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Structure and Carbon Capture of a Temperate Mixed Forest across Altitudinal Gradients in Northern Mexico

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Abstract: Maximizing the ability of forests to capture carbon (C) from the atmosphere is critical to mitigate global warming. This is a daunting task as the warming climate is adversely affecting forests with increasing forest fires, pests, and a shift to tree species that can tolerate the newer climate conditions. A large (about 1 million hectares) mixed pine–oak forest in Chihuahua, Mexico, was characterized via 151 plots to determine its floristic diversity and biomass with respect to species, age (tree diameter), and at four altitudinal gradients equally distributed between 1850 and 2850 masl. Higher richness and diversity were found at the altitudinal gradient of 2101–2350 m with 36 species and a Shannon's index (H') of 2.95, and the lowest at 2601–2850 m with 17 species and H' of 2.37. The Sorensen Index showed a high similarity in species composition, with the highest values (71% to 79%) obtained for the 2351–2600 gradient. C storage of the mixed forest increased with altitude from 7.85 Mg C ha⁻¹ in the 1850–2100 m gradient to 14.82 Mg C ha⁻¹ in the 2601–2850 m gradient. C storage in oak decreased with altitude while C storage of pine increased. Viable strategies to maximize C storage under changing climate conditions are discussed, including social safeguards and sale of carbon credits.

Keywords: carbon storage; aboveground mass; importance value index; temperate forest; *Pinus* sp.; *Quercus* sp.



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1. Introduction

Forest ecosystems are one of the most effective means to sequester carbon (C) from the atmosphere [1–3] besides providing timber and important environmental services [3,4]. Among the environmental services, forests produce rain, stabilize soils, and provide habitat to wildlife [4–6]. Management of forests historically used for timber production requires the implementation of strategies that will increase their adaptability to the foreseen impacts of climate change [1,5,7,8]. The United Nations' goal, as stated in the Paris Agreement, was to limit global warming to 1.5 °C to 2.0 °C above pre-industrial levels, a goal that relies on the reduction of atmospheric CO₂ [3,9]. The sustainable management of forests aims to optimize the growth of trees and the resilience of forest ecosystems and, in this way, protect the wood resources while sequestering atmospheric CO₂ [4,10].

Forests, in terms of the number of trees and total biomass, are declining worldwide because of deforestation and degradation; however, many uncertainties remain about the repercussions of these changes on the global C budget and on global climate [7,9,11]. An equivalent unit, CO₂e expressed in tons, is a mechanism used in the C credit market [12]. As a result, studies of the various aspects of forest management have multiplied in the past years, in both number and in the broadening of their scope, in a quest to find better

and more effective ways to manage and protect forest ecosystems. In many cases, a final product consists of the integration of the data into a model that has capabilities to run diverse scenarios [11,13]. On a global scale, computer models can integrate information about forests collected via forest inventories and/or satellite data [14,15]. A limitation to the accuracy of global models is the lack or fragmentation of data for some world regions [13,16]. Scientists agree that more information at the country or regional level is needed to generate more realistic and accurate models [14]. C storage and C emissions are unique to tree species and age, type of soil, altitude, and slope, therefore these parameters vary between tropical, temperate, or boreal forests, as well as between natural and managed forests [5]. C storage variations with altitude are crucial in the context of global warming because of their association with temperature [10,17–20].

The quantitative assessment of forests is based on a variety of ecological metrics of biomes such as richness, abundance, and diversity. C captured by plants through photosynthesis is reported as net primary production, biomass accumulation, or aboveground net primary production [14,15,21]. Since each forest responds to anthropic and natural disturbances in a particular manner, results obtained for one forest do not necessarily apply to another forest [16].

Natural disturbances such as wildfires and insect outbreaks are particularly sensitive to the changing warming and drying conditions [10,22,23]. To protect a forest, its response to these disturbances needs to be predicted to distinguish them from the normal variability of the system under undisturbed conditions [23,24].

Temperate forests of northern Mexico are characterized by the dominance of species of the genus *Pinus* and *Quercus*, many of which are managed for timber production. The change in land use, overgrazing, pests, and forest fires cause disturbances in their distribution and composition [22,25–27]. A rate of deforestation of 0.25% was measured between 1976 and 2000 in temperate pine–oak forests of Mexico, second only to tropical forests in Mexico [28]. The potential of pine–oak and mixed pine–oak forests of northern Mexico to capture C has been the focus of several studies [17,21,26–32]. However, and despite these studies, the ecological information of pine–oak forests of northern Mexico remains fragmented in location and time. Also, integrating these results onto global models may have been further deterred by many of these results being published in Spanish. In this study, the structure, diversity, and C capture potential of the pine–oak forest ecosystem are reported in a comprehensive manner and by altitudinal gradients, information that can be used as a reference in global studies and in the management of other pine–oak and mixed pine–oak ecosystems such as in northern Mexico and the Sky Islands of Arizona and New Mexico (U.S.) [25,26,33].

The objectives of this study were to (1) determine the C capture potential of a representative temperate forest of northern Mexico and its variation according to altitudinal gradient, tree diameter, and dominant species, (2) determine its species diversity and richness according to commonly reported indices, and (3) make inferences about viable strategies to capture the most possible C in this forest.

2. Materials and Methods

2.1. Description of the Study Area

The study area comprises 1,026,109 ha of forested land in the Sierra Madre Occidental within the state of Chihuahua, Mexico (Figure 1), an area known to foresters as Unidad de Manejo Forestal San Juanito A.C. [34]. This area has been selected by the Mexican Forestry Commission (CONAFOR) as representative of the forests of northern Mexico and has been used as an experimental field to test management strategies for forest protection and wildfire prevention. The elevation of this area ranges from 1850 to 2850 m above sea level (masl). Within this area there are five mayor types of vegetation, pine forest, mixed forests (pine–oak, oak–pine), oak forest, and natural and induced grassland (Table S1 in Supplementary Material). There are also areas of rainfed agriculture. Also, a 139,903 ha

nature protected area, Papigochi, is a part of the study area. Lithosol is the predominant soil type, followed by Regosol [34].

