, clay and silt content, following standard procedures (Dane et al., 2002; Sparks et al., 2020). To estimate the soil organic carbon (SOC) stock ($t\ C{\cdot}ha^{-1}$) for each vegetation type and sampled patch, we multiplied organic carbon (%), by the bulk density ($g{\cdot}cm^{-3}$) and the depth at which the samples were taken (i.e., 10 cm), multiplied by the area sampled and extrapolated to get an estimate per hectare (Griffin et al., 2013).

2.4. Data analyses

Carbon content values were compared among the patches of the vegetation types with Generalized Linear Models (GLMs), using a negative-binomial error type due to the overly dispersed nature of the data. When significant differences were found, a *post hoc* test (Tukey) was used to determine which vegetation types were different. We also assessed the variation in carbon content among the three secondary vegetation forest types defined in this study (LSF, ISF and ESF) to analyze the temporal turnover of carbon accumulation during these successional stages.

We performed Ordinary Least Squares (OLS) regressions to explore the relationship between each of the carbon values (AGC and SOC), and different variables per forest patch that summarized the heterogeneity of the 29 patches, including environmental variables and vegetation attributes (i.e., basal area, plant richness and abundance). Environmental variables per forest patch (Table S2) included maximum annual temperature (°C), mean annual precipitation (mm·year^{-1}), maximum annual precipitation (mm), elevation (m a.s.l.), slope (°), soil pH, soil organic carbon (%), soil organic matter (%), and soil content of sand, clay and silt (%). To meet the assumptions for OLS regressions, we tested for normality. Climate variables (maximum annual temperature, mean annual and maximum annual precipitation) were extracted from the high-resolution (30-arc sec; approx. 90 m per pixel) climate surfaces for Mexico (Cuervo-Robayo et al., 2014), and topographic variables (elevation, slope, and aspect) were obtained from a national Digital Elevation Model (DEM) of the study area with a resolution of 25 m per pixel (INEGI, 2009). OLS regression analysis was also used to determine if the AGC and SOC stocks per patch were related. All statistical analyses were run in R (R Development Core Team, 2019).

3. Results

3.1. Basal area

The basal area was 106.4 m^2 in a total sampling area of 87,000 m^2 (12.2 m^2·ha^{-1}), represented by 6,007 plants belonging to 157 species of woody species and 113 genera. Of all the species recorded, 29 were dominant in at least one of the six forest types in the study area, based on their IVI values in each forest type (see Table S1). These species represented 18.5% of total plant richness in the vegetation sampling, but together accounted for 60% of the total abundance and 64% of total basal area (see Supplemental section 1 and Mesa-Sierra et al., 2020a).

3.2. Carbon stocks

3.2.1. Aboveground

In a sample area of 8.7 ha within the study area, the remaining forest vegetation, both old-growth and secondary forest, stores >272 t C, with an average value of 9.4 ± 6.5 t C·ha^{-1} (±s.d.) per patch ($N = 29$ patches). Tropical oak forest (TOF) had the highest AGC, with one of its patches >23 t C·ha^{-1}. There were significant differences among the mean AGC values per forest type ($\chi^2 = 44.97$; d.f. = 5; $P < 0.05$), mainly between TOF and the other forest types (Fig. 2). The lowest value was recorded for early secondary forest (ESF). TOF had the lowest variation among the patches in terms of AGC values (Fig. 2).

Overall, wood density varied between 0.30 and 0.97 t·m^{-3} (Table 1) among the species analyzed. Carbon content values in the wood were 73.5%–99.5%. The five species with the highest percent carbon (≥98%) were *Cestrum racemosum*, *Mirandaceltis monoica*, *Quercus sapotifolia*, *Caesalpinia cacalaco* and *Senna atomaria*, while those with the lowest carbon values (<85%) were *Gliricidia sepium*, *Guazuma ulmifolia*, *Nectandra salicifolia* and *Erythrina americana* (Table 1). Some species had a remarkably high intra-specific variation in percent carbon, as revealed by extremely high coefficient of variation values (CV), particularly for *Gliricidia sepium* (CV = 49%), *Erythrina americana* (31%), *Nectandra salicifolia* (38%) and *Guazuma ulmifolia* (26%), while the CV of all the other species analyzed was lower than 5% (with the exception of *Cedrela odorata*; 10%).

When the aboveground carbon content was analyzed within the different types of secondary forest whose successional age (from Early to Late) could be regarded as a chronosequence, turnover in the species that stored the most carbon was observed. The species that made the greatest contribution to carbon stocks were *Acacia pennatula* in the Early Secondary Forest, *Gliricidia sepium* in Intermediate Secondary Forest and *Mirandaceltis monoica* in Late Secondary Forest (Fig. 3). Likewise, individual species exhibited their highest values of carbon storage at different successional stages. For example, the highest AGC values were found for *Leucaena leucocephala* in Late Secondary Forest (LSF), for *Guazuma ulmifolia* in Intermediate Secondary Forest (ISF), and for *Bursera simaruba* in Early Secondary Forest (ESF; Fig. 3).

3.2.2. Soil

For soil organic carbon stocks in the study area, the mean value of carbon stored in the forest patches sampled was 11.12 ± 7.92 t C·ha^{-1} (±s.d.) per patch ($N = 29$ patches). There were five patches whose soil organic carbon (SOC) content surpassed 20,000 t C·ha^{-1}: the tropical oak forest (TOF) patches and two of the late secondary forest (LSF) patches. TOF had the highest mean SOC value, and LSF had the highest variation in SOC content per patch (CV = 89%). SOC stock differed among forest types ($\chi^2 = 38.3$; d. f. = 5; $P < 0.001$), especially between TOF compared to SDF, ISF and ESF (Fig. 4).

3.3. Environmental variables related with carbon stocks

3.3.1. Aboveground

The variables that best explained the variation in carbon content per patch were soil attributes. None of the topographic or climate variables had a significant influence (Table S3) on the AGC values. The strongest positive relationships with the AGC values were with organic matter and organic carbon in the soil (Fig. 5a and b). Weaker relationships were found with the clay content of the soil, which was negative, and the sand content of the soil, positive (Fig. 5c and d).

3.3.2. Soil

Of all the environmental variables analyzed (Table S2), three were significantly related to the SOC stock per patch. Forest patches with a high proportion of organic matter in the soil (Fig. 6a) or with a higher number of individuals (Fig. 6c), had a higher SOC stock, though this last relationship was weak. In contrast, for forest patches with the highest values of maximum annual precipitation, the SOC values were below 10,000 t C·ha^{-1} (Fig. 6b).

Finally, contrary to expectation, there was not a strong relationship between aboveground (AGC) and soil (SOC) carbon stocks per patch (R^2

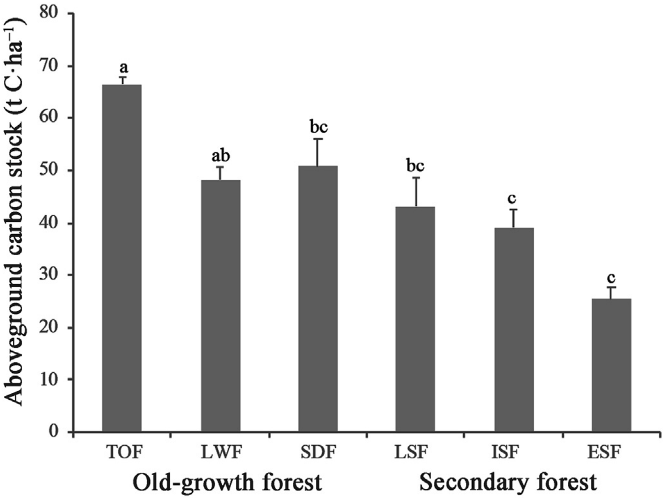

Fig. 2. Mean aboveground carbon stock (t C·ha^{-1} ± s.d.) per forest type, estimated from the dominant species of each forest type (see Methods). Forest types are: Tropical Oak Forest (TOF), Low-statured Deciduous Forest (LWF), Semi-deciduous Forest (SDF), Late Secondary Forest (LSF), Intermediate Secondary Forest (ISF) and Early Secondary Forest (ESF). Different letters indicate significant differences between forest types (Tukey test; $P < 0.05$).

