

## ORIGINAL RESEARCH ARTICLE

# Tree structure and composition of the secondary tropical deciduous forest in the Central Depression, Chiapas, Mexico

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## ABSTRACT

Tropical deciduous forest is highly threatened and transformed by agricultural activities in Chiapas; however, little is known about its successional dynamics and regeneration potential. The objective of this research was to evaluate the regenerative capacity of secondary forests through changes in richness, diversity, composition, and structure in a forest reserve in the Central Depression of Chiapas. Twenty sampling units (SU) of 1,000 m<sup>2</sup> were established in forests with different ages of abandonment (C10, C19, C35 and >C40, representing 10 years, 19 years, 35 years and 40 years, respectively), in which all individuals  $\geq 5$  cm normal diameter (ND) were measured. Attributes of structure and diversity were compared in each condition by analysis of variance and Tukey mean comparison test ( $p < 0.05$ ) and floristic composition by ordination and classification analysis. A total of 142 species grouped in 96 genera and 41 families were recorded. Leguminosae was the family with the most species and individuals. The species with the highest relative abundances were *Montanoa tomentosa* (5.1%) and *Tecoma stans* (5%). Significant differences ( $p < 0.05$ ) were found in cumulative richness, diversity (Shannon-Weiner H' and 1D), density of individuals (ind ha<sup>-1</sup>), maximum height (m), basal area (m<sup>2</sup> ha<sup>-1</sup>) and aboveground biomass (Mg ha<sup>-1</sup>). The multivariate analysis of variance procedure with permutations indicated significant differences ( $p < 0.05$ ) in species composition between early (C10 and C19) and later (C35–C40) conditions. It was concluded that the structure and floristic composition of the secondary forest is recovering slowly (low resilience), so it is necessary to implement activities conducive to its conservation in the short term.

**Keywords:** Tree Community; Disturbance; Diversity; Floristic Similarity; Ecological Succession; Resilience

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## 1. Introduction

The tropical deciduous forest (TDF) harbors an important floristic diversity and a high number of endemic species, which is why it is considered an ecosystem of high ecological value<sup>[1]</sup>. Despite its wide distribution, most of the forest in Mexico is severely disturbed; approximately 60% of its original distribution has been converted to agricultural land and the remaining fragments are severely threatened<sup>[2]</sup>. Its level of risk in some regions of the country is extremely high because it occupies fertile soils, competing with agricultural activities. In regions such as the Bajío, the central part of Veracruz and Chiapas, the original forest has practically been eliminated<sup>[3,4]</sup>. In these areas there

are now landscapes dominated by agricultural uses and fragments of secondary forest in different successional stages. Therefore, knowledge about the level of disturbance and recovery potential of secondary forests is key to promote conservation and restoration strategies for tropical forests<sup>[5,6]</sup>.

Traditionally, the study of ecological succession has sought to explain how plant communities integrate and respond to disturbance<sup>[7]</sup>. In the case of the BTC, this process is less documented compared to the rainforest<sup>[5,8]</sup>; although current evidence from deterministic and stochastic models shows the high heterogeneity in the patterns, mechanisms and trajectories followed by recovering communities in the BTC<sup>[9-11]</sup>. At the same time, the resilience of the BTC has begun to be evaluated through the analysis of the successional process<sup>[12,13]</sup>. The resilience of this ecosystem post-disturbance is fundamental for the conservation of its biodiversity. Ewel<sup>[14]</sup>, based on the ecological differences between dry and humid forests, proposed a resilience model for the BTC defined by a simpler floristic composition, with few successional stages, faster recovery of its structural attributes towards the mature forest condition; due to its low stature exhibited and high capacity to produce resprouts<sup>[15]</sup>.

The pattern of changes in the composition and structure of successions is the starting point for understanding the resilience potential of a forest<sup>[13]</sup>. In this sense, chronosequence studies, in which sites with different ages of abandonment are used to infer the successional process, have been shown to be useful to describe the basic patterns of forest regeneration in typical agricultural fields of the American tropics<sup>[5]</sup>. Results of studies have generally shown a progressive increase in terms of species richness<sup>[13,16]</sup>, height<sup>[17,18]</sup>, basal area and aboveground biomass<sup>[19]</sup>, as well as a marked difference between floristic composition and the most recent to the oldest successional stage<sup>[12]</sup>. Others on the contrary have evidenced erratic behavior of tree abundances<sup>[20]</sup> and slowly recovering species richness and aboveground biomass compared to the original forest<sup>[13]</sup>. Consequently, BTC has been shown to possess lower resilience to anthropogenic impacts compared to rainforest, where recovery

rates have been observed to be between 30 years and 60 years<sup>[21]</sup>.

