Land abandonment as driver of woody vegetation dynamics in Tamaulipan thornscrub at Northeastern Mexico

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Background: Vegetation structure is defined as the temporal and spatial distribution of plant species in a particular site. Vegetation structure includes vertical and horizontal distribution and has been widely used as an indicator of successional changes. Ecological succession plays an essential role in the determination of the mechanisms that structure plant communities under anthropogenic disturbances. After an anthropogenic disturbance, such as grazing, forests follow changes in the original composition and vegetation structure, which eventually could restore some of their attributes to become mature forests again. To know how the time of abandonment affects woody plant communities, we ask the following questions: 1) How does the species richness, diversity, and vertical structure (A index) change concerning the time of abandonment? 2) Are species similarities among woody vegetation communities determined by land abandonment? and 3) Which woody species have the highest ecological importance in each successional stage?

Methods: We explored how successional stages after land abandonment mediated the species richness, species diversity (alpha and beta), and ecological importance value index on four areas of Tamaulipan thornscrub. We selected four areas that differed in time of abandonment: 10, 20, 30, and > 30 years. The first three areas were used for cattle grazing, whereas the > 30-year area was selected as a control since it does not have a record of disturbance by cattle grazing or agriculture. During the summer of 2012, we randomly established four square plots (40 x 40 m) in each area, separated at least 200 m from each other. In each plot, we recorded all woody individuals per species with a basal diameter ≥ 1 cm at 10 cm above ground level. We estimated species richness indices, species diversity (alpha and beta), and ecological importance value index.

Results: We recorded 27 woody species belonging to 23 genera and 15 families. Fabaceae accounted for 40% of the species. *Acacia farnesiana* was the most important and abundant species in the first three successional stages. We suggested that older successional stages of Tamaulipan thornscrub promote woody plant communities, characterized by a higher complex structure than younger communities. We observed the highest species similarity between the sites with a closer time of abandonment, while the lowest similarity was shown between the sites with extreme time of abandonment. We conclude that Tamaulipan thornscrub shows a similar trend of ecological succession to other dry forests and the time of abandonment has a high mediation on plant dynamics in the Tamaulipan thornscrub. Also, we stand out the importance of secondary forests for Tamaulipan thornscrub woody plant communities. Finally, we recommended future studies include aspects of regeneration speed, the proximity of mature vegetation,

and the interactions of plants with their seed dispersers.

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Abstract

Background: Vegetation structure is defined as the temporal and spatial distribution of plant species in a particular site. Vegetation structure includes vertical and horizontal distribution and has been widely used as an indicator of successional changes. Ecological succession plays an essential role in the determination of the mechanisms that structure plant communities under anthropogenic disturbances. After an anthropogenic disturbance, such as grazing, forests follow changes in the original composition and vegetation structure, which eventually could restore some of their attributes to become mature forests again. To know how the time of abandonment affects woody plant communities, we ask the following questions: 1) How does the species richness, diversity, and vertical structure (A index) change concerning the time of abandonment?

31   2) Are species similarities among woody vegetation communities determined by land
32   abandonment? and 3) Which woody species have the highest ecological importance in each
33   successional stage?

34   **Methods**: We explored how successional stages after land abandonment mediated the species
35   richness, species diversity (alpha and beta), and ecological importance value index on four areas
36   of Tamaulipan thornscrub. We selected four areas that differed in time of abandonment: 10, 20,
37   30, and > 30 years. The first three areas were used for cattle grazing, whereas the > 30-year area
38   was selected as a control since it does not have a record of disturbance by cattle grazing or
39   agriculture. During the summer of 2012, we randomly established four square plots (40 x 40 m)
40   in each area, separated at least 200 m from each other. In each plot, we recorded all woody
41   individuals per species with a basal diameter $\geq$ 1 cm at 10 cm above ground level. We estimated
42   species richness indices, species diversity (alpha and beta), and ecological importance value
43   index.

