



# The effect of chronic disturbance on the woody plant diversity in a tropical dry forest of Central Mexico

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## ABSTRACT

After deforestation, forest fragments can be impacted by chronic disturbances (e.g., small-scale constant wood extraction), which can alter the forest's richness and composition, favoring a few generalist species while forest specialist species decline. We tested the effect of chronic disturbance along a disturbance gradient in a tropical dry forest (TDF) of central Mexico, including mature, disturbed, and secondary forests. In the Río Apatlaco sub-basin, central Mexico, we randomly chose 73 fragments (23 mature, 25 disturbed, and 25 secondaries). Along a 0.1-ha transect within each fragment, we identified and measured the diameter at breast height of all plants (DBH  $\geq$  1 cm, height  $>$ 1.30 m) and the number of dead trees (snags), stumps, trees with scars of machete/axe, and trees with carbonized trunks. We also quantified the number of cowpats within the transect. We calculated true diversity metrics and pairwise Morisita-Horn similarities. Disturbance diminished from the mature to the secondary forest, while diversity followed the opposite pattern. Along this gradient, distance to the nearest town directly increases plant diversities. An ordination based on floristic composition showed a mixture of forest types, mainly because the disturbed forest became split between secondary and mature forests. This divergence split can be explained because, in some disturbed forests, disturbance-prone pioneer species were favored, and these species were also common in secondary forests. In contrast, the most abundant species in some other disturbed forests are late-successional species. The data suggest that the main drivers of forest change are wood extraction and cattle ranching. Wood extraction generates gaps in the forest, and the cattle can then disperse seeds of pioneer species within these gaps.

## 1. Introduction

Deforestation and forest fragmentation remain the main forces threatening terrestrial biodiversity. However, the adverse effects of constant activities that restrict forest recovery (e.g., secondary vegetation removal for grass maintenance, free-range cattle grazing), the selective harvesting of forest species (e.g., selective timber/firewood extraction, the collection of non-timber forest products - NTFP), or the invasion by exotic species are factors that reduce the diversity of forest fragments and are grouped as chronic disturbance (Olden and Rooney,

2006; Ribeiro et al., 2015). Chronic disturbance can reduce the beta diversity among remaining forest fragments since it generates ecological filters (e.g., selective collection of specific species) that allow the survival of few generalist species while forest specialists disappear (Tabarelli et al., 2008; Lôbo et al., 2011; Ribeiro et al., 2015; Quisehuatl-Medina et al., 2020; Jara-Guerrero et al., 2021).

Tropical dry forest (TDF) is among the world's most threatened and less protected ecosystems and covers a large area in the neotropics (Miles et al., 2006; Banda-R et al., 2016). In the neotropics, TDF contains many endemic species in each of the 12 floristic regions, and the beta

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diversity is high at local, regional, and continental scales (Banda-R et al., 2016). In virtually all areas of TDF coexist local human populations; these populations open forested areas for agriculture or generate chronic disturbance by ranching cattle inside the forest understory or extracting NTFP (e.g., fuelwood, medicinal plants) (Challenger, 1998; Banda-R et al., 2016; Cervantes-Gutiérrez et al., 2017; Quisehuatl-Medina et al., 2020; Jara-Guerrero et al., 2021). Free-range cattle grazing and the extraction of forest plants convert mature TDF fragments into disturbed TDF where the effects of human activities become evident (e.g., scars in tree trunks, presence of exotic fruiting trees, cattle paths, higher density of scrubs) (Banda-R et al., 2016; Cervantes-Gutiérrez et al., 2017; Quisehuatl-Medina et al., 2020; Jara-Guerrero et al., 2021). These chronic disturbance also affect the TDF secondary vegetation (Ribeiro et al., 2015; Cervantes-Gutiérrez et al., 2017; Quisehuatl-Medina et al., 2020).

Several studies have explored the effect of chronic disturbance on mature TDF. It has been found that chronic disturbance can reduce species richness and stem density of woody plants in TDF of India (Sagar et al., 2003), Brazil (e.g., Ribeiro et al. 2015) and Ecuador (Jara-Guerrero et al., 2021). These effects were associated with livestock and human density (e.g., Ribeiro et al. 2015; Quisehuatl-Medina et al. 2020; Jara-Guerrero et al. 2021). Without changes in plant density, chronic disturbance can generate species replacement inside mature TDF forests, changing plant composition and causing biotic homogenization among mature TDF fragments (Ribeiro-Neto et al., 2016; Quisehuatl-Medina et al., 2020; Jara-Guerrero et al., 2021). However, these effects of chronic disturbance in the TDF could not be generalized to other regions. The fact that chronic disturbance generates changes in mature TDF fragments (Sagar et al., 2003; Ribeiro et al., 2015; Jara-Guerrero et al., 2021) points out that human disturbance affects all forest stages from those still recognized as mature to those disturbed, and those that regenerated after deforestation (secondary forest; Quisehuatl-Medina et al. 2020). Unfortunately, there is not the most basic quantitative vegetation data for several areas of the neotropics, and it is unknown how chronic anthropogenic disturbance affects them (Cervantes-Gutiérrez et al., 2017).