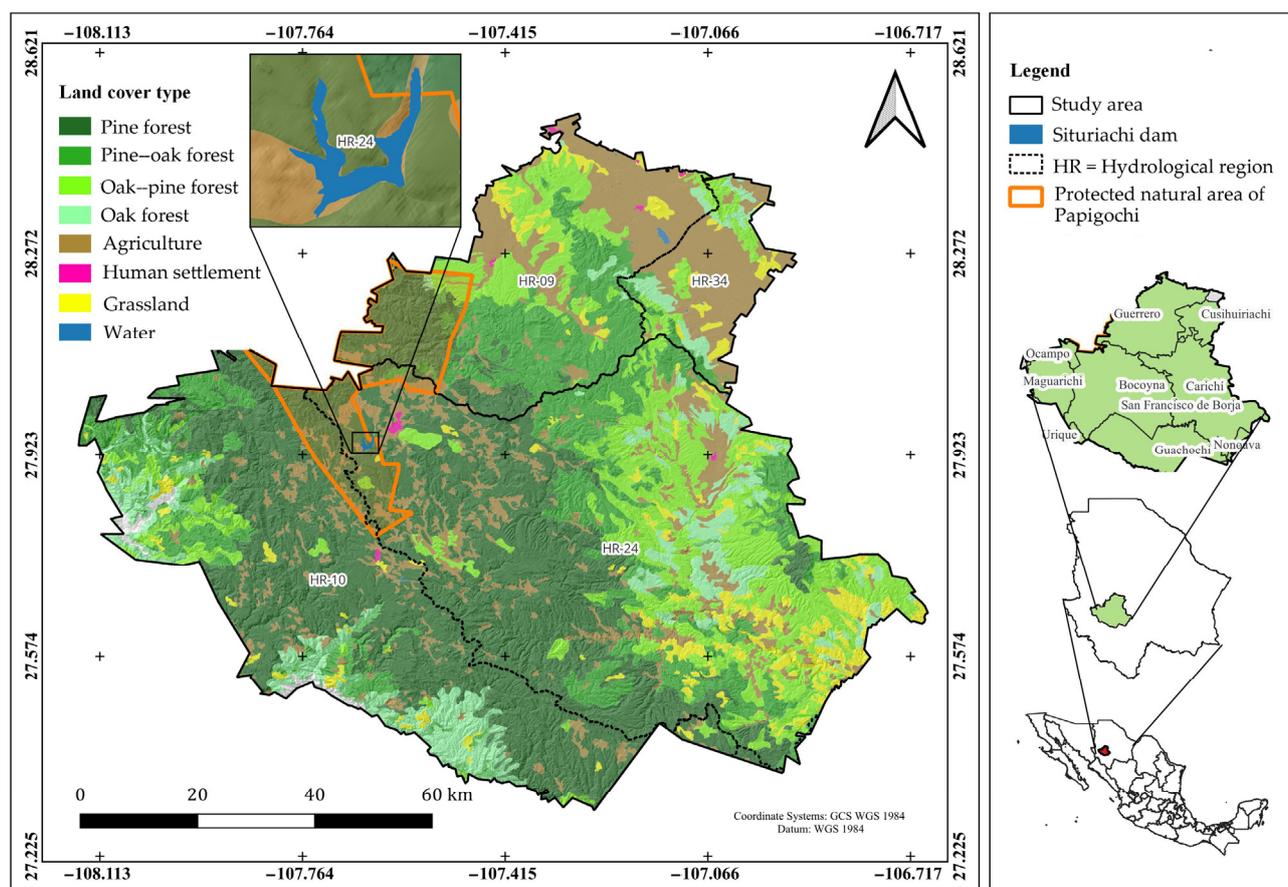


Figure 1. Study area showing the hydrological regions (RH), and the Situriachi Lake within the Natural Protected Area of Papigochi.

Hydrologically, the area comprises five hydrological basins (RH); two of them discharge into the Pacific Ocean, two of them into the Gulf of Mexico, and one into an endorheic basin in central Chihuahua. The area is crossed by numerous streams, a few of which are dammed to supply water for nearby communities and to help irrigate small-scale agriculture. One such reservoir, Situriachi, constructed in 2006, supplies water to the town of San Juanito (pop. 10,741). The climate is temperate sub-humid with an average annual temperature of 12.7 °C and average annual precipitation of 700 mm. The precipitation is of monsoon type during the months of July, August, and September [34]. Lower elevation areas are drier, with a predominance of *Quercus*.

The effects of climate change on ecosystems become reflected in the distribution and abundance of species [35], and also in the disappearance of species and populations [25,33,36]. Some species may modify their distribution to latitudes and altitudes different from where they are located [36]. However, changes in the climate could exceed the ability to migrate or survive in the new environmental conditions [21,35,36]. Disturbances affect more severely species growing in mountainous ecosystems since these are more sensitive to changes in climatic conditions [37,38].

2.2. Sampling Plots

The floristic diversity was determined using a database from Mexico's National Forest and Soil Inventory (2015–2020) that comprises a network of 151 plots distributed throughout the study area and placed at a 5 km distance between them, as shown in Figure 1 and

Table S1 in the Supplementary Material. Each plot is composed of four sampling parcels of 400 m² each, distributed within one hectare, which together make up a total area per plot of 1600 m² (Table 1). In each site, all the trees with a normal diameter and height equal to or greater than 7.5 cm were measured and registered.

Table 1. Number of plots in the study area according to altitudinal gradient.

Altitudinal Gradient, m	Number of Plots
1850–2100	19
2101–2350	64
2351–2600	61
2601–2850	7

With the data from the forest inventory and digital elevation model (DEM) using 250 m intervals between 1850 and 2850 m, four altitudinal gradients were obtained (Table 1 and Figure 2). Within each gradient, the species' richness and diversity were evaluated using each of Shannon's Index [39], Pielou's Equity (J), and Sorensen Index, applying the formulas listed in Table 2. To determine the significance of diversity variations between altitudinal gradient, a Hutcheson *t*-test was applied at $p < 0.05$ [40]. Structure was determined after grouping the trees within each gradient according to diameter, genus, and species. Lastly, the timber volume, biomass, and C storage were calculated for each of four altitudinal gradients, as described below (Section 2.3).