Table 1
Summary of percent carbon (%) and wood density ($t{\cdot}m^{-3}$) for each of the 29 species sampled ($n = 3$ individuals per species), as well as their stem volume ($m^3{\cdot}ha^{-1}$) in each forest type where they were found. Forest types: Tropical Oak Forest (TOF), Low-statured Deciduous Forest (LWF), Semi-deciduous Forest (SDF), Late Secondary Forest (LSF), Intermediate Secondary Forest (ISF) and Early Secondary Forest (ESF).

Species	%C		Wood density ($t{\cdot}m^{-3}$)*		Stem volume ($m^3{\cdot}ha^{-1}$) per forest type					
	Mean	s.d.	Mean	s.d.	TOF	LWF	SDF	LSF	ISF	ESF
Brosimum alicastrum	96.2	2.51	0.61	0.00	–	–	72.8	–	–	–
Bunchosia sp.	96.5	0.88	0.72	0.06	–	–	–	69.9	–	–
Bursera simaruba	97.6	0.36	0.34	0.11	–	186.8	–	28.3	15.1	83.2
Byrsonima crassifolia	98.7	0.52	0.61	0.06	42.5	–	–	–	–	–
Caesalpinia cacalaco	98.9	0.57	0.97	0.19	–	50.2	–	–	–	–
Casearia corymbosa	98.0	1.31	0.64	0.09	–	–	20.2	–	–	–
Cedrela odorata	91.8	9.09	0.45	0.22	–	–	198.9	–	–	36.6
Cestrum racemosum	99.5	0.18	0.48	0.05	–	058.6	–	–	–	–
Chloroleucon mangense	95.5	4.15	0.99	0.00	–	–	46.6	–	–	–
Cordia diversifolia	98.6	0.27	0.52	0.18	–	–	–	106.8	21.4	–
Diphysa americana	97.3	0.70	1.08	0.14	–	–	40.6	–	–	–
Ehretia tinifolia	96.0	1.20	0.54	0.11	–	–	109.0	–	–	–
Erythrina americana	81.8	2.80	0.30	0.15	–	–	–	–	–	3.6
Eysenhardtia polystachya	98.0	2.29	0.70	0.00	–	102.4	–	–	–	–
Gliricidia sepium	73.5	25.76	0.66	0.00	–	–	46.7	–	522.9	1.6
Guazuma ulmifolia	85.3	1.53	0.60	0.27	–	–	28.6	12.4	200.7	43.9
Leucaena leucocephala	98.8	36.27	0.78	0.13	–	55.1	70.6	132.0	0.9	74.2
Licaria capitata	97.4	22.85	0.80	0.12	–	83.4	–	–	–	–
Lysiloma divaricata	96.9	0.50	0.69	0.14	–	–	143.4	75.1	16.3	–
Mimosa tricephala	97.9	0.66	0.77	0.19	–	–	–	–	4.7	–
Mirandaceltis monoica	99.1	0.17	0.63	0.09	–	–	–	230.0	–	–
Nectandra salicifolia	81.0	0.60	0.46	0.00	–	–	89.5	–	–	–
Piscidia piscipula	95.7	0.30	0.66	0.14	–	142.4	–	15.6	–	–
Pisonia aculeata	95.7	31.01	0.35	0.13	–	–	13.9	18.5	5.9	–
Quercus olioides	93.9	0.35	0.86	0.00	177.5	–	–	–	–	–
Quercus sapotifolia	98.2	2.21	0.71	0.10	710.5	–	–	–	–	–
Senna atomaria	98.9	3.63	0.80	0.00	–	–	–	–	–	–
Senna pallida	97.8	56.38	0.60	0.13	–	129.2	–	–	–	4.0
Vachellia pennatula	98.5	0.40	0.77	0.18	–	–	–	–	–	167.2

*Data obtained from the literature (see Methods).

= 0.311; $P = 0.002$). Extremely high and contrasting spatial variability were found for these two variables; some of the sampled patches with high values of AGC had a very low SOC content, while others with a very high SOC content had an extremely low AGC content (see Table S2; patches #13 for the first case, and #1, 27 for the second).

4. Discussion

4.1. Aboveground carbon storage

The plant species associated with seasonally dry tropical forest are characterized by different growth forms that have great physiological plasticity, which allows them to adapt to different conditions and overcome the prolonged periods of drought that are typical of this ecosystem (Williams-Linera and Lorea, 2009; Alvarez-Aquino and Williams-Linera, 2012; Chaturvedi et al., 2018). Some of the traits (e.g., leaf area) of dominant species in these forests allow the trees to have efficient systems for nutrient fixation, to exploit limited resources and ensure the growth of their foliage and wood (Powers and Tiffin, 2010). In this study, we found that the dominant tree species (i.e., greater IVI) of the seasonally dry tropical region of the Gulf of Mexico are highly capable of fixing carbon in their trunks, with carbon content values (up to 99%) that are higher than those recorded in other dry Neotropical regions (47%–50%; Chave et al., 2009; Schmitt-Harsh et al., 2012; González Cásares et al., 2017; Corona-Núñez et al., 2018). Twenty-five of the twenty-nine species studied had carbon content values higher than 90%, while only two species had values lower than 85%.

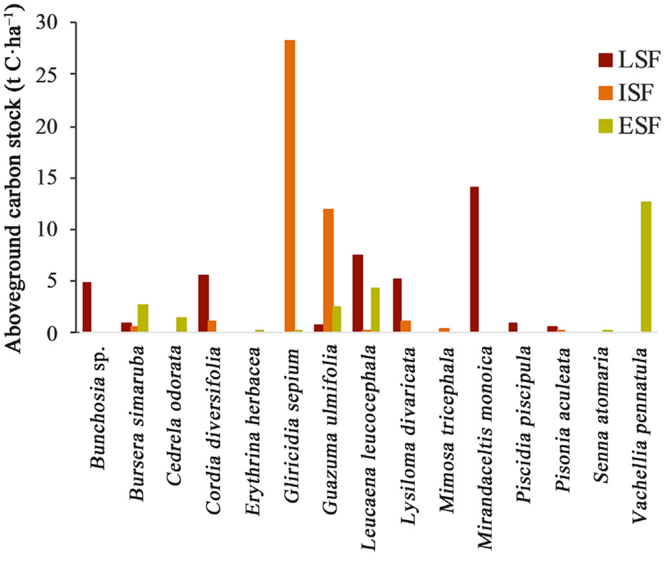

Fig. 3. Total carbon stock ($t\ C{\cdot}ha^{-1}$) for the 15 dominant species in the three types of secondary forest (i.e., different successional stages): Late Secondary Forest (LSF), Intermediate Secondary Forest (ISF) and Early Secondary Forest (ESF).