Among neotropical TDF groups, the species richness of the Mexican group is among the highest (Banda-R et al., 2016). It is the most threatened worldwide because it is poorly protected and suffers high levels of deforestation, fragmentation, and chronic disturbance (Miles et al., 2006; Cervantes-Gutiérrez et al., 2017; Quisehuatl-Medina et al., 2020). In Mexico, TDF occupies the third largest area among the eleven vegetation types of the country (Palacios-Prieto et al., 2000). It can cover more than 70% of the territory in some regions or constitute the sole primary vegetation (Sotelo-Caro et al., 2015). In Mexico, 33% (824 species) of the terrestrial vertebrates and approximately 6000 species of vascular plants (40% of which are endemic to Mexico) inhabit the TDF (Ceballos and García, 1995; Rzedowski, 1991a, 1991b). In this study, we tested the effect of chronic disturbance on the diversity of TDF fragments in the Apatlaco river sub-basin in the center of Mexico (Sotelo-Caro et al., 2015). The TDF in this area is chronically isolated, fragments have not increased in size during 2002–2012, and disturbed and secondary vegetation has not recovered to primary vegetation. Additionally, there is a high human presence, and several abandoned areas are permanently lost because they become human settlements (Sotelo-Caro et al., 2015).

We pursued the double objective to generate descriptive data on the TDF of the study area and to compare the impact of chronic disturbance on the alpha, beta, and gamma diversities of mature, disturbed, and secondary forests. In this area, all these fragments are isolated and subjected to the effects of extraction of firewood/timber and NTFP, fires, and cattle production activities. The constant human use of timber, firewood, and NTFP impedes the extracted species' regeneration, causing biotic homogenization. Free-range cattle grazing in the forest understory lowers the density of the eaten forest plants, slows forest succession, and facilitates pioneer species in the forest (e.g., *Vachellia* species) (Quisehuatl-Medina et al., 2020; Jara-Guerrero et al., 2021). Occasional fires are caused by grass management or slash-grave burn

activities and can help propagate pioneer species inside the forest (acting synergistically with cattle). All these activities: (a).- help to turn mature forests into disturbed ones; (b).- affect the regeneration of the disturbed forests, transforming these into forests more similar to secondary than to mature forests; and (c).- all the effects in plant diversity are stronger as the forest fragments are closer to human settlements, as forest distance to human settlements closely related with human intensity activity in the forest (Jara-Guerrero et al., 2021). Based on the previous, we predict that in the TDF of the Apatlaco river sub-basin: (a).- the diversity of the woody vegetation will be negatively associated with the disturbance gradient, with some species associated to each forest stage; (b).- the woody plant composition of the TDF will differ between mature, disturbed and secondary forest, and (c).- the distance to the human settlements will affect negatively the plant diversity of the TDF and its composition.

## 2. Materials and methods

### 2.1. Study area

The Río Apatlaco sub-basin, in central Mexico, covers an area of 85,312 ha between the states of Morelos, Estado de Mexico, and Distrito Federal, in Central Mexico (Fig. 1). Most of the sub-basin lies in Morelos (90%) and comprises 13% of the territory of this state. In the study area, the mean annual precipitation is 1129 mm, and the mean monthly temperature is 23 °C. The predominant soils are regosol, vertisol, and phaeozem developed on igneous and sedimentary rocks (Contreras-MacBeath et al., 2004). The TDF originally covered 73% of the sub-basin, but by 2002 had been reduced to 5%, with another 7% still recognized as disturbed TDF (Sotelo-Caro et al., 2015). Agriculture and urban development caused this high TDF deforestation since this area has the highest human population density in Morelos state (Contreras-MacBeath et al., 2004; Sotelo-Caro et al., 2015). There have been

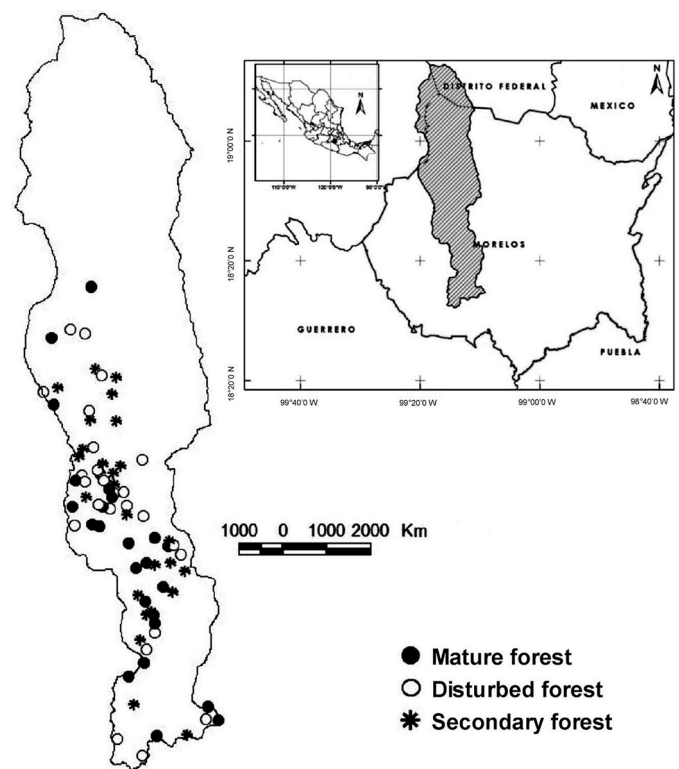


Fig. 1. Location map of the study area. The symbols correspond to the mature (solid circles), disturbed (empty circles) and secondary forest (asterisks) sampled.

no quantitative studies of the vegetation in this area, but the TDF is characterized by the low stature of the trees (<15 m) and leaf loss in most tree species for 4–6 months in the year. In the study area, characteristic species of TDF include *Bursera copallifera*, *B. fagaroides*, *B. grandifolia* (Burseraceae), *Conzattia multiflora*, *Lysiloma acapulcense*, and *L. divaricata* (Fabaceae) (Sotelo-Caro et al., 2015).