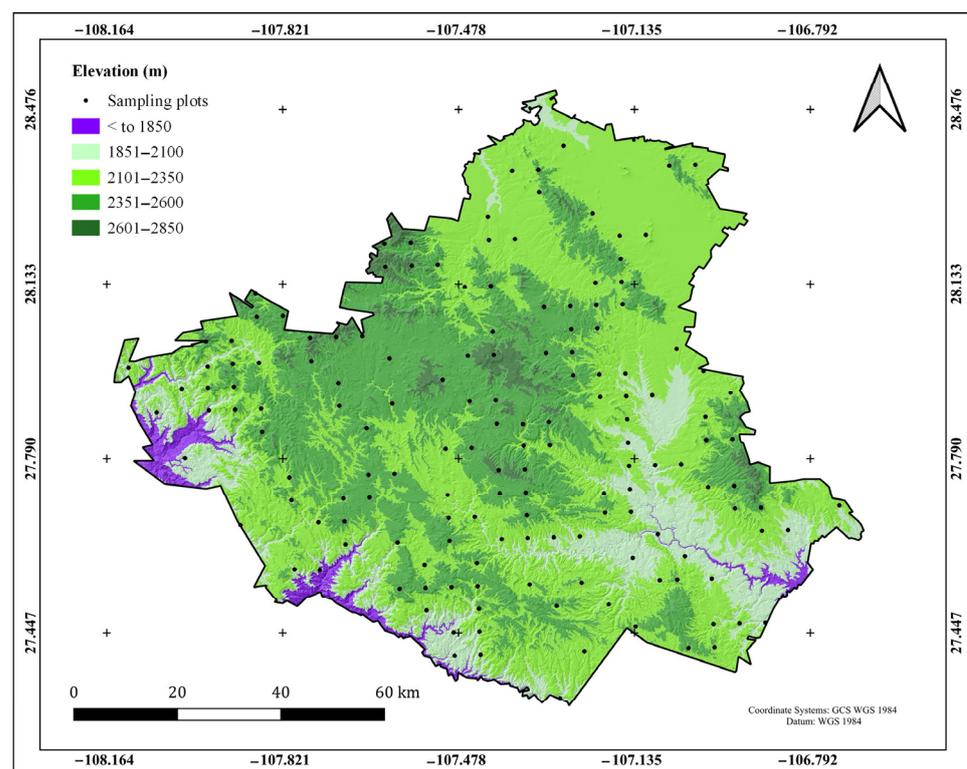


Figure 2. Spatial distribution of inventory plots and altitudinal gradients.

Table 2. Description and range of values of Shannon–Weiner Diversity Index (H'), Pielou's Equity, and Sorensen Index.

Name and Formula	Description of Terms	Range of Values
Shannon–Weiner Index $H' = - \sum_{i=1}^S P_i \times \ln(P_i)$	H' = Shannon–Weiner Index S = Total number of species P_i = proportion of individuals of species i	1–5
Pielou's Evenness Index $J = \frac{H'}{\ln(S)}$	H' : Shannon-Wiener Index S : Species richness	0–1
Sorensen Index $I_s = \frac{2c}{(a+b)}$	a : number of species community a b : number of species community b c : number of similar species in both communities	0–1
Hutchenson t -test $t = \frac{H'_1 - H'_2}{\sqrt{\text{var}H'_1 + \text{var}H'_2}}$	H'_1 : Diversity of sample 1 H'_2 : Diversity of sample 2 var: variance	Significant or not significant at $p < 0.05$

2.3. Estimation of Volume, Biomass, and C Content

The total volume of a tree, including bark, was estimated for each plot using Equation (1), whose constants are listed in Table 3.

$$V_{ta_{cc}} = b_0 \times D^{b_1} \times h^{b_2} + b_3 \times D^2 \tag{1}$$

where:

- $V_{ta_{cc}}$ = total volume of the tree;
- D = diameter of the tree i at breast height (cm);
- h = height of tree i (m);
- b_i = regionally obtained coefficients listed in Table 3.

Table 3. Coefficients utilized in the determination of tree volume according to Equation (1) [41].

Tree Species	b_0	b_1	b_2	b_3	Density g cm^{-3}
<i>Abies durangensis</i> Martínez	0.000066	1.788316	1.055175	0.000013	0.38
<i>Arbutus tessellata</i> P.D.Sørensen	0.000142	1.483474	1.121788	0.000116	0.75
<i>Arbutus xalapensis</i> Kunth	0.000142	1.483474	1.121788	0.000116	0.75
<i>Cupressus arizonica</i> Greene	0.000062	1.882421	0.946587	0.000010	0.45
<i>Cupressus lusitanica</i> Miller	0.000062	1.882421	0.946587	0.000010	0.45
<i>Fraxinus uhdei</i> (Wenz.) Lingelsh	0.000101	1.687575	1.033752	0.000050	0.46
<i>Juniperus deppeana</i> Steud.	0.000101	1.687575	1.033752	0.000050	0.46
<i>Juniperus flaccida</i> Schldtl.	0.000101	1.687575	1.033752	0.000050	0.46
<i>Juniperus monosperma</i> Engelman	0.000101	1.687575	1.033752	0.000050	0.46
<i>Pinus arizonica</i> Engelm	0.000027	2.120149	0.969354	0.000136	0.43
<i>Pinus strobiformis</i> Engelman	0.000177	1.398093	1.220451	0.000085	0.37
<i>Pinus cembroides</i> Zucc.	0.000122	1.620204	1.067986	0.000049	0.37
<i>Pinus durangensis</i> Martínez	0.00002	2.154422	1.024150	0.000100	0.47
<i>Pinus engelmannii</i> Carr.	0.000011	2.244813	1.116209	0.000149	0.43
<i>Pinus herrerae</i> Martínez	0.000122	1.620204	1.067986	0.000049	0.43
<i>Pinus leiophylla</i> var. <i>chihuahuana</i>	0.000056	1.847202	1.034216	0.000079	0.43
<i>Pinus lumholtzii</i> B.L. Rob. & Fernald	0.000122	1.620204	1.067986	0.000049	0.43
<i>Pinus oocarpa</i> Shiede	0.000056	1.847202	1.034216	0.000079	0.43
<i>Pinus teocote</i> Schiede ex Schldtl.	0.000056	1.847202	1.034216	0.000079	0.45
<i>Populus tremuloides</i> Michx.	0.000132	1.454625	1.259012	0.000100	0.45

Table 3. Cont.