Our carbon values are far higher than those used by the Intergovernmental Panel on Climate Change (IPCC; 50%) to assess carbon stocks in vegetation (AGC) worldwide, suggesting that the current potential of seasonally dry tropical regions to provide the ecosystem service of carbon fixation in aboveground biomass is greatly undervalued. Recent assessments of AGC based on remote sensing estimates of vegetation biomass (Avitabile et al., 2016; Baccini et al., 2017) do not directly measure the carbon content of the different plant species, but rather indirectly estimate biomass (based on tree height, not basal area) and apply the factor recommended by the IPCC to estimate carbon content per unit of biomass. This vastly undervalues the true carbon content of the tropical dry forests of Veracruz, and possibly that of other ecosystems not

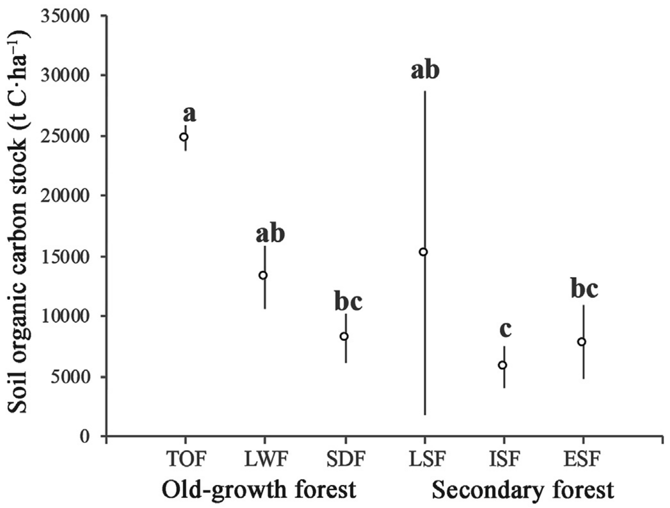

Fig. 4. Soil organic carbon stock (t C·ha^{-1}) in each forest type. Mean and standard deviation (vertical lines) are shown. Old-growth forest types: Tropical Oak Forest (TOF), Low-statured Deciduous Forest (LWF), Semi-deciduous Forest (SDF). And secondary forest types: Late Secondary Forest (LSF), Intermediate Secondary Forest (ISF) and Early Secondary Forest (ESF). Different letters indicate significant differences between forest types (Tukey test; $P < 0.05$).

revealed by coarse scale maps. While the rapid assessment of ecosystem services in tropical landscapes that takes into account the high rate of deforestation is an urgent task, it is also necessary to develop feasible methods to incorporate: *i*) remote sensing estimates of basal area (e.g., LiDAR), *ii*) existing baseline information (e.g., national forest inventories), and *iii*) datasets of carbon density for the dominant species of different ecosystems. As our results show, it is also critical to include more tree species in the carbon density datasets, since there is such high variability across species, particularly for highly diverse tropical forests and their secondary vegetation. It has been proposed that species richness could be used to predict certain ecosystem services such as carbon sequestration (Midgley, 2012; Arasa-Gisbert et al., 2018), but for tropical forests there is evidence that the predictive power of this variable is too low to obtain reliable data (Arasa-Gisbert et al., 2018). Our study provides a clear example of the disconnect between species richness and carbon storage potential; specifically, the results of the tropical oak forest where almost 90% of its basal area comes from only three tree species, which all have a relatively high capacity to fix carbon in their wood. This refutes the findings of Arasa-Gisbert et al. (2018) in a similar ecosystem in Mexico.

While the relationship between aboveground carbon stocks and soil variables was found to be weak in other seasonally dry tropical regions of Mexico (Jaramillo et al., 2003; Corona-Núñez et al., 2018; Gavito et al., 2018), our results show that the carbon stored in the aboveground biomass is strongly related to edaphological variables, mainly soil organic carbon and organic matter, as well as with the proportion of sand and clay, for which weaker relationships were detected. Some authors have reported a relationship between edaphological variables and the functional attributes of plants in dry forests, such as the carbon content of the leaves, stomatal conductivity, photosynthetic rates and biomass increase (Chaturvedi et al., 2011, 2018), which are related to the capacity of trees to fix carbon in their tissues. Additionally, and specifically in the case of clay and sand content, these variables directly influence the soil water retention capacity, since a higher sand content increases soil permeability and quick water loss, while a higher clay content increases water retention, retaining moisture for longer periods of time (Powers and Peréz-Aviles, 2013). Variation in soil water retention is particularly important in seasonally dry tropical regions where water availability is extremely low or completely absent during the months-long dry season, and access to water by the roots is a key determinant in nutrient acquisition (e.g., carbon fixation) and wood growth (Becknell and Powers, 2014; Corona-Núñez et al., 2018). The evidence for the mechanisms that explain the influence of edaphic attributes on the capacity of carbon storage in the aboveground biomass is scarce, indicating the need to carry out more in-depth studies.

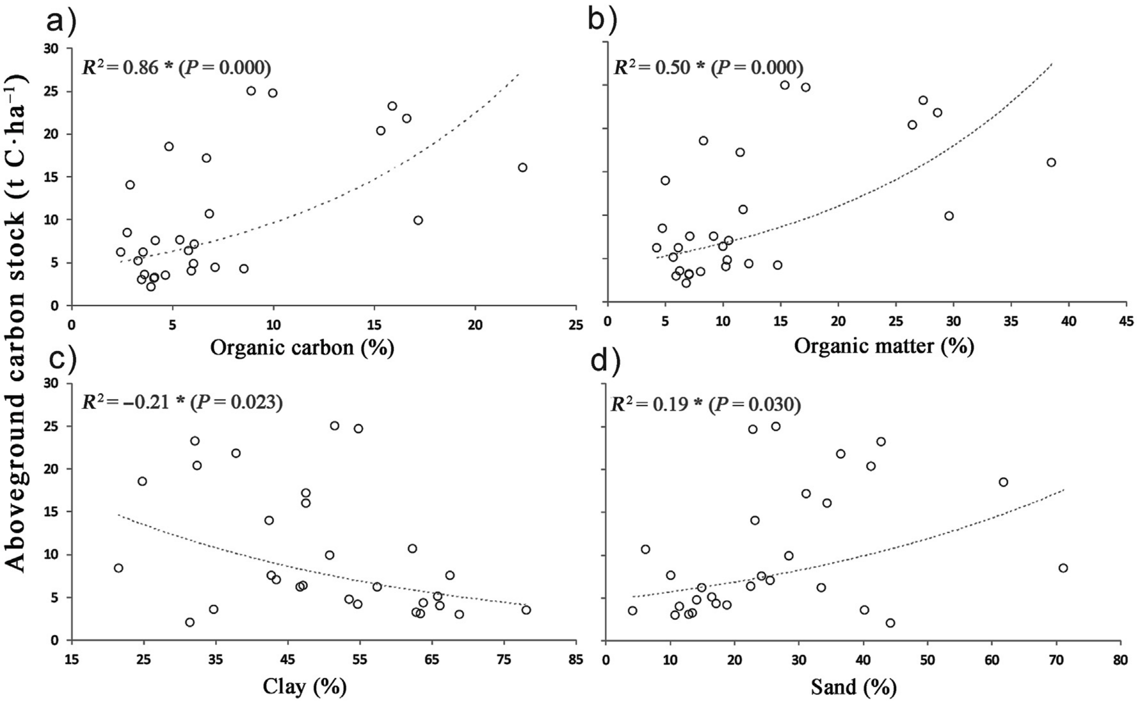

Fig. 5. Significant relationships (i.e., $R^2 > 15\%$) between aboveground carbon stock per forest patch (t C·ha^{-1}) and environmental variables: (**a**) soil organic carbon (%), (**b**) soil organic matter (%), (**c**) soil clay (%) and (**d**) soil sand (%) content for the patches ($N = 29$) sampled in the seasonally dry tropical region of the Gulf of Mexico.