44   **Results**: We recorded 27 woody species belonging to 23 genera and 15 families. Fabaceae
45   accounted for 40% of the species. *Acacia farnesiana* was the most important and abundant
46   species in the first three successional stages. We suggested that older successional stages of
47   Tamaulipan thornscrub promote woody plant communities, characterized by a higher complex
48   structure than younger communities. We observed the highest species similarity between the
49   sites with a closer time of abandonment, while the lowest similarity was shown between the sites
50   with extreme time of abandonment. We conclude that Tamaulipan thornscrub shows a similar
51   trend of ecological succession to other dry forests and the time of abandonment has a high
52   mediation on plant dynamics in the Tamaulipan thornscrub. Also, we stand out the importance of
53   secondary forests for Tamaulipan thornscrub woody plant communities. Finally, we
54   recommended future studies include aspects of regeneration speed, the proximity of mature
55   vegetation, and the interactions of plants with their seed dispersers.

56   *Keywords*: Cattle grazing, Ecological succession, Plant dynamics, Plant diversity, Tamaulipan
57   thornscrub, Vegetation disturbance, Vegetation structure.

58

Introduction

59

60   Tropical dry forests are among the most threatened ecosystems in Latin America (Garcia-Millán
61   & Sánchez-Azofeifa, 2018), due to the land-use change for many productive activities among we
62   can include agriculture and cattle expansion (Portillo-Quintero & Sánchez-Azofeifa, 2010).
63   These activities affect directly the dry forest biodiversity and structure since these ecosystems
64   have one of the most endemisms in the globe (Sánchez-Azofeifa et al., 2009).

65   Vegetation structure is defined as the temporal and spatial distribution of plant species in a
66   particular site; it has been widely used as an indicator of successional changes through time after
67   a process of disturbance in natural ecosystems (Domínguez-Gómez et al., 2013; Kulmatiski &
68   Beard, 2019). Vegetation structure includes vertical and horizontal distribution of vegetation,
69   spatial patterns, and size and age of trees (Oliver & Larson, 1996). These factors are important in
70   ecosystem studies since it can be inferred whether an ecosystem reached the mature successional
71   stage (Domínguez-Gómez et al., 2013). Studies of ecological succession play an important role
72   in the determination of the relative importance of mechanisms that structure plant communities
73   under different environmental conditions (Choung et al., 2020; McCook, 1994; van Andel,
74   Bakker & Grootjans, 1993). Additionally, understanding the forest successional dynamics in
75   forests is a crucial issue for the establishment and design of conservation strategies (Sánchez-
76   Azofeifa et al., 2005; Quesada et al., 2009). According to Falkowski, Chankin & Diemont
77   (2020), several factors affect secondary forest succession, among them: abiotic conditions, the
78   surrounding space, and land-use history (Quesada et al., 2009). The latter has been recognized as
79   one of main drivers of changes in vegetation successional dynamics (Baeza et al., 2007; Quesada
80   et al., 2009; Pequeño-Ledezma et al., 2018). The land-use change is defined as the modification
81   of native vegetation into areas for productive purposes (Alanís et al., 2015; Falkowski, Chankin
82   & Diemont, 2020; Pequeño-Ledezma et al., 2018; Zhang et al., 2018) like cattle grazing,
83   agriculture, or mineral extraction.

84   After an anthropogenic disturbance, such as logging, grazing, or farming, forests follow a
85   revegetation process characterized by changes in the original floristic composition and
86   vegetation structure (Kitenberga et al., 2020; Lohbeck et al., 2020; Tálamo et al. 2020; Zhang et
87   al., 2018). These natural successional processes eventually could restore the attributes of
88   degraded ecosystems in old-growth forests (DeWalt, Maliakal & Denslow, 2003). Nevertheless,
89   despite their importance, the successional trajectories of plant communities (mainly in dry or
90   deciduous forests) after land abandonment are still poorly understood (Bonet & Pausas, 2004;
91   Quesada et al., 2009). Thus the changes in vegetation structure, composition, and abundance are
92   important to understand the potential driver of long-term land abandonment on the configuration
93   of mature ecosystems of Tamaulipan thornscrub.