Tree Species	b_0	b_1	b_2	b_3	Density g cm^{-3}
<i>Pseudotsuga menziesii</i> (Mirb.) Franco	0.000062	1.882421	0.946587	0.000010	0.45
<i>Quercus arizonica</i> C.S. Sargent	0.000048	1.878022	0.996633	0.000149	0.61
<i>Quercus crassifolia</i> Bonpl.	0.000132	1.454625	1.259012	0.000100	0.45
<i>Quercus rugosa</i> Née	0.000038	1.818784	1.158475	0.000191	0.61

Note: The equation for *Quercus arizonica* Sarg. was applied to *Q. chihuahuensis* Trel., *Q. depressipes* Trel., *Q. durifolia* Seemen ex Loes., *Q. emoryi* Torr., *Q. fulva* Liebm., *Q. greggii* (A.DC.) Trel., *Q. grisea* Liebm., *Q. hypoleucoides* A.Camus, *Q. jonesii* Trel., *Q. laeta* Liebm., *Q. laurina* Bonpl., *Q. macvaughii* Spellenb., *Q. magnoliifolia* Née, *Q. oblonguifolia* Torr., *Q. potosina* Trel., *Q. sideroxyla* Bonpl., *Q. tarahumara* Spellenb., J.D.Bacon & Breedlove, and *Q. viminea* Trel., and a density of 0.61 g cm^{-3} [41–48].

The biomass was then obtained by multiplying the volume of the tree by the density of the wood for each species and by the number of individuals registered for that species (N ha^{-1}). Next, the amount of C was obtained by multiplying the biomass by the C concentration, a factor calculated for this specific forest following the LUCS model and values reported for regional species, resulting in a value of 0.50 [49]. The CO_2e stocks were estimated after multiplying the C content by a conversion factor of 3.67 [50].

3. Results

3.1. Tree Composition and Diversity across Altitudinal Gradients

3.1.1. Tree Composition

Within the altitudinal gradient 1850–2100 m, oak and oak–pine forests predominated, with 25 taxa identified. The predominant oak species included *Quercus grisea*, *Quercus laeta*, *Quercus emory*, *Quercus sideroxyla*, *Q. arizonica*, and *Q. Fulva*. The most common species of the genus *Pinus* were *P. leiophylla*, *P. lumholtzii*, *P. cembroides*, and in lesser amounts *P. engelmannii* and *P. arizonica*. Other species found were *Juniperus deppeana* and *Arbutus xalephensis*.

In the intermediate altitudinal gradients 2101–2350 m and 2351–2600 m, the forests were predominantly mixed oak–pine and mixed pine–oak, respectively, with 36 and 28 species. The predominant species in both of these gradients were *P. durangensis*, *P. cembroides*, *P. arizonica*, *P. strobiformis*, *P. engelmannii*, and *P. leiophylla* for pine, and oak species were *Q. grisea*, *Q. laeta*, *Q. rugosa*, *Q. sideroxyla*, *Q. oblonguifolia*, and *Q. arizonica*. The richness in the study area was slightly less than that of the close by pine–oak forest of Guadalupe y Calvo [51].

In the 2601–2850 m altitudinal gradient, pine forest predominated among the 17 taxa identified. The species more abundant were *P. arizonica* and *P. strobiformis* and in lesser amounts *P. durangensis*, *P. leiophylla*, and *P. lumholtzii*, and the oak species were drastically reduced. Oaks included species *Q. arizonica*, *Q. sideroxyla*, and *Q. grisea*. Other trees present in this gradient included *Populus tremuloides*, *Pseudotsuga menziesii*, *Abies durangensis*, *Juniperus deppeana*, and *Arbutus xalephensis* (Figure 3).

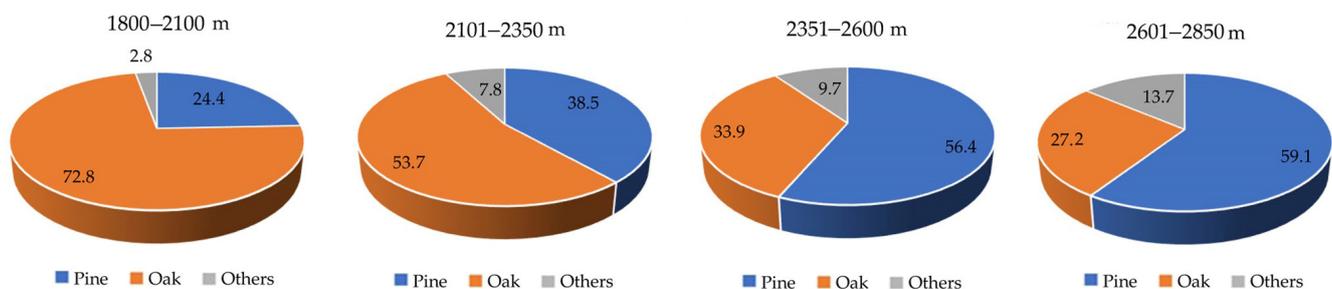


Figure 3. Percentage of trees by genus in the four altitudinal gradients.

3.1.2. Diversity

The higher values of species richness and diversity corresponded to the intermediate gradient 2101–2350 m with 36 species and a H' value of 2.95. On the other hand, the lowest values corresponded to the altitudinal gradient 2600–2850 m with 17 taxa and H' of 2.37. According to Margalef (1972) [52], all H' values found here correspond to medium diversity. The results agree with the hypothesis (mid-domain) that intermediate altitudes contain a larger number of species and that the number of species decreases at high elevations. This as a result of more species finding the environmental conditions of intermediate elevations as favorable [53,54]. Also, values above 0.80 in the Pielou Equity (J) obtained for these gradients agree on the high equity in relative abundance of species present (Table 4).

Table 4. Diversity indexes by altitudinal gradient.

Altitudinal Gradient, m	No. Sampled Trees	No. Species (S)	H'	Evenness (J')
1850–2100	861	26	2.75 b ¹	0.84
2101–2350	3829	36	2.95 a	0.82
2351–2600	4164	28	2.73 b	0.82
2601–2850	378	17	2.37 c	0.83

¹ Letters a, b, and c represent significative differences according to Hutchenson *t*-test.