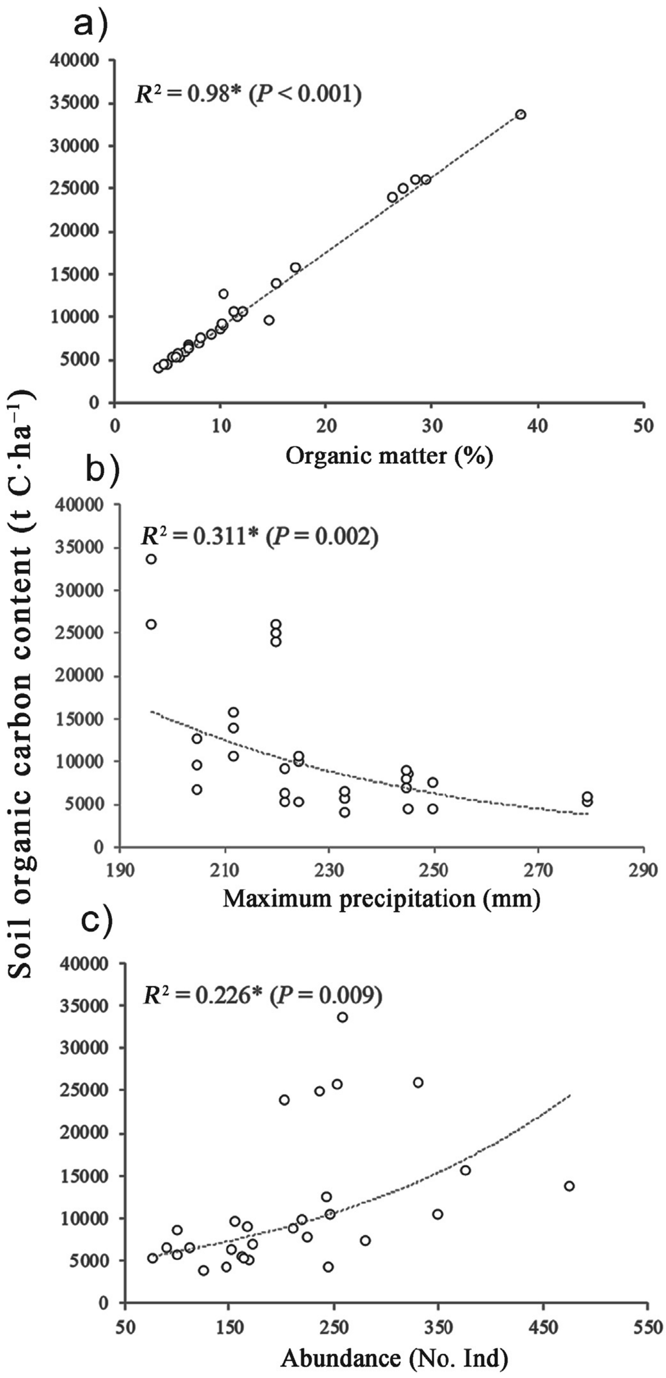

Fig. 6. Significant relationships between soil organic carbon stock (t C·ha^{-1}) and environmental variables: (**a**) soil organic matter (%), (**b**) maximum annual precipitation (mm) and (**c**) plant abundance (number of stems) for the forested patches sampled in the seasonally dry tropical region of the Gulf of Mexico. Precipitation data is from Cuervo-Robayo et al. (2014).

4.2. *Soil organic carbon storage*

It has been reported that the conversion of natural vegetation cover into different types of land use does not have particularly strong consequences for soil organic carbon stocks, and even that while the conversion of a forest into a pasture reduces the amount of nitrogen in the soil, it does not reduce its carbon content (Cairns et al., 2000; Jaramillo et al., 2003; Ibrahim et al., 2006). However, on average the old-growth forest types in the region we studied have a higher soil organic carbon stock than secondary forest patches of different successional stages do, providing evidence that past changes in land use result in degraded soils by diminishing nutrients stocks, including those of carbon (Becknell and Powers, 2014; Gavito et al., 2018). Still, despite the high rates of deforestation in the study area, the soils of this landscape have a high capacity for recovery after the agricultural disturbance stops and secondary succession progresses, as shown by some of the patches of secondary forest whose soil carbon content was as high as that of old-growth forest patches.

Tropical oak forest (TOF) had the highest soil carbon content, likely due to the fact that these patches have remained relatively undisturbed in their forest structure and species composition over the past few centuries (Mesa-Sierra et al., 2020a). The rough, extremely poor soils of this forest type are not suitable for agricultural activities, and thus soil degradation has been prevented. This forest type is regarded as a Pleistocene relic (Arriaga et al., 2000), where it is possible to find species that are not distributed in any other zone of the tropical dry region of the Gulf of Mexico (e.g., *Quercus sapotifolia*). Today, tropical oak forest is one of the most threatened vegetation types in the region due to open-pit mining projects focused on precious metals located directly underneath the remaining patches of this forest type (Laborde, 2018). However, this study demonstrates that in addition to its relevance as a biodiversity refuge (e.g., millennial-old cycads), TOF also has a great deal of potential to provide ecosystem services, including the highest carbon stocks per unit area within the region studied.

Soil organic matter is directly related to vegetation structure (especially the number of woody plants) and species composition, whose spatial variation has explicit effects on leaf litter production, and rates of organic matter decomposition and nutrient exchange (Jaramillo et al., 2003; Gavito et al., 2018). However, our results in this respect, as well as the weak relationship between aboveground and soil organic carbon stocks, demonstrate the need for further edaphological analyses in the seasonally dry tropical region of the Gulf of Mexico; particularly to increase our understanding of how the spatial variation in species composition and edaphic properties influence soil carbon stocks, regardless of the amount of organic matter in the soil. This would allow us to generate a database of the most desirable tree species for assisted restoration projects and to enrich vegetation patches during secondary succession, and to more quickly and completely recover forest attributes in terms of the edaphological processes (e.g., carbon cycle) and soil nutrients, not only at the local patch level, but also for the whole anthropic landscape.

4.3. *Forest resilience*

Regardless of the structural similarities among the old-growth and secondary forest patches, particularly in terms of tree size distribution, the basal area of secondary forest types was lower than that of two of the old-growth forest types: the tropical oak forest (TOF) and the semi-deciduous forest (SDF), though it was similar to or even greater than that of the low-statured deciduous forest (LWF). These structural differences have usually been attributed to differences in stand age (Hernández-Stefanoni et al., 2011; Dupuy et al., 2012; Becknell and Powers, 2014; Poorter et al., 2016), which can be the direct result of chronic human disturbance, natural disturbances (e.g., hurricanes) or both. However, large trees (DBH ≥60 cm) were recorded in patches of early secondary forest (ESF), whose presence during the early stages of secondary succession is explained by specific tree management practices along with agricultural uses of the plot. For example, leaving large canopy trees in the middle of pastures during forest clearing provides shade for cattle, or along rivers that cross properties protects the riverbanks, or by directly planting trees as living fence posts. These large trees that remain within farmers' plots improve the heterogeneity and quality of the agricultural matrix, as well as landscape connectivity (Guevara et al., 1998; Arroyo-Rodríguez et al., 2020), and they also increase the basal area of regenerating secondary vegetation during the fallow period after plot abandonment. These forest patches have a profuse, dense advance regeneration, i.e., plenty of juvenile trees, to maintain forest regeneration (Chazdon et al., 2007; Hernández-Stefanoni et al., 2011; Mesa-Sierra and Laborde, 2017; Corona-Núñez et al., 2018).