In Chiapas, the distribution of BTC currently occurs in the regions: Coastal Plain<sup>[22]</sup>, Sierra Madre<sup>[23]</sup> and the Central Depression<sup>[24]</sup>. The latter is considered the most critically threatened region of the Mexican Pacific, since more than 95% of the original distribution area of the BTC has been replaced by agricultural land<sup>[25]</sup>. In this region, basic information to describe the BTC succession process is very limited. The few studies conducted particularly in secondary forests record a species richness between 119 and 157 tree species in fragments with lower levels of disturbance<sup>[26,27]</sup>. Meanwhile, the floristic composition of the less disturbed remnants is confirmed by late tree species, whose assemblages change due to the combined effect of environmental heterogeneity and anthropogenic disturbance<sup>[28]</sup>. There are practically no studies available that document the ecological changes and processes of succession in the face of anthropogenic disturbance, which serve as a basis for understanding the phenomenon, planning conservation and restoration actions for the BTC in this region.

## 2. Objectives

The purpose of this study was to evaluate changes in the structure, diversity and floristic composition of the tree community in the BTC of the Central Depression of Chiapas, in pasture sites with different ages of abandonment and types of human disturbance. The hypothesis to be confirmed was that the structure of the secondary forest is resilient, with a gradual recovery in species richness, diversity, altitude, basal area and aerial biomass as the time of abandonment advances, but with a lower similarity in its floristic composition.

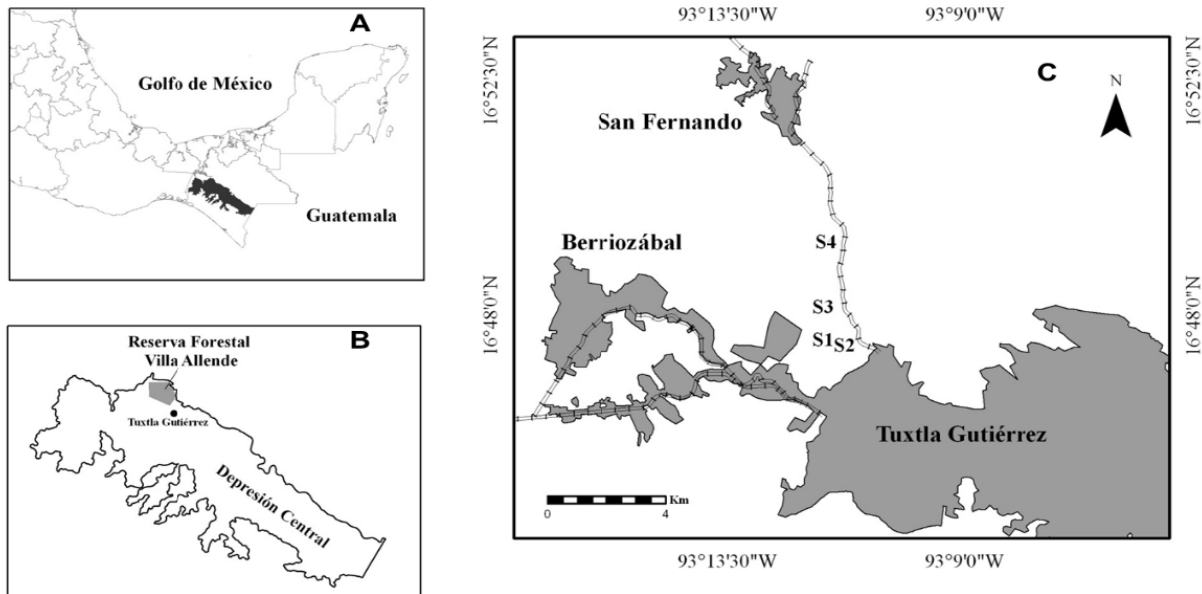
## 3. Materials and methods

### 3.1 Study area

This work was carried out in the southwestern sector of the Vedada de Villa Allende forest reserve, in the municipalities of San Fernando, Berriozábal and Tuxtla Gutiérrez, Chiapas (southern Mexico), between parallels 16°47'N–93°12'W and

16°48'S–91°11'E (**Figure 1**). The dominant climate type (Koppen classification modified by García<sup>[29]</sup>) is warm sub-humid, with summer rainfall, mean annual temperature of 22 °C and total annual precipitation of 955.8 mm<sup>[30]</sup>. The geological strata are represented by Upper Cretaceous and Eocene sedimentary rocks made up of limestone, shale and

sandstone<sup>[31]</sup>. The soil is a medium-textured lithosol and feozem, with a dominant agricultural use, but with a strong tendency to transition to urban use<sup>[32]</sup>. On gently sloping hillsides, there is predominantly BTC<sup>[1]</sup> and, to a lesser extent, sub-deciduous tropical forest and *Quercus* forest.



**Figure 1.** Location of the Central Depression, Chiapas, Mexico (A), Villa Allende Forest Reserve (B) and sampling sites (C). Abandonment conditions: S1 = 35 years, S2 = 40 years, S3 = 19 years, S4 = 10 years.