3.1.3. Sorensen Index

The Sorensen Index reflected a high similarity in species richness among the lowest three altitudinal gradients, with values fluctuating between 0.71 and 0.79 (Table 5). The highest similitude values were obtained for the altitudinal gradient of 2351 to 2600 masl, likely because starting at an elevation of 2350 m, pine and pine-oak forests become predominant. The Sorensen value for the altitudinal range of 2600 to 2850 masl was different than the other gradients. (Figure 4 and Table 5).

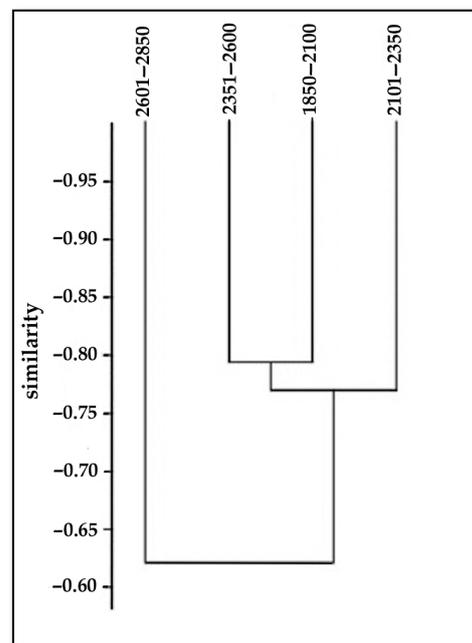


Figure 4. Dendrogram for Sorensen Index of similarity for the four altitudinal gradients.

Table 5. Sorensen Index by altitudinal range.

Altitudinal Gradient, m	1850–2100	2101–2350	2351–2600	2601–2850
1850–2100	1	0.78	0.79	0.61
2101–2350	0.78	1	0.75	0.52
2351–2600	0.79	0.75	1	0.71
2601–2850	0.61	0.52	0.71	1

3.2. Volumetric Inventory

The results ranged between $12.47 \text{ m}^3 \text{ ha}^{-1}$ and $83.98 \text{ m}^3 \text{ ha}^{-1}$. The aerial distribution of volume values is depicted in Figure 5 as well as land use types for comparison purposes. As shown in Figure 5, the volume is two to three times larger in the western part compared to the rest of the study area.

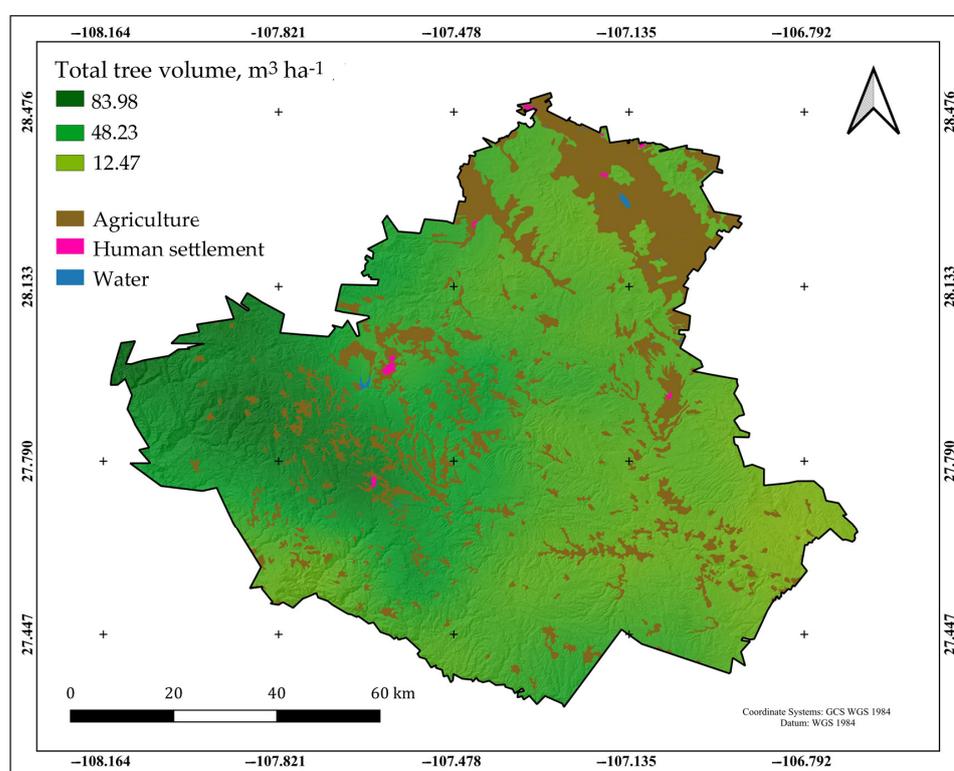


Figure 5. Distribution of volume values in $\text{m}^3 \text{ ha}^{-1}$ based on the 2015–2020 inventory.

3.3. C Storage in Aboveground Biomass

After the timber volume was obtained, the conversion of wood volume to C captured in aboveground biomass was carried out according to the conversion factors listed in Table 3. Once the amount of C captured was grouped according to altitudinal gradient, the results showed an increase of C storage with increasing altitude, from $7.85 \text{ Mg C ha}^{-1}$ to $14.82 \text{ Mg C ha}^{-1}$. The smaller values of C storage fluctuated between $0.93 \text{ Mg C ha}^{-1}$ and $2.04 \text{ Mg C ha}^{-1}$ and the highest values between $21.03 \text{ Mg C ha}^{-1}$ and $40.87 \text{ Mg C ha}^{-1}$. Yet, 83% of the study area was comprised between 2101 m and 2600 m elevation; therefore, at this altitudinal gradient most of the C storage occurred, amounting to $7,594,672 \text{ Mg C}$ (Table 6).

Table 6. C storage in Mg ha^{-1} and equivalent CO_2 according to elevation after 152 inventoried plots, each plot occupying a surface area of 1600 m^2 .