In the Apatlaco river sub-basin, the TDF deforestation rate decreased from 1.40% per year (Trejo and Dirzo, 2000) to 0.13% per year (Sotelo-Caro et al., 2015). Still, recovery of primary forest patches has not been observed. In this area, the individual size of the TDF fragments remained unchanged from 2002 to 2012, and these fragments remain chronically isolated. Disturbed TDF fragments of the same region presented low tree density and are chronically isolated. The lack of primary and disturbed TDF recovery is probably due to chronic disturbance. Furthermore, 23% of the secondary vegetation derived from TDF has not become primary vegetation and has been lost to grassland and urban settlements (Sotelo-Caro et al., 2015).

## 2.2. Vegetation sampling

Using the maps we developed previously, and for which we did verification fieldwork (Sotelo-Caro et al., 2015), we randomly chose 73 fragments (23 of mature TDF, 25 of disturbed TDF, and 25 of secondary forest fragments). Our previous criteria (Sotelo-Caro et al., 2015) to classify forest fragments as mature, disturbed, or secondary were: Mature TDF fragments have the tallest trees, a low density of shrubs, and a lower frequency of human activities; disturbed forests have a high density of shrubs, a higher frequency of human activities (e.g., cowpats, stumps) and species linked to these activities (e.g., *Acacia* spp., *Vachellia* spp., exotic fruiting trees); secondary forest develops in deforested areas or abandoned planting areas, there are no tall trees, or they are scarce, dominant trees are short, and there is a high density of thorn shrubs or grass areas (Cervantes-Gutiérrez et al., 2017). However, until the present work, no quantitative data supports these criteria in the study area. Still, these are similar to those used in other neotropical TDF (e.g., Jara-Guerrero et al. 2021).

We attempted to sample all the size variability of fragments in the study area. We sampled the woody vegetation in each fragment along a 0.1-ha transect (10 × 100 m, Muller-Dombois and Elleberg 1974). Each transect was 50 m from the nearest edge or at the center of the fragment (in small fragments). In each transect, we identified and measured the diameter at breast height (DBH) of all plants with DBH ≥ 1 cm and height >1.30 m. Where possible, plants were identified in the field, but even with easily identified plants, we collected herbarium vouchers (Lot et al., 1986), which were deposited in the herbarium of the Universidad Autónoma del Estado de Morelos (HUMO). We determined for each plant species its seed dispersal syndrome (anemochory, barochory, and zoochory) and successional role (pioneer or late successional). These data come from herbaria vouchers, local floras (e.g., Vester and Martínez 2007; Dorado et al. 2012; Dorado-Ruiz et al. 2013), genus information, or our experience.

## 2.3. Chronic disturbance factors

In each sampling transect, we measured one variable of forest maturity (abundance of dead-standing trees = snags) and five variables related to sources of disturbance. In healthy forests, snags result from tree competition, and their frequency must increase as the forest ages; additionally, deadwood is essential for some birds, insects, and orchids (Westoby, 1984; Alvarez-Buylla and Martínez-Ramos, 1990; Grove, 2001; Cruz-Fernandez et al., 2011; Vázquez and Renton, 2015; Torres-Manjarrez, 2017; Martínez-Hernández et al., 2019).

The first disturbance factor was the distance from the sampling transect to the nearest human settlement. This distance was measured with the help of our previous maps (Sotelo-Caro et al., 2015); and is the most common chronic disturbance measure taken because the closer

humans are to a forest, the higher intensity of forest use they do (Jara-Guerrero et al., 2021). To measure the intensity of timber extraction, we counted the number of stumps per transect; this second disturbance factor should reduce the frequency of timber species. We also measured the number of trees with machete or axe scars deliberately made by the Campesinos to kill the tree; this measure points out tree species used for firewood exclusively because in Mexico, it is legal to collect firewood from dead trees, so campesinos furtively damage trees (Torres-Manjarrez, 2017). We counted the frequency of carbonized trunks to measure the presence and intensity of recent fires. Finally, we also quantified the number of cowpats within the transect to measure cattle presence.

## 2.4. Diversity pattern analyzes

True diversity ( ${}^qD$ ) was analyzed for each forest type (mature, disturbed, secondary), with multiplicative diversity decomposition (Jost, 2007). In the true diversity index (see Jost 2007),  $q$  determines the index's sensitivity to species' relative abundance (Jost, 2007). When  $q$  is 0,  ${}^qD$  measures the species richness, ignoring species abundance. When  $q$  is 1, the diversity is equal to the inverse of the Shannon diversity ( $e^{H'}$ ) and perfectly weights the proportional abundance of each species; in this case,  ${}^1D$  can be interpreted as the number of typical species. When  $q$  is 2,  ${}^2D$  diversity equals the inverse of the Simpson dominance ( $1/D$ ) and measures the number of abundant species (Jost, 2007). The true diversity index can describe one community, a set of samples of the same community, or different communities (Jost, 2007).

When used in a group of samples or communities, true diversities follow the multiplicative diversity decomposition, and gamma diversity is equal to the product of alpha and beta diversities (Jost, 2007). We calculated alpha diversity as the average number of species in each sampled transect for each forest type (Jost, 2010), and we also calculated evenness factors (EF; Jost 2010), which are the ratio between  ${}^qD_{alpha}$  and  ${}^0D_{alpha}$  (e.g.,  $EF_{0,1} = {}^1D_{alpha} / {}^0D_{alpha}$ ; Jost, 2010). Evenness factors take a value of 1 when all species are equally abundant in the community and approach 0 when the community is over-dominated by a single species (Jost, 2010).  $EF_{0,1}$  is equivalent to the Pielou evenness index (Jost, 2010).