### 3.2 Selection of sampling sites

Abandoned fields were selected that had previously been used for cattle ranching, with similar characteristics in geological substrate and topographic position. Abandonment times were first estimated with data from surveys and walks with local inhabitants and then corroborated by photointerpretation of Landsat TM satellite images (1992 and 2000), SPOT 5 (2009), orthophotos from 2001 (black and white, scale 1:75,000) and 2007 (color, scale 1:40,000); aerial photographs from 1972 (black and white, scale 1:50,000) and Landsat 2015 satellite data consulted in the Google Earth platform. Four post-disturbance abandonment time conditions were defined: (a) 10 years (C10), site used for grazing until the year 1992 (some trees of the original forest exist), cleared again in 2009 and excluded by fencing since 2011 to establish the ejido reserve, disturbed by clearing practices with elimination of natural regeneration; (b) 19 years

(C19), pastures were cultivated for more than 46 years, its last cycle of use was 2000, disturbed by constant collection of sand; (c) 35 years (C35), used as pasture until it was abandoned in 1982, occasionally disturbed by forest fires (last in 2007) and extraction of poles; (d) More than 40 years (C40), the site was used for 30 years for cattle without totally eliminating the forest, the activity was abandoned at the end of the seventies, little disturbed site, wood is eventually harvested.

### 3.3 Vegetation sampling

We measured 20 sampling units (SU) of 1,000 m<sup>2</sup> (20 m × 50 m). To assign the sample size to each abandonment condition, the protocol proposed by Kalacska *et al.*<sup>[17]</sup> was used, which recommends measuring a minimum of three plots for each abandonment age; because some abandonment conditions were more frequent than others, additional SS were assigned to them, leaving the sample distributed as follows: five SS in C10, six in C19, six in

C35 and three in C40. The completeness of the floristic inventory was also estimated by comparing the observed and estimated richness through non-parametric indicators<sup>[33]</sup>. In each MU, the diameter at breast height (DBH) and total height (from the ground to the apex of the tree) of all ligneous plants with DBH greater than 5 cm and height greater than 1.30 m were measured. The botanical species of each of the plants measured was also identified. Botanical samples were collected from individuals that were not identified in the field, which were determined by comparison using specimens from the vascular plant collection of the Eizi Matuda Herbarium (EMH) of the Universidad de Ciencias y Artes de Chiapas, Herbarium of the Secretaría de Medio Ambiente e Historia Natural (CHIP) and by consultation with specialists of some families. The classification system APGIV<sup>[34]</sup> angiosperms was followed. The taxonomic names were corroborated with The Plant List Database.

### 3.4 Data analysis

Species-area curves were generated from which rarified richness ( $S_{obs}$ ) was obtained by abandonment condition in a given area. The expected richness ( $S_{est}$ ) was also estimated using non-parametric indicators based on 100 randomizations without replacement, choosing for each abandonment condition those that most accurately matched the  $S_{est}$ . All calculations were performed in the program EstimateS v. 8.2.0<sup>[33]</sup>. Species diversity for each abandonment condition was calculated using the following diversity indices  $\alpha$ :

Simpson's reciprocal:

$$(D_2 = \frac{1}{\sum_{i=1}^S p_i^2})$$

Shannon-Wiener:

$$(H = \sum_{i=1}^S p_i \log_b p_i)$$

and their respective measure of fairness:

$$(J = \frac{H}{\log(S)})$$

and true diversity:

$$(^1D = \exp(H))$$

where:

$p_i$  = relative abundance of species  $i$

$S$  = number of species composing the community

$\log_b$  = logarithm in base  $b$  of  $p_i$ <sup>[35,36]</sup>

and  $^1D$  = true diversity<sup>[37]</sup>

The latter index was calculated using the SpadeR program<sup>[38]</sup>.

To characterize species dominance by condition, the relative importance value index of each species was calculated by measuring and summing the values of density (number of individuals per species/total individuals of species  $\times$  100), frequency (number of sample units in which a species was counted/total number of sample units  $\times$  100) and dominance (basal area of each species/total basal area of all species  $\times$  100) recorded in each vegetation class analyzed<sup>[39]</sup>.

The average values of the following metrics of structural attributes were calculated between the different conditions of time of abandonment: density of individuals (ind  $m^{-2}$ ), maximum height (of the 10 tallest individuals; m), basal area ( $m^2 ha^{-1}$ ) and biomass area ( $Mg ha^{-1}$ ). Aboveground biomass was quantified by applying the allometric model proposed by Martínez-Yrizar *et al.*<sup>[40]</sup> for the dry forest of Mexico:

$$\log_{10}(\text{mass}) = a + 0.9011(\log_{10}AB) + 0.5715(\log_{10}DW) + 0.5654(\log_{10}H)$$

where:

mass = aerial biomass (kg)

$a$  is the constant = -0.7590

$AB$ : Basal area ( $cm^2$ )

$DW$ : density of wood ( $g/cm^3$ )

$H$ : height (m)

Height was taken directly from the field inventory data. Wood density for each species was obtained by consulting the Functional and Ecological Tree Attributes Database<sup>[41]</sup>. Average values of wood density at the family or genus scale were considered for species for which no record was available.