No. of Plots	Altitudinal Gradient, m	Minimum (Mg C ha^{-1})	Maximum (Mg C ha^{-1})	C Average (Mg C ha^{-1})	Area (ha)	Total (Mg C) per Gradient	MgCO_2e
19	1850–2100	0.99	21.03	7.85	98,355.98	745,983	2,737,759
64	2101–2350	1.50	31.32	9.35	361,111.81	3,377,069	12,393,845
61	2351–2600	0.93	40.87	14.33	294,245.79	4,217,602	15,478,600
7	2601–2850	2.04	35.90	14.82	33,180.56	491,844	1,805,067

The highest C capture in the higher altitudinal gradient coincides with that recorded by Álvarez et al., 2013 [55]. The differences in C storage by altitudinal gradient may be due to the structure and floristic composition of the plant communities [56]; for this region the highest C sequestration values may be due to the predominance of species of the genus *Pinus* that are managed for timber production, whereas at lower elevations there are more trees of genus *Quercus* and the species of *Pinus* present (Figure 6), such as *Pinus cembroides* and *Pinus leiophylla*, grow at a slower rate and result in a less biomass production [34].

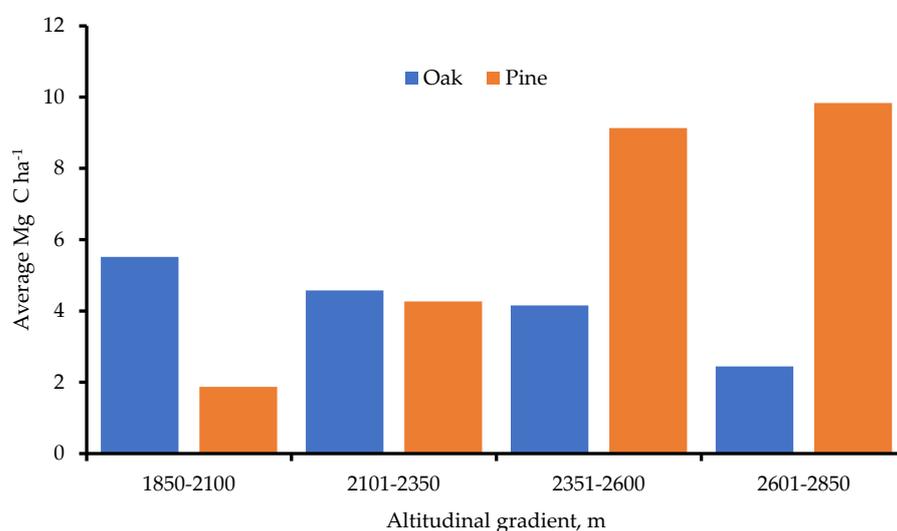


Figure 6. Average C capture according to altitudinal gradient for pine and oak.

The resulting C capture value up to $14.82 \text{ Mg C ha}^{-1}$ (Table 6), is low compared to values reported for other forests of northern Mexico: $26.87 \text{ Mg C ha}^{-1}$ [57], $36.42 \text{ Mg C ha}^{-1}$ [58], and $66.42 \text{ Mg C ha}^{-1}$ [59] in Durango, and 37 Mg C ha^{-1} in Nuevo Leon [60]. In other forests of Chihuahua, C storage is reported as $45.20 \text{ Mg C ha}^{-1}$ for a *Pseudotsuga menziesii* forest [61] and $46.71 \text{ Mg C ha}^{-1}$ for a temperate mixed pine–oak forest [62], while CONAFOR [63] obtained 6.3 to $16.5 \text{ Mg C ha}^{-1}$ and 16.5 to $28.2 \text{ Mg C ha}^{-1}$ using algorithms.

The differences in C storage in the above studies may result from differences in the methodology followed, species and age of trees, as well as other factors such as climate and type of soil [64]. The results showed that the annual timber growth in the study area can be up to $1.49 \text{ m}^3 \text{ ha}^{-1} \text{ year}^{-1}$ [17], whereas for the nearby forest of Guadalupe y Calvo Chihuahua values of up to $3 \text{ m}^3 \text{ ha}^{-1} \text{ year}^{-1}$ were found [65], while Nuevo Leon reported an annual timber growth of $2 \text{ m}^3 \text{ ha}^{-1} \text{ year}^{-1}$ [60]. The species richness and C storage values are likely higher, since neither individuals smaller than 7.5 cm in diameter nor the understory were considered in this study. In this regard, a study in a temperate forest in Durango found that 5% of the total C was stored in shrubs, herbaceous plants, leaf litter and necromass [59].

3.4. C Capture and Structure by Altitudinal Gradient

The diametric structure in all four altitudinal gradients shows an inverted J or Liocurt curve which corresponds to irregular growth, indicating a forest that is undergoing regeneration and changes in the mature individuals [66–69]. This same trend is observed in structure by genus (Tables 7 and 8) in all diameters below 60 cm. (Figure 7). In general, foresters recommend maintaining a natural regeneration that would allow different diameters as a measure of forest protection as well as sustainable growth [59,70].

Table 7. C storage by pine trees according to diameter (cm) and altitude (masl), in Mg ha⁻¹.

Altitude	1850–2100 m		2101–2350 m		2351–2600		2601–2850	
Diameter, cm	Sampled Trees	C Storage Mg ha ⁻¹	Sampled Trees	C Storage Mg ha ⁻¹	Sampled Trees	C Storage Mg ha ⁻¹	Sampled Trees	C Storage Mg ha ⁻¹
10	45	0.07	352	0.18	464	0.25	37	0.22
15	67	0.26	513	0.53	786	0.93	52	0.65
20	44	0.36	289	0.68	498	1.42	31	0.86
25	26	0.39	153	0.65	269	1.47	26	1.29
30	14	0.34	83	0.66	150	1.38	17	1.70
35	5	0.22	43	0.51	91	1.29	14	1.58
40	4	0.22	23	0.42	56	1.15	10	1.79
45	--	--	10	0.28	22	0.60	4	1.07
50	--	--	8	0.25	7	0.31	3	0.68
55	--	--	2	0.09	4	0.20	--	--
60	--	--	--	--	2	0.14	--	--
Total	205	1.87	1476	4.27	2349	9.13	194	9.83

-- no record was found.

Table 8. C storage by oak trees according to diameter (cm) and altitude (masl), in Mg ha⁻¹.