Beta diversity was measured as the ratio:  ${}^qD_{gamma} / {}^0D_{alpha}$ . The maximum value of  ${}^qD_{beta}$  is the number of communities (or samples inside a community) compared and occurs when all communities are different (no shared species); in this case, 23 transects for the mature forest, 25 for disturbed, and 25 for the secondary forest. We reported the ratio between the observed  ${}^qD_{beta}$  and its expected maximum value to avoid misinterpretations. All the true diversity values were calculated with the library Entropart (Macron and Hérault, 2015).

We used gamma diversity as the number of species ( ${}^0D_{gamma}$ ) for each forest type in the study area (mature, disturbed, or secondary). We only used  ${}^qD_{gamma}$  when  $q$  is 0 and compared this value between forest types at a similar sample coverage value ( $\hat{C}_n$ ; Chao and Jost, 2012). Comparisons of species richness based on sample coverage rather than sampling effort, are conducted on the same proportion of community completeness (Chao and Jost, 2012). We used the iNext library (Chao and Jost, 2012) to estimate the expected richness ( $\hat{S}_m$ ) at the same sample coverage value and the 95% confidence intervals. All analyses were done in R version 3.6.3 (R Core Team, 2018).

## 2.5. Forest composition structure - floristic ordination

To test if the sampled transects were more similar in their floristic composition within each forest type than between forest types, we performed a non-metric multidimensional scaling analysis (NMDS; Johnson and Wichern, 2002). This multivariate analysis tests whether the floristic distances between samples (transects) belonging to several groups (three forest types) are more cohesive inside than between the groups. If this is the case, the transects will form clumps that belong to

the same forest type rather than mixing the transects between forest types. Some crucial differences with other multivariate techniques are that the groups are not defined *a priori*, and the distance matrix must have values between 0 and 1 (Johnson and Wichern, 2002). This latter property is essential because NMDS works with the similarity distances used mainly in ecology (e.g., the Jaccard index).

With the Morisita-Horn index (M-H, Jost et al. 2011), we built a squared matrix of paired similarities between the 73 transects. The M-H index is insensitive to rare species and helps compare communities' ecological structure instead of just species' presence. M-H indexes were calculated with the basal area per species. The M-H index takes a value of one when the same species, with the same proportional abundance, are in both samples. A value near one is found when the same species over-dominate both communities, while non-shared species are rare. It takes a value of 0 when no species are shared; or near 0 if species are shared but their proportional abundance is quite different between samples (e.g., the dominant species differs). The values of the M-H index are equivalent to the  $1/D_{beta}$  when two communities are compared (Jost, 2007). The library *vegan* (Oksanen et al., 2019) was used to calculate the M-H index matrix and perform the NMDS analysis.

We used a Mantel test to assess whether floristic similarity was related to distance (log-transformed) between transects. P values were obtained with a Monte-Carlo test using the software TFPGA (Miller, 1997).

## 2.6. Data analyses

In addition to the previously mentioned libraries, for different analyzes, we use the libraries: *ggplot2* (Wickham 2016, graphics), *ggsci* (Xiao and Miao, 2018, graphics), *multcomp* (Hothorn et al. 2008, multiple comparisons procedures), and *olsrr* (Hebbali 2020, testing statistical assumptions). We used one-way ANOVA to compare single variables between forest types. We used Kruskal-Wallis tests where some variables did not fulfill the ANOVA assumptions (Zar, 2010). When differences were detected, we used Tukey multiple comparison tests (ANOVA) or the Nemenyi multiple comparison procedure for medians (Zar, 2010).

With their 95% confidence intervals, gamma and beta diversities were compared between forest types (mature, disturbed, secondary). With generalized and general linear models, we tested the effect of forest type (a factor with three levels: mature, disturbed, secondary), and the covariables fragment size and the distance to the nearest town (a variable associated with human use) in the diversity of the transects (gamma diversity). For  $^0D$  diversity (species richness), we built generalized linear models with Poisson error adjusted for overdispersion (Crawley, 1993). We used general linear models for  $^1D$  and  $^2D$  because the best model's residuals fulfilled the assumptions of normality and homoscedasticity (Crawley, 1993). Models were constructed and selected with the library *AICcmodavg* (Mazerolle, 2020).

For each response variable, we performed 12 models (see Supplementary Material), including the null model (i.e., the model including only the intercept) and the full model. Model selection was based on Akaike information criteria (AIC, Andersen 2008). The best model was the one with the lowest AIC. When several models were equally probable (their AIC differences were less than 2) (Andersen, 2008), we reviewed the parameters' coefficients and chose the model where the coefficients differed from zero.