The attributes of the structure were analyzed with a Shapiro-Wilks test to determine the normality assumption; all variables were adjusted to this behavior. Therefore, a one-way analysis of var-

iance (ANOVA, where each condition represented a treatment and each plot a replicate) was applied to identify differences between attributes and dropout times. When ANOVA values were significant ( $p \leq 0.05$ ), Tukey's multiple comparison tests were performed posteriori, to learn which of the treatments were statistically different. This same procedure was performed to determine if the time of abandonment affects the cumulative richness and the true diversity index ( ${}^1D$ ) in each study condition.

Significant differences between Simpson's reciprocal ( $1/D$ ), Shannon-Wiener ( $H$ ) and equitability ( $J$ ) indices with the abandonment conditions were obtained through a Kruskal-Wallis test. In order to know the statistical differences between treatments, the rank sum comparison was obtained (Mann-Witney U,  $p < 0.05$ ), under the null hypothesis of equality of conditions<sup>[42]</sup>.

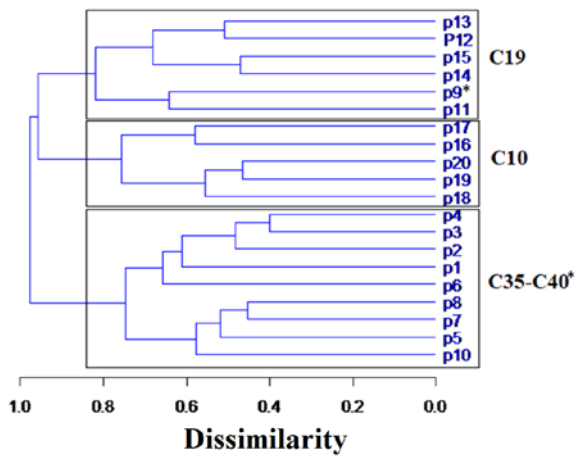
Variation in tree composition among the different abandonment conditions was analyzed through the average values of the Bray-Curtis Beta index ( $S_B$ ),  $(S_B) = \Xi(X_{ij} - X_{ik})/\Xi(X_{ij} + X_{ik})$ , where  $X_{ij}$  is the abundance of species  $i$  at site  $j$  and  $X_{ik}$  is the abundance of species  $i$  at site  $k$ . Values for this measure range from 0 to 1; a value of 0 indicates total identity and a value of 1 indicates units with no species in common. Prior to this analysis, the matrix of sampling plots and their corresponding species was standardized by transforming it to a square root scale. Subsequently, a nonmetric multidimensional ordination (NMDS) analysis<sup>[43]</sup> was performed, which integrated the sample plots based on species composition. The ordination used a similarity matrix between sample plots belonging to the four abandonment conditions, which contained the values of the Bray-Curtis index. A multivariate analysis of variance per-mutational analysis of variance test<sup>[44]</sup>, using the distance matrix was used to determine statistical differences in species ordination dimensions among the abandonment conditions, under the null hypothesis of equality among tree composition. Bonferroni-type a posteriori tests were applied to identify species groups that differed from each other on these management dimensions. Finally, all statistical analyses were performed in R version 3.5.3<sup>[45]</sup>.

## 4. Results

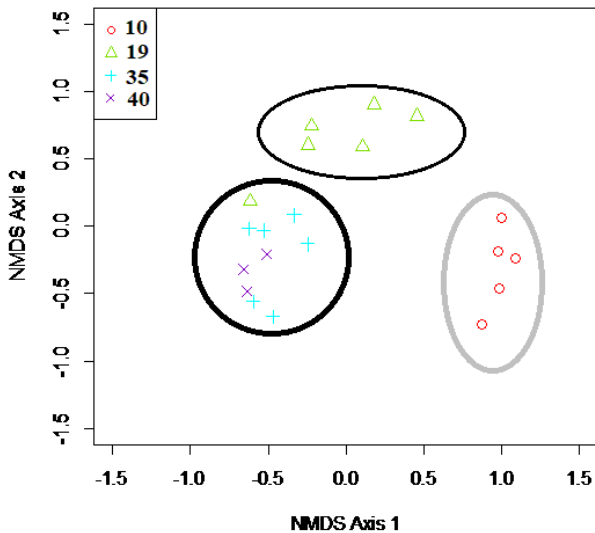
### 4.1 Floristic composition

A total of 142 species corresponding to 96 genera and 41 families were recorded. The families with the highest number of species were Leguminosae (35), Euphorbiaceae (10), Rubiaceae (10) and Compositae (9). The rest of the families contributed six or fewer species. *Lonchocarpus* was the best represented genus with 4.2% of the total, followed by *Eugenia* with 3.5%, *Acacia*, *Bursera*, *Cordia* and *Leucaena*, all with 2.8%. Seventeen species concentrated half of the total abundances, of which *Montanoa tomentosa* Cerv. with 129 individuals (5.1% of the total individuals sampled), *Tecoma stans* (L.) Juss. ex Kunth. with 123 (5%), *Perymenium gfande* Hemsl. with 117 (4.7%), *Eugenia savannarum* Standl. & Steyerl. with 109 (4%) and *Machaerium arboreum* (Jacq.) Benth. with 102 (4%) were the most abundant.