These attributes of secondary forest patches can be interpreted as indirect evidence of resilience (Mesa-Sierra et al., 2020b), at least in forest physiognomy, which is explained not only by the distribution of tree sizes but also by the spatial and temporal turnover of the species that dominate the biomass of the different successional stages. *Vachellia pennatula*, for example, is dominant in the early stages of succession (i.e., ESF), but declines over time and is replaced by later stage species such as *Gliricidia sepium* or *Guazuma ulmifolia*, having facilitated more suitable microclimatic conditions for the arrival of those later species. Similar successional trends have been reported for other seasonally dry regions within the Neotropics, where resilience is also represented by changes in the species that dominate the biomass through succession (Kalacska et al., 2004; Powers et al., 2009; Griscom, 2020). Such resilience confers ecological stability and the long-term maintenance of other ecosystem services in addition to carbon sequestration, particularly those that are directly related to forest biomass, such as the availability of high-quality habitat for forest fauna, efficient nutrient fixation and cycling, and the mitigation of natural disturbances (e.g., hurricanes), among others (Balderas Torres and Lovett, 2013; Becknell and Powers, 2014; Poorter et al., 2016; Prado-Junior et al., 2016). This resilience is of vital importance, considering the global crisis of forest ecosystems (i.e., high rates of deforestation) and their capacity to regulate climate (Anderegg et al., 2020), making these tropical dry forests a high priority for carbon offset projects.

4.4. Landscape management implications

At first sight from a satellite image (e.g., Google Earth) our study region seems to be devastated and devoid of its original forest cover. However, on closer inspection as in our study, we can appreciate that numerous small forest patches are still present in this landscape, and that they also have a notable richness of forest plants and contribute substantially to carbon sequestration.

We are aware that our methods underestimate carbon stocks because we were unable to take into account every stem in our transects. This was related to constraints in available funding and time for field sampling, but also because it was not possible to carry out the extraction and analysis of samples for all the species detected. While we only obtained carbon sequestration data for 29 of the 157 species present in the study area, the data obtained clearly indicates that this vegetation is making a substantial contribution. However, the procedure we followed allowed us to compare not only the six different vegetation types present in our study site, but also the spatial variability among the 29 patches sampled in a systematic way, based on the dominant species of the region.

Quantifying both the aboveground and also the soil organic carbon stocks is essential to recognizing the full conservation value of the remnant patches of native vegetation that are still present in human-modified landscapes but rarely taken into account in GIS analyses. In the seasonally dry tropical region of the Gulf of Mexico, despite the great impact of human activities, there is an important pool of tree species that seem to maintain landscape functionality, providing essential ecosystem services such as carbon sequestration, and that ensure the capacity of soils to perform critical processes such as nutrient and carbon cycling. In the secondary forests of different ages that we sampled (LSF, ISF, ESF), successional turnover results in successive floristic transitions that contribute to increasingly higher values of AGC stocks, if allowed to grow undisturbed. Thus, in order to enrich a plot of land after agricultural disturbance, our results suggest that the best trees to reintroduce would be secondary species of the Fabaceae family (formerly Leguminosae) such as *Vachellia pennatula*, *Gliricidia sepium* and *Leucaena leucocephala*, or other species with high growth rates and carbon storage potential such as *Bursera simaruba* and *Cedrela odorata*.

These species would rapidly regenerate biomass and modify biotic and abiotic conditions, promoting the arrival and growth of the shade-tolerant species typical of old-growth forest. Fabaceae species have a high carbon content and fast rates of wood growth, and are able to attain high densities in patches of secondary forest. They are also recognized for their ability to restore biogeochemical cycles in the soil, such as nitrogen fixation (Gavito et al., 2018; Bakhoum et al., 2018; Castellanos Barliza et al., 2019). Even though in this region there was no evidence of a direct relationship between aboveground and soil organic carbon stocks, it has been proposed that these tree species are able to promote an increase in soil carbon stocks (Castellanos Barliza et al., 2018; Gavito et al., 2018). More research is needed to determine the best management practices to enhance the carbon stocks of the region and similar landscapes, and to improve our understanding of how biogeochemical processes and nutrient distribution are related to the environmental variables that are vulnerable to climate change.

5. Conclusions

Our results reveal that patches of remnant old-growth and secondary forest together and under appropriate conservation and management actions, can make a substantial contribution to meeting climate mitigation objectives through their carbon stocks. This may help set priorities for land-use planning and in the development of programs for landscape restoration at the national scale, with the aim of achieving the international goals of increasing forest cover and carbon stocks. Combining local information on biodiversity and organic carbon stocks to produce maps that are accurate at a finer resolution will enable governments and other stakeholders to geospatially identify where different management actions can help them to meet their conservation and restoration objectives, as well as understand how local and national actions contribute to global goals.

Funding

This study was funded by The Rufford Foundation (Rufford small grant #206761, to N.M.-S.); the Instituto de Ecología, A. C. (project INECOL, 20030–10281, to J.L.); and the Consejo Nacional de Ciencia y Tecnología (CONACYT, Scholarship #263474, to N.M.-S.).

Availability of data and material

All the data generated or analyzed during this study are included in this published article and its supplementary information files.

Authors' contributions

N.M.-S., J.L., R.C-K., and F.E. conceived the ideas and hypotheses, and designed the study. N. M.-S. collected data. N.M.-S., J.L., R.C.-K., and F.E. ran the statistical analyses and interpreted the results. N.M.-S. coordinated the writing of the manuscript. All the authors substantially contributed to the manuscript and agreed with the final version for submission.

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Declaration of competing interest

The authors declare that they have no competing interests.

Acknowledgments

We are grateful to Victor Vázquez, Noé Cardona, Miguel Ramirez, Evodio Martínez, Tomás Higueredo, and Enrique Romero for their help during field work and to those in charge of the Amelco UMA. René Altamirano, Noé Cardona, and the Higueredo Family generously granted us permission to work on their properties, and Ariadna Martínez Virués provided expert advice on the methods for estimating carbon content of wood. We thank Bianca Delfosse her editorial work on the final English version of the manuscript.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.fecs.2022.100016.

References

Alvarez-Aquino, C., Williams-Linera, G., 2012. Seedling survival and growth of tree species: site condition and seasonality in tropical dry forest restoration. Bot. Sci. 90, 313. https://doi.org/10.17129/botsci.395.

Anderegg, W.R.L., Trugman, A.T., Badgley, G., Anderson, C.M., Bartuska, A., Ciais, P., Cullenward, D., Field, C.B., Freeman, J., Goetz, S.J., Hicke, J.A., Huntzinger, D., Jackson, R.B., Nickerson, J., Pacala, S., Randerson, J.T., 2020. Climate-driven risks to the climate mitigation potential of forests. Science 368. https://doi.org/10.1126/science.aaz7005.

Arasa-Gisbert, R., Vayreda, J., Román-Cuesta, R.M., Villela, S.A., Mayorga, R., Retana, J., 2018. Forest diversity plays a key role in determining the stand carbon stocks of Mexican forests. For. Ecol. Manag. 415–416, 160–171. https://doi.org/10.1016/j.foreco.2018.02.023.

Arriaga, L., Espinoza, J., Aguilar, C., Martínez, E., Gómez, L., 2000. Regiones terrestres prioritarias de México. Comisión Nacional para el Conocimiento y uso de la Biodiversidad. México.

Arroyo-Rodríguez, V., Fahrig, L., Tabarelli, M., Watling, J.I., Tischendorf, L., Benchimol, M., Cazetta, E., Faria, D., Leal, I.R., Melo, F.P.L., Morante-Filho, J.C., Santos, B.A., Arasa-Gisbert, R., Arce-Peña, N., Cervantes-López, M.J., Cudney-Valenzuela, S., Galán-Acedo, C., San-José, M., Vieira, I.C.G., Slik, J.W.F., Nowakowski, A.J., Tscharntke, T., 2020. Designing optimal human-modified landscapes for forest biodiversity conservation. Ecol. Lett. 23, 1404–1420. https://doi.org/10.1111/ele.13535.