## 3. Results

The three forest types studied did not differ regarding the density of tree individuals and stems per transect (Table 1). As expected for a mature forest, transects of mature TDF had the largest cumulative basal area of live trees, the fewest trees with machete/axe scars, and the fewest cowpats (Table 1). The numbers of stumps and the number of trees with carbonized trunks were statistically similar between the three

**Table 1**

Structural variables, and species richness measured in mature, disturbed, and secondary tropical dry forest transects at the Río Apatlaco sub-basin, central Mexico. For each variable, the mean ( $\pm$  SD), the test statistic used for comparing the means ( $F$  for one way ANOVA tests), or the medians ( $H$  for Kruskal-Wallis test;  $U$ , for Mann-Whitney tests), and the associated P value are presented. Different letters indicate significant differences (Tukey test for the means or Nemenyi test for medians,  $P < 0.05$ ). Except for species richness and the percentages, multiplying each variable by 10 gives the units/ha. For example,  $55,940.7 \pm 26,934.9 \text{ cm}^2/0.1 \text{ ha}$  will be  $559,407 \pm 269,349 \text{ cm}^2/\text{ha}$ . In the basal area, dividing by 1000 will give the units in  $\text{m}^2/\text{ha}$  ( $55.9 \pm 26.4 \text{ m}^2/\text{ha}$ ).

Variable	Forest type			Test statistic
	Mature	Disturbed	Secondary	
Number of sampled transects 0.1 ha	23	25	25	
Number of live trees /0.1 ha	112.3 <sup>ns</sup> $\pm$ 44.6	111.2 $\pm$ 49.6	86.1 $\pm$ 31.8	$H = 5.4, P > 0.05$
Number of live stems /0.1 ha	225.9 <sup>ns</sup> $\pm$ 107.3	222.7 $\pm$ 106.8	285.6 $\pm$ 163.8	$H = 2.0, P > 0.05$
Pooled basal area of live trees ( $\text{cm}^2/0.1 \text{ ha}$ )	55,940.7 <sup>a</sup> $\pm$ 26,934.9	38,091.4 <sup>b</sup> $\pm$ 17,812.6	27,862.0 <sup>b</sup> $\pm$ 20,423.0	$F_{2,70} = 11.0, P < 0.001$
Number of snags /0.1 ha	5.5 <sup>a</sup> $\pm$ 3.9	4.8 <sup>a</sup> $\pm$ 4.0	2.4 <sup>b</sup> $\pm$ 5.3	$H = 19.6, P < 0.001$
Number of stumps /0.1 ha	0.8 <sup>ns</sup> $\pm$ 1.3	2.4 $\pm$ 4.1	3.3 $\pm$ 6.8	$H = 3.7, P > 0.05$
Number of trees with machete or axe scars /0.1 ha	1.0 <sup>b</sup> $\pm$ 1.7	5.5 <sup>a</sup> $\pm$ 8.5	6.8 <sup>a</sup> $\pm$ 6.8	$H = 15.1, P < 0.001$
Number of trees with carbonized trunks /0.1 ha	–	0.2 <sup>ns</sup> $\pm$ 0.6	0.2 $\pm$ 0.7	$U = 0.2, P > 0.05$
Numbers of cow pats/0.1 ha	0.8 <sup>b</sup> $\pm$ 1.2	5.8 <sup>a</sup> $\pm$ 8.0	31.6 <sup>a</sup> $\pm$ 70.6	$H = 27.5, P < 0.001$
Number of species /0.1 ha	21.5 <sup>a</sup> $\pm$ 5.8	20.0 <sup>a</sup> $\pm$ 7.2	11.8 <sup>b</sup> $\pm$ 6.0	$F = 18.1, P < 0.0001$
Percentage of pioneer species dispersed by anemochory	22.3 <sup>b</sup> $\pm$ 9.8	27.5 <sup>ab</sup> $\pm$ 7.9	32.2 <sup>a</sup> $\pm$ 11.3	$H = 10.21, P < 0.0001$
Percentage of pioneer species dispersed by zoochory	11.1 <sup>b</sup> $\pm$ 8.1	16.8 <sup>b</sup> $\pm$ 12.7	37.6 <sup>a</sup> $\pm$ 18.6	$H = 27.7, P < 0.0001$
Percentage of late successional species dispersed by anemochory	26.0 <sup>a</sup> $\pm$ 8.0	22.3 <sup>a</sup> $\pm$ 8.6	12.0 <sup>b</sup> $\pm$ 11.2	$H = 17.17, P < 0.05$
Percentage of late successional species dispersed by zoochory	40.6 <sup>a</sup> $\pm$ 8.0	33.4 <sup>a</sup> $\pm$ 7.2	18.2 <sup>b</sup> $\pm$ 16.2	$H = 30.1, P < 0.0001$

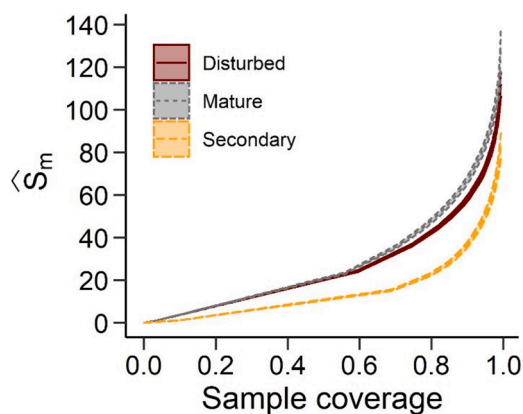
forest types (Table 1), suggesting that the timber extraction and fire frequency levels were similar. The disturbed forest transects were similar to the mature transects only in the density of snags (Table 1). While the number of trees with machete/axe scars and the number of cow pats were similar between disturbed and secondary forests (Table 1).

### 3.1. Diversity patterns

We sampled 7516 individuals of 142 species between the 73 transects (See Appendix Table A in Supplementary material). We found 122 species in the mature forest (2580 individuals), with a sample coverage ( $\hat{C}_n$ ) of 0.991. In the disturbed forest, we found 112 species (2781 individuals,  $\hat{C}_n = 0.993$ ) and 83 in the secondary forest (2153 individuals,  $\hat{C}_n = 0.993$ ). When this richness was compared at the same coverage (0.993), the three forests had different  $^0D_{gamma}$  diversities, with the mature forest presenting the highest ( $\hat{S}_m = 128$ ), followed by the disturbed forest, and finally, the secondary forest (Fig. 2).