Comparisons of floristic similarity between the abandonment conditions according to the Bray-Curtis index showed almost total dissimilarity between the older forests (88% to 92%) versus the 10-year abandoned forest, as well as between the C35 (79%) and C40 (83%) abandonment conditions with respect to the 19-year-old forest. The highest floristic similarity (66%) was between the C35–C40 forests (**Figure 2**). Corresponding to these results, the non-metric multidimensional scaling analysis (NMDS) revealed the conformation of three statistically different ecological groups (stress: 0.13; **Figure 3**). The first group (A) consisted of forest plots with 10 years of abandonment, the second (B) consisted of five forest plots with 19 years of abandonment and the third (C) group consisted of one plot with 19 years of abandonment with all plots corresponding to forests with 35 years and >40 years of abandonment. The ADONIS showed significant differences ( $p < 0.05$ ) in tree composition among all the ecological groups previously formed in the NMDS (**Table 1**). This trend shows the complementarity existing between the species composition of the oldest abandoned sites (35 years and >40 years of abandonment) versus the most recently abandoned conditions (C19 and C10).



**Figure 2.** Hierarchical clustering dendrogram based on the Bray-Curtis dissimilarity index. The number of plots (P) corresponding to each abandonment condition (uncertain black lines in the dendrogram) in the study area were grouped.



**Figure 3.** Non-metric multidimensional ordination based on the square root of abundances of all species and by abandonment condition (years). Lines indicate plot affinity according to abundances: Group A: thin black line; Group B: thick black line; and Group C: gray line.

**Table 1.** Tests for differences in tree composition among ecological groups based on the ADONIS procedure in the Central Depression, Chiapas, Mexico

Comparison between ecological groups	F	R <sup>2</sup>	Value of p
Group A vs Group B	6.58	0.46	0.008
Group A vs Group C	3.8	0.22	0.001
Group B vs Group C	6.59	0.33	0.001

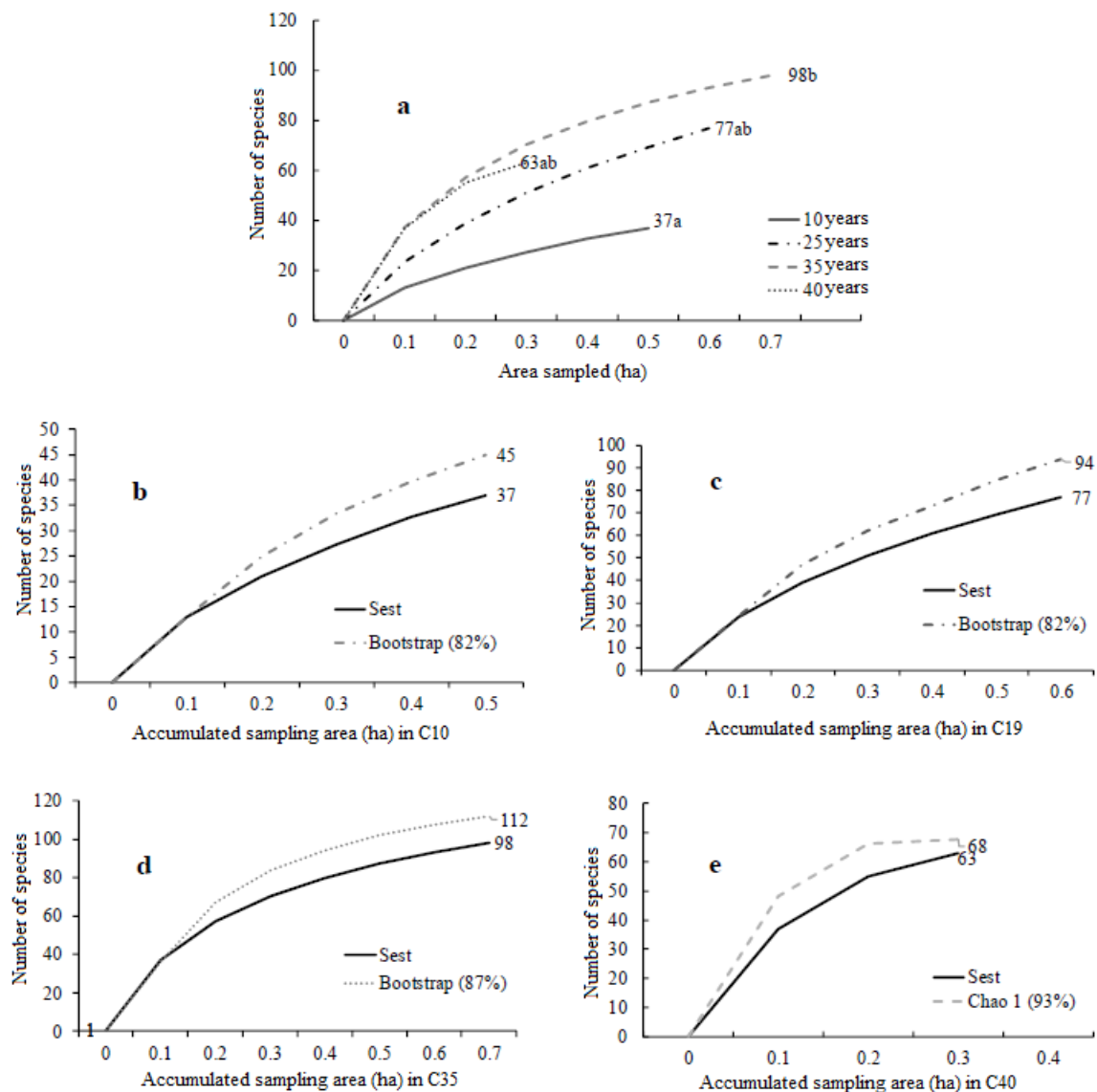
Statistical significance:  $p < 0.05$ ; Bonferroni correction adjusted  $\alpha$  value: 0.016.