Avitabile, V., Herold, M., Heuvelink, G.B.M., Lewis, S.L., Phillips, O.L., Asner, G.P., Armston, J., Ashton, P.S., Banin, L., Bayol, N., Berry, N.J., Boeckx, P., de Jong, B.H.J., DeVries, B., Girardin, C.A.J., Kearsley, E., Lindsell, J.A., Lopez-Gonzalez, G., Lucas, R., Malhi, Y., Morel, A., Mitchard, E.T.A., Nagy, L., Qie, L., Quinones, M.J., Ryan, C.M., Ferry, S.J.W., Sunderland, T., Laurin, G.V., Gatti, R.C., Valentini, R., Verbeeck, H., Wijaya, A., Willcock, S., 2016. An integrated pan-tropical biomass map using multiple reference datasets. Global Change Biol. 22, 1406–1420. https://doi.org/10.1111/gcb.13139.

Baccini, A., Walker, W., Carvalho, L., Farina, M., Sulla-Menashe, D., Houghton, R.A., 2017. Tropical forests are a net carbon source based on aboveground measurements of gain and loss. Science 358, 230–234. https://doi.org/10.1126/science.aam5962.

Bakhoum, N., Fall, D., Fall, F., Diouf, F., Hirsch, A.M., Balachandar, D., Diouf, D., 2018. *Senegalia senegal* (synonym: *Acacia senegal*), its importance to sub-Saharan Africa, and its relationship with a wide range of symbiotic soil microorganisms. South Afr. J. Bot. 119, 362–368. https://doi.org/10.1016/j.sajb.2018.10.007.

Balderas Torres, A., Lovett, J.C., 2013. Using basal area to estimate aboveground carbon stocks in forests: La Primavera Biosphere's Reserve, Mexico. Forestry 86, 267–281. https://doi.org/10.1093/forestry/cps084.

Banda, K., Delgado-Salinas, A., Dexter, K.G., Linares-Palomino, R., Oliveira-Filho, A., Prado, D., Pullan, M., Quintana, C., Riina, R., Rodríguez, M.G.M., Weintritt, J., Acevedo-Rodríguez, P., Adarve, J., Álvarez, E., Aranguren, B.A., Arteaga, J.C., Aymard, G., Castaño, A., Ceballos-Mago, N., Cogollo, Á., Cuadros, H., Delgado, F., Devia, W., Dueñas, H., Fajardo, L., Fernández, Á., Fernández, M.Á., Franklin, J., Freid, E.H., Galetti, L.A., Gonto, R., González-M, R., Graveson, R., Helmer, E.H., Idárraga, Á., López, R., Marcano-Vega, H., Martínez, O.G., Maturo, H.M., McDonald, M., McLaren, K., Melo, O., Mijares, F., Mogni, V., Molina, D., Del Pilar Moreno, N., Nassar, J.M., Neves, D.M., Oakley, L.J., Oatham, M., Olvera-Luna, A.R., Pezzini, F.F., Dominguez, O.J.R., Ríos, M.E., Rivera, O., Rodríguez, N., Rojas, A., Särkinen, T., Sánchez, R., Smith, M., Vargas, C., Villanueva, B., Pennington, R.T., 2016. Plant diversity patterns in neotropical dry forests and their conservation implications. Science 353, 1383–1387. https://doi.org/10.1126/science.aaf5080.

Bastin, J.-F., Finegold, Y., Garcia, C., Mollicone, D., Rezende, M., Routh, D., Zohner, C.M., Crowther, T.W., 2019. The global tree restoration potential. Science 365, 76–79. https://doi.org/10.1126/science.aax0848.

Becknell, J.M., Powers, J.S., 2014. Stand age and soils as drivers of plant functional traits and aboveground biomass in secondary tropical dry forest. Can. J. For. Res. 44, 604–613. https://doi.org/10.1139/cjfr-2013-0331.

Brown, S., 1997. Estimating Biomass and Biomass Change of Tropical Forests: a Primer. Food and Agriculture Organization of the United Nations, Rome.

Cairns, M.A., Haggerty, P.K., Alvarez, R., Olmsted, I., 2000. Tropical Mexico's recent land-use change: a region's contribution to the global carbon cycle. Ecol. Appl. 10, 1426–1441.

Castellanos Barliza, J., Blanco Rodríguez, O., León Peláez, J.D., Chávez, L.F., 2019. Planted forests for open coal mine spoils rehabilitation in Colombian drylands: contributions of fine litterfall through an age chronosequence. Ecol. Eng. 138, 180–187. https://doi.org/10.1016/j.ecoleng.2019.07.018.

Castellanos Barliza, J., León Peláez, J.D., Campo, J., 2018. Recovery of biogeochemical processes in restored tropical dry forest on a coal mine spoil in La Guajira, Colombia. Land Degrad. Dev. 29, 3174–3183. https://doi.org/10.1002/ldr.3069.

Chaturvedi, R.K., Pandey, S.K., Rahul, B., Shivam, S., Raghubanshi, A.S., 2018. Woody species in tropical dry forest exhibit plasticity in physiological traits in response to variations in soil properties. MOJ Ecol. Environ. Sci. 3, 364–367. https://doi.org/10.15406/mojes.2018.03.00114.

Chaturvedi, R.K., Raghubanshi, A.S., Singh, J.S., 2011. Carbon density and accumulation in woody species of tropical dry forest in India. For. Ecol. Manag. 262, 1576–1588. https://doi.org/10.1016/j.foreco.2011.07.006.

Chave, J., Andalo, C., Brown, S., Cairns, M.A., Chambers, J.Q., Eamus, D., Fölster, H., Fromard, F., Higuchi, N., Kira, T., Lescure, J.-P., Nelson, B.W., Ogawa, H., Puig, H., Riéra, B., Yamakura, T., 2005. Tree allometry and improved estimation of carbon stocks and balance in tropical forests. Oecologia 145, 87–99. https://doi.org/10.1007/s00442-005-0100-x.

Chave, J., Coomes, D., Jansen, S., Lewis, S.L., Swenson, N.G., Zanne, A.E., 2009. Towards a worldwide wood economics spectrum. Ecol. Lett. 12, 351–366. https://doi.org/10.1111/j.1461-0248.2009.01285.x.

Chazdon, R.L., 2014. Second Growth: the Promise of Tropical Forest Regeneration in an Age of Deforestation. University of Chicago Press, Chicago.

Chazdon, R.L., Broadbent, E.N., Rozendaal, D.M.A., Bongers, F., Zambrano, A.M.A., Aide, T.M., Balvanera, P., Becknell, J.M., Boukili, V., Brancalion, P.H.S., Craven, D., Almeida-Cortez, J.S., Cabral, G.A.L., de Jong, B., Denslow, J.S., Dent, D.H., DeWalt, S.J., Dupuy, J.M., Durán, S.M., Espírito-Santo, M.M., Fandino, M.C., César, R.G., Hall, J.S., Hernández-Stefanoni, J.L., Jakovac, C.C., Junqueira, A.B., Kennard, D., Letcher, S.G., Lohbeck, M., Martínez-Ramos, M., Massoca, P., Meave, J.A., Mesquita, R., Mora, F., Muñoz, R., Muscarella, R., Nunes, Y.R.F., Ochoa-Gaona, S., Orihuela-Belmonte, E., Peña-Claros, M., Pérez-García, E.A., Piotto, D., Powers, J.S., Rodríguez-Velazquez, J., Romero-Pérez, I.E., Ruíz, J., Saldarriaga, J.G., Sanchez-Azofeifa, A., Schwartz, N.B., Steininger, M.K., Swenson, N.G., Uriarte, M., van Breugel, M., van der Wal, H., Veloso, M.D.M., Vester, H., Vieira, I.C.G., Bentos, T.V., Williamson, G.B., Poorter, L., 2016. Carbon sequestration potential of second-growth forest regeneration in the Latin American tropics. Sci. Adv. 2, e1501639. https://doi.org/10.1126/sciadv.1501639.