Transects of the mature and disturbed forests had the highest species





**Fig. 2.** Relationship between the expected number of species ( $\hat{S}_m$ ) and the sample coverage for the woody plants sampled in mature, disturbed, and secondary tropical dry forest transects of the Apatlaco river sub-basin, Central Mexico. Shadow areas represent the 95% CI.

richness and proportion of late-successional species (Table 1) and the lower proportion of pioneer species dispersed by zoochory (Table 1). Secondary forest transects presented a higher proportion of pioneer species dispersed by anemochory than mature-forest transects (Table 1).

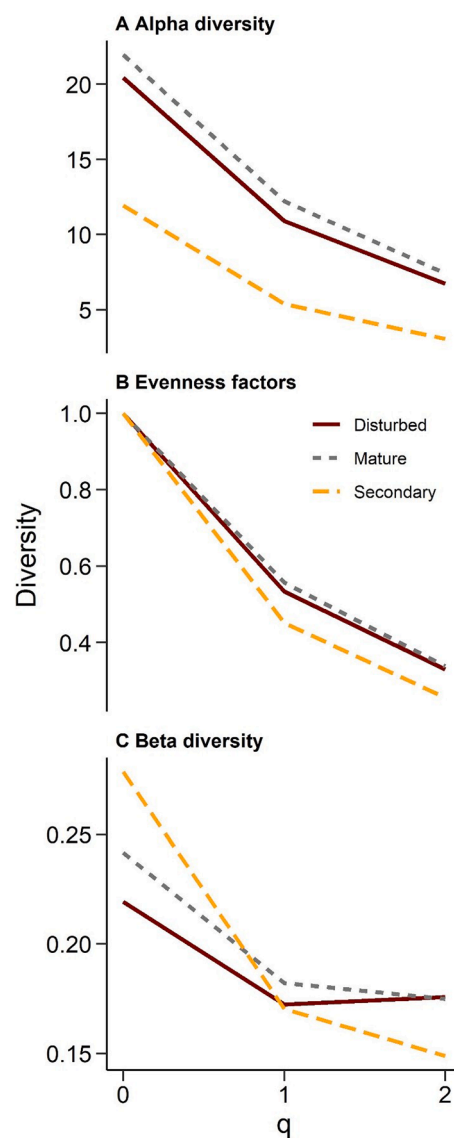
All of the  ${}^qD_{\alpha}$  diversity values showed the same pattern as those of the  ${}^0D_{\alpha}$  diversity, and the mature forest had the highest alpha diversity for all orders of  $q$ , followed by disturbed and secondary forests (Fig. 3A). All evenness factors followed the same pattern, showing that evenness was higher in the mature than in the secondary forest (Fig. 3B).

Contrary to previous patterns, the secondary forest had the highest  ${}^0D_{\beta}$  diversity. In contrast, the mature forest had the highest  ${}^1D_{\beta}$  diversity, and the lowest was in disturbed and secondary forests (Fig. 3C). The highest  ${}^2D_{\beta}$  was found in mature and disturbed forests (Fig. 3C).

### 3.1.1. Forest composition structure - floristic ordination

We found no significant correlation between geographical distance and floristic similarity between transects (Mantel  $R = -0.21$ ,  $P > 0.05$ ). Two dimensions of the NMDS analysis graphically represent the original matrix with an error  $< 25\%$  (stress = 0.22). In this analysis, dimension one correlated positively with species richness in each transect ( $R = 0.65$ ), the richness of late-successional species dispersed by zoochory ( $R = 0.75$ ), and richness ( $R = 0.70$ ) and proportional abundance ( $R = 0.75$ ) of late-successional species dispersed by anemochory; while it correlated negatively with the proportional abundance of pioneer species dispersed by zoochory ( $R = -0.80$ ). Other correlations explored, with either dimension one or two, were weak (all  $R$  values were between  $-0.54$  and  $0.57$ ).

NMDS ordination (Fig. 4) separated most of the transects of mature forest to the right of dimension 1, showing that species richness, the richness of late-successional species dispersed by zoochory, and richness and proportional abundance of late-successional species dispersed by anemochory increases within these transects; while the proportional abundance of pioneer species dispersed by zoochory decreases (e.g., *Acacia*, *Pithecelobium*, and *Vachellia*). However, five mature forest transects were mixed with secondary transects on the left of the graph; in two of these transects, the most abundant species was *Ipomoea pauciflora*, a frequent species among all the transects, but highly abundant between disturbed and secondary forests (See Appendix Table A in Supplementary material), while *Guazuma ulmifolia* was present in all transects, being the most abundant in one transect (45.6% of the pooled basal area), and the second or third most abundant in the other three (12.5–15.9% of the pooled basal area, Fig. 4). These two species can be found in other mature forests but at a lower abundance. At the right side of the NMDS ordination were mature transects where *Conzattia*



**Fig. 3.** Diversity profiles (alpha, beta, and evenness factor) for woody plants sampled in mature, disturbed, and secondary transects of tropical dry forest of the Apatlaco river sub-basin, Central Mexico.  $q$  determines the sensitivity of the diversity value ( ${}^qD$ ) to species' relative abundance. When  $q$  is 0,  ${}^0D$  measures the species richness; when  $q$  is 1, the diversity is equal to the inverse of the Shannon diversity ( $e^{H'}$ ) and when  $q$  is 2,  ${}^2D$  diversity equals the inverse of the Simpson dominance (Jost, 2007).