## 4.2 Richness, diversity and structure

The accumulated richness showed significant differences with time of abandonment ( $F_3 = 7.1$ ,  $p < 0.05$ ), especially between conditions C10-C35 (**Figure 4a**). In the latter abandonment condition, the highest number of cumulative species (98) was also recorded. This same trend followed the expected richness, whose highest value was concentrated in the plots with 35 years of abandonment (**Figure 4d**). Similarly, significant differences in diversity were found only between the H' (Kruskal-Wallis  $\chi^2 = 12.54$ ,  $p < 0.05$ ) and <sup>1</sup>D ( $F_3 = 7.3$ ,  $p < 0.05$ ) indices with the C10 and C35 conditions (**Table 2**). The rest of the dominance and evenness indices showed no significant statistical differences.

The total abundance of trees in the four study conditions was 2,488 individuals. Condition C40 registered the highest number of trees per hectare and only significant differences were found between C10 and the rest of the abandonment conditions (**Table 2**). In the cases of height and aerial biomass, the highest values were recorded in the C40 condition, while in basal area the highest value was found in C35. Significant differences ( $p > 0.05$ ) were found in all conditions against time of abandonment, but these were more noticeable between conditions C10 and C40 (**Table 2**).

The assemblage of the most important species in the structure was consistent among the C25, C35 and C40 conditions, although it showed great variation in the 10-year condition. According to the cumulative IVIR values, *Luehea candida* (Moç. & Sessé ex DC.) Mart. dominated the C10 condition with 33.52%. While *T. stans*, *Lysiloma acapulcense* (Kunth) Benth., *M. tomentosa* and *E. savannarum* were the species with the highest IVIR values in the rest of the study conditions (Supplement). Regarding species exclusivity, the highest number of species was recorded in the 19-year condition (27 species), followed by the 35-year condition (21 species); and the lowest number of exclusive species was recorded in C40 (Supplement).



**Figure 4.** Species-area curves by time of abandonment in the Central Depression, Chiapas, Mexico. **a)** Cumulative richness. Different letters between curves indicate significant differences (Tukey,  $p < 0.005$ ); **b), c), d)** and **e)** richness expected by nonparametric estimates with higher precision.

**Table 2.** Mean values and standard deviation (in parentheses) of structural attributes and diversity by time of abandonment of secondary forests in the Central Depression, Chiapas, Mexico

Conditions	H' <sup>(*)</sup>	<sup>1</sup> D	Density (ind. ha <sup>-1</sup> )	Maximum height (m)	Basal area (m <sup>2</sup> ha <sup>-1</sup> )	Biomass area (Mg ha <sup>-1</sup> )
10 years	1.7(0.8) <sup>a</sup>	8.5(0.6) <sup>a</sup>	410(99) <sup>a</sup>	6.7(0.5) <sup>a</sup>	6.5(2.8) <sup>a</sup>	16.0(7.1) <sup>a</sup>
19 years	2.6(0.2) <sup>abc</sup>	13.8(4.1) <sup>ab</sup>	1,341(398) <sup>b</sup>	10.2(1.23) <sup>bc</sup>	11.1(4.7) <sup>ab</sup>	25.8(9.8) <sup>ab</sup>
35 years	3.0(0.3) <sup>bc</sup>	21.7(6.8) <sup>b</sup>	1,581(423) <sup>b</sup>	9.08(2.19) <sup>ab</sup>	16.7(3.5) <sup>b</sup>	37.7(11.0) <sup>b</sup>
>40 years	2.8(0.2) <sup>abc</sup>	18.1(4.9) <sup>ab</sup>	1,730(384) <sup>b</sup>	12.2(0.0) <sup>c</sup>	15.0(0.6) <sup>b</sup>	42.8(0.7) <sup>b</sup>

The standard deviation is presented in parentheses. Different letters indicate statistical differences between study conditions (Tukey,  $p > 0.05$ ; <sup>(\*)</sup> U Mann-Whitney,  $p < 0.05$ ).