Chazdon, R.L., Letcher, S.G., van Breugel, M., Martínez-Ramos, M., Bongers, F., Finegan, B., 2007. Rates of change in tree communities of secondary Neotropical forests following major disturbances. Philos. Trans. R. Soc. B Biol. Sci. 362, 273–289. https://doi.org/10.1098/rstb.2006.1990.

Corona-Núñez, R.O., Campo, J., Williams, M., 2018. Aboveground carbon storage in tropical dry forest plots in Oaxaca, Mexico. For. Ecol. Manag. 409, 202–214. https://doi.org/10.1016/j.foreco.2017.11.014.

Cuervo-Robayo, A.P., Téllez-Valdés, O., Gómez-Albores, M.A., Venegas-Barrera, C.S., Manjarrez, J., Martínez-Meyer, E., 2014. An update of high-resolution monthly climate surfaces for Mexico. Int. J. Climatol. 34, 2427–2437. https://doi.org/10.1002/joc.3848.

Dane, J., Topp, C., Campbell, G., 2002. Methods of Soil Analysis: Part 4-Physical Methods. Soil Science Society of America, Inc Madison, WIS, USA.

Dirzo, R., 2011. Seasonally Dry Tropical Forests: Ecology and Conservation. Island Press, Washington.

Dupuy, J.M., Hernández-Stefanoni, J.L., Hernández-Juárez, R.A., Tetetla-Rangel, E., López-Martínez, J.O., Leyequién-Abarca, E., Tun-Dzul, F.J., May-Pat, F., 2012. Patterns and correlates of tropical dry forest structure and composition in a highly replicated chronosequence in Yucatan, Mexico: tropical dry forest structure and composition. Biotropica 44, 151–162. https://doi.org/10.1111/j.1744-7429.2011.00783.x.

FAO, 2011. RED++ Reducción de las emisiones derivadas de la deforestación y la degradación de los bosques. http://www.fao.org/redd/overview/es/. (Accessed 15 September 2021).

García, E., 2004. Modificaciones al sistema de clasificación climática de Köppen. Universidad Nacional Autónoma de México, México.

Gavito, M.E., Sandoval-Pérez, A.L., del Castillo, K., Cohen-Salgado, D., Colarte-Avilés, M.E., Mora, F., Santibáñez-Rentería, A., Siddique, I., Urquijo-Ramos, C., 2018. Resilience of soil nutrient availability and organic matter decomposition to hurricane impact in a tropical dry forest ecosystem. For. Ecol. Manag. 426, 81–90. https://doi.org/10.1016/j.foreco.2017.08.041.

González Cásares, M., Yerena-Yamallel, J.I., Pompa García, M., 2017. Measuring temporal wood density variation improves carbon capture estimates in Mexican forests. Acta Univ. 26, 11–14. https://doi.org/10.15174/au.2016.1206.

Griffin, E., Hoyle, F.C., Murphy, D.V., 2013. What is soil organic carbon? https://www.agric.wa.gov.au/measuring-and-assessing-soils/what-soil-organic-carbon. (Accessed 15 September 2021) accessed.

Griscom, H.P., 2020. The long-term effects of active management and landscape characteristics on carbon accumulation and diversity within a seasonal dry tropical ecosystem. For. Ecol. Manag. 473, 118296. https://doi.org/10.1016/j.foreco.2020.118296.

Guevara, S., Laborde, J., Sánchez, G., 1998. Are isolated remnant trees in pastures a fragmented canopy? Selbyana 19, 34–43.

Harja, D., Rahayu, S., Pambudi, S., 2010. Tree functional attributes and ecological database. http://db.worldagroforestry.org//wd. (Accessed 15 September 2021).

Heilmayr, R., Echeverría, C., Lambin, E.F., 2020. Impacts of Chilean forest subsidies on forest cover, carbon and biodiversity. Nat. Sustain. 3, 701–709. https://doi.org/10.1038/s41893-020-0547-0.

Hernández-Stefanoni, J.L., Dupuy, J.M., Tun-Dzul, F., May-Pat, F., 2011. Influence of landscape structure and stand age on species density and biomass of a tropical dry forest across spatial scales. Landsc. Ecol. 26, 355–370. https://doi.org/10.1007/s10980-010-9561-3.

Ibrahim, M., Chacón, M., Cuartas, C., Naranjo, J., Ponce, G., Vega, P., Casasola, F., Rojas, J., 2006. Almacenamiento de carbono en el suelo y la biomasa arbórea en sistemas de usos de la tierra en paisajes ganaderos de Colombia, Costa Rica y Nicaragua. Agroforestería En Las Américas 45, 27–36.

INEGI, 2009. Instituto nacional de Estadística y geografía. http://www.inegi.org.mx/. (Accessed 15 September 2021).

IPBES, 2019. In: Brondizio, E.S., Settele, J., Díaz, S., Ngo, H.T. (Eds.), Global Assessment Report on Biodiversity and Ecosystem Services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. IPBES, Bonn, Germany.

Jaramillo, V.J., Kauffman, J.B., Rentería-Rodríguez, L., Cummings, D.L., Ellingson, L.J., 2003. Biomass, carbon, and nitrogen pools in Mexican tropical dry forest landscapes. Ecosystems 6, 609–629. https://doi.org/10.1007/s10021-002-0195-4.

Kalacska, M., Sanchez-Azofeifa, G.A., Calvo-Alvarado, J.C., Quesada, M., Rivard, B., Janzen, D.H., 2004. Species composition, similarity and diversity in three successional stages of a seasonally dry tropical forest. For. Ecol. Manag. 200, 227–247. https://doi.org/10.1016/j.foreco.2004.07.001.

Laborde, J., 2018. Explotación de oro a cielo abierto en Veracruz y sus consecuencias potenciales sobre el capital natural veracruzano. In: En Defensa del Patrimonio Natural y Cultural de Veracruz: el caso del proyecto de la mina La Paila, Municipio de Alto Lucero, Veracruz. SEDEMA, pp. 43–68.

López-Barrera, F., Manson, R.H., Landgrave, R., 2014. Identifying deforestation attractors and patterns of fragmentation for seasonally dry tropical forest in central Veracruz, Mexico. Land Use Pol. 41, 274–283. https://doi.org/10.1016/j.landusepol.2014.06.004.

Melo, F.P.L., Arroyo-Rodríguez, V., Fahrig, L., Martínez-Ramos, M., Tabarelli, M., 2013. On the hope for biodiversity-friendly tropical landscapes. Trends Ecol. Evol. 28, 462–468. https://doi.org/10.1016/j.tree.2013.01.001.

Mesa-Sierra, N., 2020. Capital natural del trópico seco de Veracruz. Dissertation, Instituto de Ecología, Mexico.

Mesa-Sierra, N., Escobar, F., Laborde, J., 2020a. Appraising forest diversity in the seasonally dry tropical region of the Gulf of Mexico. Rev. Mex. Biodivers. 91, e913175. https://doi.org/10.22201/ib.20078706e.2020.91.3175.

Mesa-Sierra, N., Laborde, J., 2017. Insights for the conservation of native tree species gleaned from the advance regeneration community in a seasonally dry tropical landscape. Trop. Conserv. Sci. 10, 1–15. https://doi.org/10.1177/1940082917714228.