94   Sarmiento-Muñoz (2019) found that the Tamaulipan thornscrub areas used for grazing
95   could affect the natural ecological succession of the ecosystem. Recently, several studies
96   highlighted the structure of regenerated woody communities resulting from secondary succession
97   (Alanís-Rodríguez et al., 2008; González-Rodríguez et al., 2010; Jiménez-Pérez et al., 2009,
98   2012, 2013; Patiño-Flores et al., 2021), but none of them explored the successional trajectories
99   after land abandonment under a well-defined chronosequence. Although plant diversity has been
100   considered in many studies on Tamaulipan thornscrub and its importance is well known (Alanís-
101   Rodríguez et al., 2015a). It is not yet clear how land abandonment (successional changes)
102   contributes to the changes in woody plant diversity, how the tree and shrub species are replaced

103 by others, or how these replacement contributes to the general structure of Tamaulipan
104 thornscrub.

105   In this study, we explored how the successional stages of four areas of Tamaulipan
106 thornscrub drive the changes in species richness, species diversity (alpha and beta), vertical
107 structure of vegetation, and ecological importance value index. Specifically, we wanted to know
108 (1) how species richness, diversity, and vertical structure (A index) change concerning the time
109 of abandonment? (2) Species similarities among vegetation communities are related to land-use
110 abandonment?, and 3) Which species are the most important within each successional stage?
111 According to this background and questions, we elaborated three main hypotheses: 1) the earlier
112 successional areas would have lower values of species richness, species diversity, and the species
113 height profile index than sites with the longest time of abandonment; 2) the species similarity
114 among sites will be related to the time of abandonment; therefore we would find the lowest
115 species similarity between the sites with early and late years of abandonment; and 3) the species
116 with a higher ecological importance value in early successional stages will not have high
117 importance values in sites with vegetation on late-successional stage.

118

Materials & methods

119 **Materials & methods**

120 *Study area*

121 The study area was located in a Tamaulipan thornscrub in Linares, Nuevo Leon state,
122 Northeastern Mexico (25°09′ - 24° 33′ N and 99° 54′ - 99° 07′ W; Figure 1) at an elevation of
123 350 - 411 m a.s.l. This area has an arid desert-warm climate with a maximum amount of rainfall
124 during September (INEGI, 1986). The area has an annual average temperature of 23.7 °C and
125 annual cumulative precipitation of 810 mm (Martínez-Adriano et al., 2021). Low hills with
126 gentle slopes are predominant in the area, mainly with Vertisol soils (INEGI, 1986). The four
127 selected areas had similar topographic conditions and only differed in the years of abandonment.

128   We selected four areas with different time of abandonment after last recorded human
129 disturbance occurs (10, 20, 30, and > 30 years). The first three areas were used for cattle grazing,
130 whereas the > 30-year area was selected as a control. The native vegetation in the three grazed
131 areas was removed with heavy machinery and replaced with forage grass (*Cenchrus ciliaris* L.)
132 as food for cattle. Grazing areas were excluded 10, 20, 30, and > 30 years before the start of this
133 study and it allowed the natural plant succession. The evaluated areas were located next to plant
134 communities that are growing after livestock activity. The control area (> 30 yr) shows
135 Tamaulipan thornscrub vegetation without evidence of disturbance or land-use changes. Local
136 people used the control area exclusively to collect wild fruits and firewood from the ground. This
137 information was corroborated by satellite images and personal interviews. Additionally, we

138 highlighted that EA obtained verbal permission from the owners of the four sites used to conduct
139 this study.

Experimental design

141 During summer of 2012, we randomly established four square plots (40 x 40 m) in each
142 condition of abandonment separated by a minimum distance of 200 m. In each plot, we recorded
143 all woody individuals per species with a basal diameter $\geq$ 1 cm at 10 cm above ground level.
144 Total height (h) and basal diameter ($d_{0,10}$) were measured in all individuals of woody species.