## 5. Discussion

The null hypothesis, which proposes an in-

crease in the richness, diversity and structure of the tropical deciduous forest with time of abandonment, is rejected because in all the attributes evaluated

only highly significant statistical differences were found between the oldest age conditions (35 years and >40 years of abandonment) and the 10-year category (**Table 2**). On the contrary, each attribute analyzed followed different paths, which coincides with the results found in recent studies for tropical forest, in which age is discarded among the main determinants of changes during the succession process<sup>[11,46]</sup>. Thus, a slow recovery of floristic composition is also evident<sup>[13,21,47]</sup>. The results found for each attribute are discussed below:

### 5.1 Floristic composition

In terms of number of species, Leguminosae and all the best represented genera in the study area are results that agree with the pattern of dominant floristic elements for BTC of Mexico<sup>[4,48]</sup>. In terms of abundances, the floristic composition of the forests is preponderantly represented by species highly tolerant to disturbance and drought. It is known that *T. stans* is a pioneer species that easily progresses in disturbed areas with stony soils and highly resistant to water stress<sup>[49]</sup>. Also, *M. tomentosa* is a typical secondary forest species that has a high capacity to colonize sites of highly disturbed condition such as soils with high nitrogen concentrations<sup>[50]</sup>.

Arboreal dissimilarity between study conditions was generally high (79% to 92%) between the conditions with the shortest time of abandonment (C10 and C19) compared to those with the longest time of abandonment (C35 and C45). These results are in agreement with those found in several secondary BTCs in Mexico, which support the existence of a high rate of species turnover among sites<sup>[12,47,51]</sup>. Based on the *p*-value of the significant test based on ADONIS, it is confirmed that species composition changes with time of abandonment and it is shown that conditions of lower abandonment age (C10 and C19) are floristically different from each other and with respect to those of higher abandonment age (C35–C40). Similar results have been recorded in other Neotropical secondary forests, suggesting that species composition recovery in these forests changes slowly over time<sup>[9,13,52]</sup>. Although the recovery rates of species composition of new assemblages are attributed to the availability

of seeds from remnant vegetation<sup>[11]</sup>, disturbance is also an important factor that has led to variations in environmental conditions that influence the recovery rates of species in the study area<sup>[28]</sup>. Likewise, the similarity of species between conditions of longer time of abandonment can be explained due to the proximity between the sampled sites<sup>[53]</sup>.

### 5.2 Richness, diversity and structure

Accumulated richness and diversity reached high values in the intermediate stage at 35 years, which are close to what was observed for secondary forests in other regions of the country (Oaxaca, 141 species,  $H'$  3.34, minimum diameter 1.0<sup>[12]</sup>; Morelos, 79 species,  $H'$  between 2.39 and 2.73, minimum diameter  $\geq 2.5$  cm<sup>[47]</sup>) and even to the conserved forest ( $H'$  between 2.9 and 4.17, minimum diameter  $\geq 2.5$  cm<sup>[2]</sup>). As already demonstrated for other Neotropical secondary forests, intermediate stages seem to exceed in richness and diversity to advanced stages or even to conserved forests because of the process of establishment and persistence of pioneer species favored by disturbance<sup>[16]</sup>. This maximum peak of species accumulation consistent with the intermediate disturbance hypothesis described by Connell<sup>[54]</sup>, is ruled out for the study area, because no statistical differences were recorded between C35 and C40. Therefore, the higher species accumulation in C35 is explained by the confluence of early-appearing species with those of advanced stages<sup>[9]</sup>, the high floristic similarity between the older conditions and due to disturbances, which could have created favorable environmental conditions for the presence of species with high tolerance to disturbance<sup>[17]</sup> and limited the regeneration of mature forest species via dispersal and seed bank in the more advanced abandonment condition<sup>[55]</sup>.

Plant density presented a different behavior to that shown in other neotropical BTCs, as it did not stabilize in the first conditions of abandonment<sup>[9,17,52]</sup>. According to Chazdon *et al.*<sup>[20]</sup>, changes in dry forest plant density are generally inconsistent with the time of abandonment, because these are influenced by factors such as species composition, dense-dependence, and disturbance. The gradual



increase in tree density in the study area was mainly due to the contribution of the high number of young tree individuals (5 cm–10 cm, 80%) coexisting in the intermediate-aged forests ( $\approx$  35 years and 40 years). Individuals, generally, belong to species with a high capacity for growth and adaptation to current disturbance conditions<sup>[9,51]</sup>.