Altitude	1850–2100 m		2101–2350 m		2351–2600 m		2601–2850 m	
Diameter, cm	Sampled Trees	C Storage Mg ha ⁻¹	Sampled trees	C Storage Mg ha ⁻¹	Sampled Trees	C Storage Mg ha ⁻¹	Sampled Trees	C Storage Mg ha ⁻¹
10	181	0.43	581	0.39	392	0.28	17	0.11
15	244	1.21	856	1.23	527	0.76	41	0.63
20	104	1.12	360	1.05	219	0.66	15	0.42
25	34	0.65	156	0.83	131	0.67	8	0.46
30	29	0.74	50	0.43	69	0.56	5	0.44
35	12	0.64	26	0.27	38	0.45	3	0.38
40	3	0.21	11	0.17	15	0.27	--	--
45	5	0.28	3	0.05	7	0.15	--	--
50	1	0.10	5	0.14	6	0.17	--	--
55	1	0.15	3	0.11	6	0.19	--	--
60	--	--	3	0.10	--	--	--	--
Total	614	5.52	2054	4.78	1410	4.16	89	2.45

-- no record.

The C captured in aboveground biomass in the lower altitudinal gradients (Figure 7a) was concentrated in the 15–30 cm diametric categories with an average percentage of 68%, while in the higher gradients (Figure 7b), 60% of C stored was accumulated in the 20–35 cm classes. In contrast, Rascón et al. (2022) [62] found that 48% of the C was stored in the 30–45 cm diametric categories in a mixed forest, which may be due to the fact that in that region the trees had higher diametric categories than those recorded in the present study. In this study, the highest C storage value for the lower two gradients corresponded to the 15 cm diametric category and in the 2351 to 2600 m gradient the highest C storage value was found in the 20 and 25 cm categories. In the highest elevation gradient, the highest value was recorded in the 30 cm category, following a pattern in which as the altitude increases the highest value of C storage is recorded in the next higher diametric category.

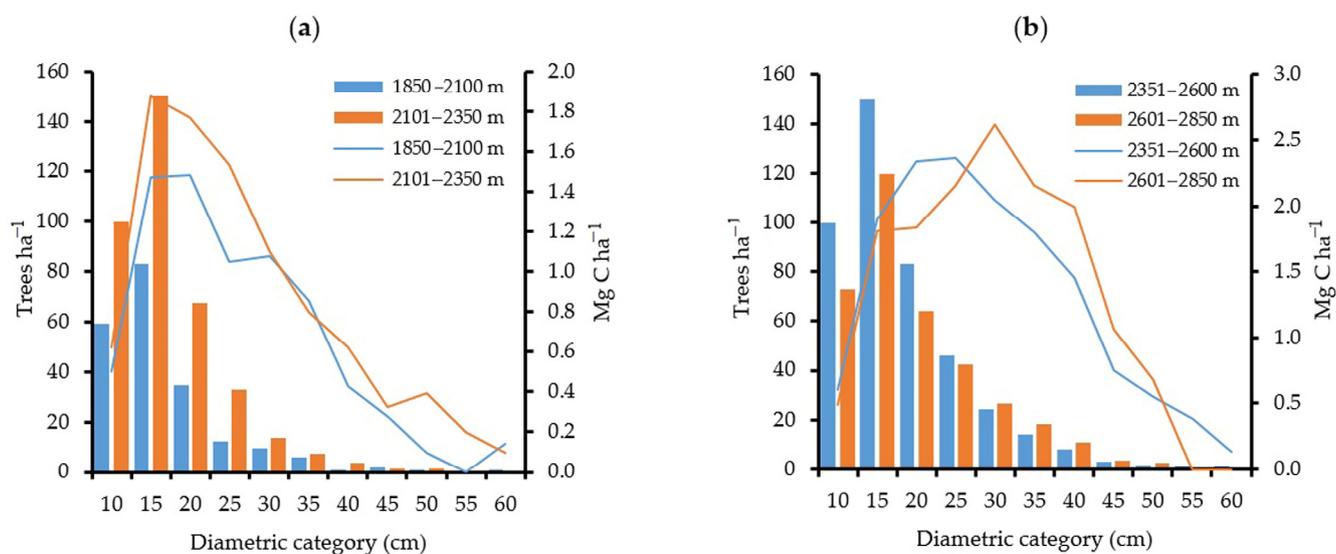


Figure 7. C stored by diameter class and altitudinal gradient (a) 1850 to 2350 masl, and (b) 2351 to 2850 masl.

4. Discussion

4.1. Carbon Storage by Altitudinal Gradient and by Diametric Classification

The *Pinus* genus concentrated the highest C capture in the first three gradients (1800–2600 m) in the diameter categories of 15–30 cm with a percentage ranging from 57 to 72% of the C stored. In contrast, in the 2601–2850 m gradient, C was concentrated in the diameter categories of 25 to 45 cm with 75% (Table 7), due to the fact that in this gradient the pine forests with larger diameters are concentrated. The *Quercus* genus behaved similarly to the *Pinus* genus, concentrating 64 to 80% of C in the same diameter classes (15 to 30 cm) (Table 8), in agreement with a study reporting that *Pinus spp.* and *Quercus spp.* have their greatest annual C storage increase in the diameter classes of 15 to 35 cm [59].

In *Pinus*, from the 2351 gradient onwards, C storage increases significantly with respect to the lower gradients, while in *Quercus* the highest storage rates occurred in the lower three gradients. It should be noted that in the 2601–2850 gradient the *Quercus* genus only presented individuals up to 35 cm diameter while the other gradients had trees with diameters up to 55 and 60 cm. This result validates that the ecological conditions in the lower elevation gradients favor the development and growth of the genus *Quercus* whereas the higher altitude areas are more suitable to produce biomass in the genus *Pinus* in this region.

Tables 7 and 8 show a maximum C storage value (9.83 Mg ha^{-1}) for pine was observed for the 2601–2850 masl altitude, and a distant second value at 2351–2600 masl. In contrast, the differences in C storage were not as marked for oak, with 5.52 and 4.78 Mg ha^{-1} for altitudes of 1850–2100 masl and 2101–2350 masl, respectively.

The results listed in Table 7 show that C storage is larger in a pine-dominated forest and smaller in an oak-dominated forest, and that this difference becomes noticeable for diameters greater than 17.6 cm. The expected effects of global warming on this ecosystem include changes in the distribution, abundance, and composition of species [33] and also in the disappearance of species [25,35,36]. Some species may modify their distribution to latitudes and altitudes different from the present location [37], whereas species that live in mountainous areas will be more severely affected since these are more sensitive to changes in climatic conditions [21,33,37,38]. A shift from pine to oak is an expected consequence of a warming climate [25,33] as oak is more tolerant to warmer and drier climates. Having precise values of the amount of C storage under the various conditions of the gradual replacement of pine by oak provides a way to calculate the changes that will take place regarding C storage. Compensation for this decrease in C storage can then be planned

by implementing strategies in forest management, possibly an increase in reforestation or allowing trees to grow to an optimal age.