*multiflora* was most abundant, along with *Bursera* and *Lysiloma* species (Fig. 4). The dominance of *Bursera* species can define the upper right quadrant of Fig. 4. In contrast, the dominance of *Conzattia multiflora* and *Bursera* species defines the lower quadrant.

Disturbed forest transects were mixed in the ordination between mature and secondary forests, showing their composition is highly variable (Fig. 4). Secondary forests were mostly separated to the left of dimension 1. On the left side of the ordination were the transects where species of *Vachellia*, *Ipomoea*, and *Guazuma ulmifolia* dominated. The transects with less species richness (2–6) were found on the extreme left side, where the most abundant species were *Vachellia* species dispersed by livestock. The upper left quadrant can be defined by the dominance of *Vachellia* species along with *Guazuma ulmifolia*, while the dominance of *Vachellia* and *Ipomoea* species defines the bottom left quadrant (Fig. 4).



TDF of Morelos and, in some protected areas, dictates the forest physiognomy (e.g. the TDF of the Chichinautzin reserve; Vergara-Torres et al. 2010). *Lysiloma* species are hardwood species, probably of slow growth (Vester and Martínez, 2007), and are among the preferred species used for firewood (Torres-Manjarrez, 2017), so their presence also suggests less human impact. *Bursera* species are animal-dispersed and have low germination rates (Hernández-Pérez et al., 2011), suggesting they can only prosper in mature areas. Additionally, some *Bursera* species, such as *B. copallifera* (the most frequent in the study area), constitute key elements of the TDF of Morelos because they host most of the epiphytes present in this forest, and a rich ant community (Vergara-Torres et al., 2010, 2017). Our previous classification of the forest was based on satellite images and orthophotos (Sotelo-Caro et al., 2015); however, the present survey confirms that the forests dominated by *Conzattia*, *Lysiloma*, and *Bursera* could be considered as mature, while the secondary forest in which these species dominated, should be considered as areas of successful TDF recovery.

In the secondary forest, the most characteristic species are pioneer species of the genera *Ipomoea* and *Vachellia*. While species of both genera are found in open areas, *Ipomoea* has wind-dispersed seeds, and *Vachellia* has seeds that are dispersed by endozoochory, suggesting that their success in these areas depends on different vectors (by the wind or by vertebrates) and anthropogenic chronic factors (e.g., gap dynamics or free-range cattle grazing, see below).

#### 4.2. Disturbance factors

Our data show that chronic disturbance occurs in all the forest fragments in the studied landscape, but as expected, chronic disturbance diminishes from disturbed and secondary to mature TDF. As expected, we found that the distance from the sampling transect to the nearest human town was negatively correlated with the woody plant diversity (Jara-Guerrero et al., 2021). This distance directly measures the general impact of chronic human activities in the fragments. Unfortunately, the distance from the sampling transect to the nearest town is a black box, and with this single variable, it can not be detected which chronic disturbance factor is responsible for the vegetation changes. We measured four disturbance factors, but our measurements were limited because they were done in a single moment. However, these four factors help us infer what could happen in the studied fragments. We counted the number of stumps and trees with machete or axe scars; these variables show the cumulative effect of two practices of woody plant extraction: timber and firewood extraction, respectively. The number of trees with scars was five to six times greater in the disturbed and secondary forests, showing that firewood extraction is much more frequent in these forest stages. In contrast, the number of stumps was similar among all three forest types and lower than that of trees with machete/axe scars, suggesting that firewood extraction may be more frequent than timber extraction for construction. These differences in the intensity of firewood extraction between the forest stages could explain the higher abundance of some species (e.g., *Lysiloma*; Torres-Manjarrez, 2017) in mature forests and their scarcity in disturbed and secondary forests. Livestock production activity was considerably greater in disturbed and secondary forests and probably explains the dominance of cattle-dispersed pioneer species (e.g. *Vachellia* species and *Pithecellobium dulce*) in some of these forest fragments, as reported previously (Olivares-Pérez et al., 2011; Jara-Guerrero et al., 2021).

#### 4.3. Diversity effects

The study area has a high human population, and most of the original vegetation has been transformed (Sotelo-Caro et al., 2015). Still, the general diversity (142 species richness) appears higher than that reported in TDF sites of the neotropics (13.8–106.1, Banda-R et al., 2016) or that found in close Mexican TDF. For example, in the lower Balsas basin, Guerrero, 82 species of woody plants were found in four 0.1 ha

transects (Pineda-García et al., 2007), while Trejo and Dirzo (2002) found 115 species of woody plants in four localities (sampling 40, 2 × 50-m transects), in the entire Balsas river basin.

The  ${}^0D_{\alpha}$ ,  ${}^1D_{\beta}$  and  ${}^0D_{\gamma}$  diversities were greater in the mature forest than in the other two forests. However, among the latter, chronic disturbance's alpha, gamma, and  ${}^1D_{\beta}$  diversity cost is lower for the disturbed forest than for the secondary forest. This evidence is in perfect concordance with the chronic disturbance gradient. However, the  ${}^0D_{\beta}$  and  ${}^2D_{\beta}$  diversities did not follow the previous pattern.