The maximum tree height interval (9 m–12 m) recorded for the study area showed an increase according to the time of abandonment (**Table 2**), with values approximating those observed for secondary forests in Yucatan<sup>[46]</sup>  $\approx$  10 m–12 m) and the BTC conserved in Mexico ( $\approx$  8 m–12 m)<sup>[56]</sup>. In neotropical secondary forests, it has been observed that the recovery of their height depends on the life history of the dominant species during succession. In the early stages, pioneer species employ an early placement strategy for resource acquisition, grow fast and dominate the canopy early<sup>[7]</sup>. The data from the present study agree with this approach, because pioneer species such as *M. tomentosa*, *Cochlospermum vitifolium* (Willd.) Spreng., *Heliocarpus terebinthinaceus* (DC.) Hochr. and *Bauhinia divaricata* L. dominated canopy at C10, C19 and C35.

Basal area and aboveground biomass showed a monotonic tendency to increase with time of abandonment. It is generally known that these structural parameters are correlated and tend to stabilize in the early stages of succession, and then continue to accumulate slowly for several more decades before reaching values approximating those of conserved forests<sup>[20]</sup>. Several studies in BTCs in Mexico have shown that both attributes tend to accumulate rapidly in the early stages of succession [Lebrija-Trejos *et al.*<sup>[12]</sup>:  $\geq 1$  cm DBH, 15 m<sup>2</sup>/ha; Dupuy *et al.*<sup>[46]</sup>:  $> 5$  cm DBH, 20 m<sup>2</sup>/ha, Read and Lawrence<sup>[57]</sup>:  $\geq 1$  cm DBH, 34 m<sup>2</sup>/ha; Rozendaal *et al.*<sup>[58]</sup>: 31.0 Mg ha<sup>-1</sup>  $\pm$  25.1 Mg ha<sup>-1</sup>], until reaching the maximum average after 3 to 5 decades. The results of this study had a behavior contrary to these approaches, because both parameters registered low values compared to the previously cited forests. This situation could be due to the cumulative effect of agricultural land use in the region on species composition<sup>[59]</sup> and the various current disturbances (timber extraction, fires, etc.), which have led to a slow recovery

of basal area and areal biomass.

The structural index IVIR showed that *L. candida* was the most important species in the youngest abandonment condition, which is explained by the high adaptability of this species to disturbed environments<sup>[60]</sup> and by the contribution of remnant trees, product of the encouragement by producers to favor vegetation that protects the watershed in the ejido Viva Cárdenas. The forests of 19 years and 35 years of abandonment were dominated by the heliophilous species *T. stans* and *M. tomentosa*. In contrast, the older age condition was dominated by late species belonging to the genera *Eugenia* and *Machaerium*, recorded by Rocha *et al.*<sup>[28]</sup> for the Central Depression.

### 5.3 Resilience of secondary forests

The present study found a rapid recovery of tree richness versus a slow recovery of floristic structure and composition. The resilience of the BTCs, represented by the high recovery capacity in terms of species diversity and richness in the early stages of succession, is due to the large number of species with anemochorous dispersal<sup>[61]</sup>, which have a greater capacity to grow and progress in disturbed environments<sup>[8,62]</sup>. In contrast, the lower resilience of the structure and composition of the forests in the reserve, agree with the approaches of Mora *et al.*<sup>[52]</sup>, Derroire *et al.* (2016)<sup>[13]</sup> and Poorter *et al.* (2016)<sup>[21]</sup>, by pointing out that these forests have lower resilience compared to humid forests, because they are more sensitive to site factors, such as previous land use, type and intensity of disturbance. The Central Depression has a long history of disturbance; until before the 20th century it was subject to intense forest exploitation<sup>[63]</sup> and associated with the rotational use of extensive agricultural crops and livestock. In turn, the scarce presence of large-sized trees (<60 cm) as a result of illegal logging, still observed during field surveys, is a proxy indicator<sup>[64]</sup> of the negative changes of disturbances on the structure and resilience of these forests.

## 6. Conclusions

The secondary deciduous forests of the Central Depression were different in diversity, structure and

floristic composition between early conditions and those of longer abandonment. Consequently, most of the ecological attributes evaluated did not follow the same pattern as post-disturbance abandonment time, so that forest recovery rates did not follow a unidirectional trajectory. On the other hand, the secondary forests with the longest time of abandonment (C35–C40) presented the highest specific richness, confirming (high resilience) their ecological importance in safeguarding local tree diversity. On the other hand, the composition and structure showed a slow recovery (low resilience), due to the different disturbances present in the conditions of abandonment, the time of post-disturbance abandonment, as well as the dominance of a group of generalist species tolerant to disturbance.

Finally, it is recommended that future action plans for the reserve incorporate forests in their different stages of succession. The BTCs are important sources of propagules, the basis for conservation and restoration programs, which also require more detailed studies to understand the effect of disturbances on the successional dynamics and resilience of the forests, which are under constant threat from human activities.

## Conflict of interest

The authors declare that they have no conflict of interest.

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