The structure and diversity values obtained for this forest agree with values reported for northern Mexico and the Sky Islands of Arizona [29,33] but differ from results obtained for other mixed forests, e.g., India [20], that report an increase in diversity and tree density with altitude. With regard to C capture in mixed forests, studies agree that C capture increases with elevation. Besides this general pattern, specific values are difficult to compare as some studies include only the arboreal mass while others report all aboveground mass, some do not include certain tree diameters in their calculations, etc.

4.2. Forest Management Strategies to Increase C Storage

Strategies to increase C storage for timber production in intensively managed forests continue to be investigated, with a renewed focus on increasing the C storage and resilience of forest ecosystems [71,72]. These strategies vary widely in their scope. Some of the most utilized include genetic improvements [73], reforestation with genotypes that can successfully thrive and repel pest insects [74], mechanical preparation of soil, clearing of cut branches and competing vegetation [75], and finding the optimum depth at which saplings are to be planted [76,77].

An increase of 10% to 20% in C storage can be obtained by selecting genotypes capable of rapid growth [71]. Similarly, C storage increases after mechanical preparation of the forest soil. Although it first promotes decomposition of organic matter that releases CO₂ to the atmosphere, in the long-term, pine trees offset this loss and end up storing more C [78]. Reforestation and afforestation are also strategies utilized to sequester C, especially when using genotypes that are fully adapted to the region and are tolerant to, or repel, pest insects. Also, mixed stands reduce the risk of pathogens and pests when compared to monocultures [66]. A commonly utilized practice is pre-commercial thinning, which redistributes C among the different pools of biomass in soil, increasing the capacity of C capture in the long-term while reducing competition of trees for water, light, and nutrients [79]. With respect to this practice, Ruano et al. [80] report that the base area of pine trees grew by 20% after a 5-year period since pre-thinning was conducted. In intensively managed forests, a variable that affects C storage is the rotation period since this is an efficient way to manage C balance [63]. Therefore, forests of a uniform age sequester more C than those of various ages, and fertilization and nutrient supplements can increase the capacity of sequestration of C by forests [20,80–83].

Lastly, species richness, mixed stands, and the conservation of old forests increase productivity and have a higher potential to capture C [84–87]. The foreseen shifts in pine versus oak in a mixed pine–oak forest are crucial information in maximizing the amount of CO₂ sequestered by these forests. Precise measurements, continuing monitoring, and enforceable policies will be required, in addition to any of the practices described above that would likely result in an increase of C capture.

4.3. C Trade and Social Aspects

In an effort to reduce C in the atmosphere and as an incentive to meet regulatory guidelines in greenhouse emissions, countries have signed accords to implement programs towards reducing C emissions. A popular plan is the cap-and-trade program, where industries that release C above the limit buy the emission permit from another industry that emits less than the limit. According to this program, forest owners are paid for the removal of atmospheric C under a voluntary cap-and-trade program. Although C trade payments represent additional income to forest owners its implementation is far from simple and sometimes controversial [2]. Experts in this field recommend a more in-depth study on this issue and the quantification of the value of the forest overall [88]. To estimate its rentability, critical variables such as the costs of logging time, shifts in tree species to plant, and C prices need to be calculated in detail [89].

In Mexico, the participation of the forestry sector in the voluntary C market has been limited [12,90]. In 2016, the country began implementing its own emissions reduction initiative (IRE) and proposed that five Mexican states collaborate with California's Reducing Emissions from Deforestation and Forest Degradation (REDD+) program [91]. Once implemented, participation in these programs is expected to produce important environmental and social benefits to the regions adopting them.

The importance of stakeholders' participation in sustainable forest management is recognized by foresters and policy makers alike. However, this topic has received little attention in the published literature. Most reports consist of dispersed case studies that cannot be applied to other areas [92] as social aspects of management vary widely from region to region and are infused by cultural values that are unique to each locality [1,93,94]

The forest studied here supplies critical water for drinking and agriculture to about one million people downstream and helps prevent soil erosion and flooding during high intensity precipitation events that are common to the area [6]. Therefore, the stakeholders are not confined to nearby residents but include communities and productive sectors (farmers) directly downstream. Participatory policies, e.g., bottom-up forest management, land ownership (Mexican ejidos), illegal logging, illegal removal of firewood, and lack of environmental education programs have all been identified as social factors whose impact to the forest may be of consequence [6]; however, none have been either quantified or formally reported for this region [94].

5. Conclusions

The results of this study provide detailed information about the floristic diversity, structure, and C storage potential of the forest according to four different altitudinal gradients within 1850 to 2850 masl of a large (about one million hectares) mixed pine–oak forest in northern Mexico. C storage was calculated according to tree density values obtained for the trees growing in this area, therefore adding precision to the calculations. The average C storage potential was higher at 2600–2850 m elevation, where pines dominate. Among the biome at different altitudinal gradients, aboveground C storage varied between 0.93 Mg C ha⁻¹ and 40.87 C ha⁻¹, and a total of 4,217,602 Mg C capture was calculated for the study area. The C storage obtained was less than the values reported for other pine–oak forests in northern Mexico. Observed changes in pine–oak forest ecosystems with elevation translate to a gradual shift from pine to mixed pine–oak to oak and a decrease in aboveground C storage as the expected response to increasing temperatures. To compensate for the foreseen reduction in C storage, careful management of these forests will be needed, a task that may require the help of models able to integrate a variety of scenarios. Accurate and detailed data provided to modelers and climate scientists will ensure the best results. The variation of structure and C capture values with altitudinal gradient obtained in this study agreed with some mixed pine–oak forests (e.g., Southwest U.S.) but not to others (e.g., Himalaya), highlighting the use of own data as the best practice to study a forest.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/land13040461/s1>, Table S1: Sampled trees and average values of aboveground biomass and carbon capture according to four altitudinal gradients.

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