Low alpha and high beta diversity are key features of the TDF (Trejo and Dirzo, 2002). These characteristics have been used to explain the high plant diversity found in this ecosystem (Trejo and Dirzo, 2002; Arroyo-Rodríguez et al., 2013). Forest fragments that are chronically isolated and subjected to plant invasions and extraction of NTFP, can present lower beta diversity (Arroyo-Rodríguez et al., 2013). In the study landscape, the beta diversity shows that secondary forests can be highly variable in terms of the presence of certain species but also that a few of these species highly dominate them. When  $q$  was 0, the beta diversity was greater in the secondary forest. The diversity of the  $q$  order zero shows differences caused by the presence/absence of species (Jost, 2007). As a consequence, the high  ${}^0D_{\beta}$  diversity found among the secondary forest transects shows high heterogeneity in the presence of species. In the secondary forest, we found the largest proportion of species that appear only in one or two transects (59%), while in the disturbed (48%) and mature (46%) forests, this proportion was low. However, the beta diversities of  $q$  orders 1, and 2 show that even when many species were not shared between the secondary forest fragments, some species had a high dominance, lowering beta diversity below that of the mature forest transects.

#### 4.4. Mechanisms affecting the diversity and composition

Mature and secondary TDF fragments were our reference points; in the mature forest, we expect to find the largest values of variables that define forest maturity (e.g., basal area, snag abundance), and in the secondary forest, the maximum values of variables associated with disturbance. The mature forest, as expected, has a larger cumulative basal area, a high abundance of snags, and a lower human activities impact. In comparison, the secondary forest shows a lower cumulative basal area and a higher frequency of human activities. The larger cumulative basal area and the higher presence of snags are indicators of forest maturity. Snags could be the result of competition between trees and are critical elements in the forest dynamic; because they allow the regeneration of pioneer species that depend upon gap dynamics (Westoby, 1984; Alvarez-Buylla and Martínez-Ramos, 1990), mobilize resources, and create habitat for some animal (e.g., amphibians, birds, insects), fungus, and plant species (e.g., orchids) (Cruz-Fernández et al., 2011; Vázquez and Renton, 2015; Torres-Manjarrez, 2017; Martínez-Hernández et al., 2019). However, the importance of snags is scarcely studied in TDF (Vázquez and Renton, 2015; Torres-Manjarrez, 2017; Martínez-Hernández et al., 2019).

Our data show that for the TDF of the studied zone, mature fragments are still diverse and can generally be recognized as mature. Still, floristic ordination showed that several of these forest fragments have a more similar structure to secondary or disturbed forests. In contrast, the disturbed fragments split between those in which the disturbance has been insufficient to facilitate the abundance of pioneer species (being more similar to mature forest), and those more similar to secondary vegetation. *Guazuma ulmifolia*, *Vachellia*, and *Ipomoea* were the dominant taxa in the secondary forest, and in those mature/disturbed forest fragments ordered between secondary forests. *Guazuma ulmiflora* and species of *Vachellia* are among the most widespread species in the Neotropical TDF (Banda-R et al., 2016). For example, *Guazuma ulmiflora* appears in 10 of the 12 floristic TDF groups delimited by Banda-R et al. (2016). In five floristic TDF groups, its frequency is above 35% among each group's sites (36.7–86.2, Banda-R et al., 2016). In the Mexican TDF



group, *G. ulmifolia* (45.5% of the sites), *Vachellia farnesiana* (63.6%), and *V. pennatula* (54.5%) are among the most common species found in the TDF sites (Banda-R et al., 2016).

Cattle disperse seeds of *Vachellia* species; in fact, *Guazuma ulmifolia* and *Vachellia* species are locally maintained because their leaves and fruits provide food for cattle (Villa-Herrera et al., 2009). Additionally, some *Vachellia* species are sources of firewood (Torres-Manjarrez, 2017) and, in pristine conditions, were probably eaten and dispersed by deer. *Ipomoea* species are frequently found in gaps and rocky outcrops inside mature forests, forest edges, and secondary areas along roads or abandoned mining areas. The dominance of *Vachellia* and *Ipomoea* species within mature forests can be promoted by wood extraction (generating gaps) and cattle's free movement. Additionally, deliberate fires are used for grass management within some forests, but fires can also facilitate the germination of some *Vachellia* species. Suppose the forest composition becomes dominated by *Ipomoea* species. In that case, other forest guilds can be negatively affected since at least *I. pauciflora* and *I. murucoides* can exert adverse allelopathic effects on epiphytic plants (Valencia-Díaz et al., 2010).

#### 4.5. Concluding remarks

In the study area, all forest fragments are subject to chronic disturbance. While the effect of disturbance on plant diversity depends on the closeness of the forest fragment to the towns; two sources of disturbance appear as the main affecting plant diversity. The first mechanism is firewood extraction, which lowers the abundance of late-successional species (e.g., *Lysiloma*) and could increase the number of gaps inside the forest. The second is free-range cattle grazing, which reduces the abundance of other forage species and facilitates the introduction of pioneer species (e.g., *Vachellia*) inside the mature forest fragments. In the past, the extraction of NTFP has been suggested as a sustainable method of using resources (Singh 1998; González-Insusti and Caballero, 2007); however, studies are urgently required in order to guide the generation of management practices that warrant the conservation and regeneration of TDF, since livestock production and wood extraction are converting mature forest into disturbed ones, and these into secondary vegetation.

#### Credit authors statement

OSC and AFP carried out the field measurements. SVD, OSC, and AFP performed the statistical analysis. AFP, OSC, SVD, GCC, and DMIM conceive the study and wrote the article.

#### Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper

#### Data availability

Data will be made available on request.

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#### Supplementary materials

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