Mesa-Sierra, N., Laborde, J., Escobar, F., 2020b. Seasonally dry tropical forests of the Gulf of Mexico: a degraded landscape undergoing homogenization or a promising, resilient reservoir? Acta Oecol. 106, 103583. https://doi.org/10.1016/j.actao.2020.103583.

Midgley, G.F., 2012. Biodiversity and ecosystem function. Science 335, 174–175.

Ordóñez Díaz, J.A.B., Galicia Naranjo, A., Venegas Mancera, N.J., Tejeda, T.H., de Jesús Ordóñez Díaz, M., Dávalos-Sotelo, R., 2015. Densidad de las maderas mexicanas por tipo de vegetación con base en la clasificación de J. Rzedowski: compilación. Madera Bosques 21, 77–216.

Pennington, R.T., Lavin, M., Oliveira-Filho, A., 2009. Woody plant diversity, evolution, and ecology in the tropics: perspectives from seasonally dry tropical forests. Annu. Rev. Ecol. Evol. Syst. 40, 437–457. https://doi.org/10.1146/annurev.ecolsys.110308.120327.

Petrokofsky, G., Kanamaru, H., Achard, F., Goetz, S.J., Joosten, H., Holmgren, P., Lehtonen, A., Menton, M.C.S., Pullin, A.S., Wattenbach, M., 2012. Comparison of methods for measuring and assessing carbon stocks and carbon stock changes in terrestrial carbon pools. How do the accuracy and precision of current methods compare? A systematic review protocol. Environ. Evid. 1, 6. https://doi.org/10.1186/2047-2382-1-6.

Poorter, L., Bongers, F., Aide, T.M., Almeyda Zambrano, A.M., Balvanera, P., Becknell, J.M., Boukili, V., Brancalion, P.H.S., Broadbent, E.N., Chazdon, R.L., Craven, D., de Almeida-Cortez, J.S., Cabral, G.A.L., de Jong, B.H.J., Denslow, J.S., Dent, D.H., DeWalt, S.J., Dupuy, J.M., Durán, S.M., Espírito-Santo, M.M., Fandino, M.C., César, R.G., Hall, J.S., Hernandez-Stefanoni, J.L., Jakovac, C.C., Junqueira, A.B., Kennard, D., Letcher, S.G., Licona, J.-C., Lohbeck, M., Marín-Spiotta, E., Martínez-Ramos, M., Massoca, P., Meave, J.A., Mesquita, R., Mora, F., Muñoz, R., Muscarella, R., Nunes, Y.R.F., Ochoa-Gaona, S., de Oliveira, A.A., Orihuela-Belmonte, E., Peña-Claros, M., Pérez-García, E.A., Piotto, D., Powers, J.S., Rodríguez-Velázquez, J., Romero-Pérez, I.E., Ruíz, J., Saldarriaga, J.G., Sanchez-Azofeifa, A., Schwartz, N.B., Steininger, M.K., Swenson, N.G., Toledo, M., Uriarte, M., van Breugel, M., van der Wal, H., Veloso, M.D.M., Vester, H.F.M., Vicentini, A., Vieira, I.C.G., Bentos, T.V., Williamson, G.B., Rozendaal, D.M.A., 2016. Biomass resilience of Neotropical secondary forests. Nature 530, 211–214. https://doi.org/10.1038/nature16512.

Portillo-Quintero, C., Sanchez-Azofeifa, A., Calvo-Alvarado, J., Quesada, M., do Espirito Santo, M.M., 2015. The role of tropical dry forests for biodiversity, carbon and water conservation in the neotropics: lessons learned and opportunities for its sustainable management. Reg. Environ. Change 15, 1039–1049. https://doi.org/10.1007/s10113-014-0689-6.

Powers, J.S., Becknell, J.M., Irving, J., Pèrez-Aviles, D., 2009. Diversity and structure of regenerating tropical dry forests in Costa Rica: geographic patterns and environmental drivers. For. Ecol. Manag. 258, 959–970. https://doi.org/10.1016/j.foreco.2008.10.036.

Powers, J.S., Peréz-Aviles, D., 2013. Edaphic factors are a more important control on surface fine roots than stand age in secondary tropical dry forests. Biotropica 45, 1–9. https://doi.org/10.1111/j.1744-7429.2012.00881.x.

Powers, J.S., Tiffin, P., 2010. Plant functional type classifications in tropical dry forests in Costa Rica: leaf habit versus taxonomic approaches: leaf habit and functional traits of dry forest trees. Funct. Ecol. 24, 927–936. https://doi.org/10.1111/j.1365-2435.2010.01701.x.

Prado-Junior, J.A., Schiavini, I., Vale, V.S., Arantes, C.S., van der Sande, M.T., Lohbeck, M., Poorter, L., 2016. Conservative species drive biomass productivity in tropical dry forests. J. Ecol. 104, 817–827. https://doi.org/10.1111/1365-2745.12543.

R Development Core Team, 2019. R: a language and environment for statistical computing. Version 2.14.10. http://www.r-project.org. (Accessed 15 September 2021).

SARE, 2012. Sustainable agriculture research and education. Organic matter: what it is and why it's so important. https://www.sare.org/Learning-Center/Books/Building-Soils-for-Better-Crops-3rd-Edition/Text-Version/Organic-Matter-What-It-Is-and-Why-It-s-So-Important. (Accessed 15 September 2021).

Schmitt-Harsh, M., Evans, T.P., Castellanos, E., Randolph, J.C., 2012. Carbon stocks in coffee agroforests and mixed dry tropical forests in the western highlands of Guatemala. Agrofor. Syst. 86, 141–157. https://doi.org/10.1007/s10457-012-9549-x.

Soto-Navarro, C., Ravilious, C., Arnell, A., de Lamo, X., Harfoot, M., Hill, S.L.L., Wearn, O.R., Santoro, M., Bouvet, A., Mermoz, S., Le Toan, T., Xia, J., Liu, S., Yuan, W., Spawn, S.A., Gibbs, H.K., Ferrier, S., Harwood, T., Alkemade, R., Schipper, A.M., Schmidt-Traub, G., Strassburg, B., Miles, L., Burgess, N.D., Kapos, V., 2020. Mapping co-benefits for carbon storage and biodiversity to inform conservation policy and action. Philos. Trans. R. Soc. B Biol. Sci. 375, 20190128. https://doi.org/10.1098/rstb.2019.0128.

Sparks, D.L., Page, A., Helmke, P., Loeppert, R.H., 2020. Methods of Soil Analysis, Part 3: Chemical Methods. John Wiley & Sons, Madison.

Stoner, K.E., Sánchez-Azofeifa, G.A., 2009. Ecology and regeneration of tropical dry forests in the Americas: implications for management. For. Ecol. Manag. 258, 903–906. https://doi.org/10.1016/j.foreco.2009.05.019.

Travieso-Bello, A.C., Campos, A., 2006. Los componentes del paisaje. Entornos Veracruzanos: la Costa de La Mancha, pp. 245–280.

Williams-Linera, G., Lorea, F., 2009. Tree species diversity driven by environmental and anthropogenic factors in tropical dry forest fragments of central Veracruz, Mexico. Biodivers. Conserv 18, 3269–3293. https://doi.org/10.1007/s10531-009-9641-3.

WWF, 2020. In: Almond, R.E.A., Grooten, M., Petersen, T. (Eds.), Living Planet Report 2020 - Bending the Curve of Biodiversity Loss. WWF, Gland, Switzerland.

Zanne, A.E., Lopez-Gonzalez, G., Coomes, D., Ilic, J., Jansen, S., Lewis, S.L., Miller, R.B., Swenson, N.G., Wiemann, M.C., Chave, J., 2009. Data from: towards a worldwide wood economics spectrum. https://datadryad.org/stash/dataset/doi:10.5061/dryad.234. (Accessed 15 September 2021).