145 We collected botanical samples of the woody plant species found in each plot for
146 taxonomic identification. The taxonomical identification was carried out by botanical experts and
147 by comparing our samples with specimens stored in the herbarium at Facultad de Ciencias
148 Forestales at Universidad Autónoma de Nuevo León. To confirm the current scientific names,
149 we used The Plant List web database (TPL, 2013).

Species richness and diversity

151 We determined the species richness as the number of species in each plot. Additionally, with the
152 identity and abundance of each woody species, we calculated Shannon's diversity index ($H' = -$
153 $\sum_{i=1}^{S} p_i \log_e p_i$), where S is the number of species, and pi is the proportion of individuals of species
154 i concerning the total number of individuals (Shannon, 1948). With H' values per site, we
155 estimated the effective number of species (^1D), based on the exponential of Shannon's index
156 (exp (H')) (Cultid-Medina & Escobar 2019; Jost 2006; Moreno et al. 2011). Additionally, we
157 calculated the vertical distribution of the species through the species height profile index (A-
158 index), which is also based on Shannon's index (H'). The A-index takes classifies the vertical
159 distribution of species into three height zones, zone I goes from 100-80 % (where the tallest tree
160 is 100%), zone II(80-50 %), and zone III (50-0 %) (see Pretzsch, 2009). Additionally, to know if
161 years of abandonment affect species similarity, we performed a cluster analysis of species
162 similarity in PAST software ver. 3.24 (Hammer, Harper & Ryan, 2011). This analysis was
163 performed with Bray-Curtis similarity and UPGMA algorithm and 9999 permutations (this
164 procedure allows to support each branch of the resultant grouping tree; Hammer, Harper & Ryan,
165 2011).

Importance values index

167 The importance value index is composed of three elements (*Abundance, Dominance, and*
168 *Frequency*) given by species within the studied community. We estimated the absolute
169 abundance per species (A_i) through dividing the number of records of species I (N_i) by the
170 sampling plot area (S, in m^2). We calculated the relative abundance of species using the
171 equation: $RA_i = (A_i/\Sigma A_i)*100$, where RA_i is the relative abundance of species i and ΣA_i is the
172 total abundance of species (Mostacedo & Fredericksen, 2000). To estimate dominance, we
173 extrapolated the basal area per hectare (G ha^{-1}) for each species. Absolute dominance is given by

174 $D_i = Ba_i/S$, where D_i is the absolute dominance of species i, Ba_i is the basal area of species i, and S
175 is the area of the sampling plot. Relative dominance was calculated using the equation
176 $Rd_i = (D_i/\Sigma D_i)*100$, where Rd_i is the relative dominance of species i, and ΣD_i is the total
177 dominance of species. Finally, the relative frequency is $Rf_i = (F_i/\Sigma F_i)*100$, where Fr_i is the relative
178 frequency of species i, F_i is the number of sites where the species i is present and ΣF_i is the total
179 frequency of all species (Edwards, May & Webb, 1994; Mostacedo & Fredericksen, 2000). Thus
180 the importance value index (IVI) per species (i) was computed as follows: $IVI_i = (Ar_i + Dr_i + Fr_i)/3$
181 (Mueller-Dombois & Ellenberg, 1974).

182 The volume above the ground of each site (m^3 ha^{-1}) was calculated as a measure of
183 woody plants per area. The volume per individual was estimated with the formula: $V = g*h*MC$.
184 Where V is the volume, g is the assumed circular section of the stem diameter ($d_{0.10}$), h is the
185 total height of the individual, and MC is the morphic coefficient. The value of MC for the
186 Tamaulipan thornscrub is a constant of 0.5 (Alanís-Rodríguez, Mora-Olivo & Marroquín de la
187 Fuente, 2020).

188 *Effect of years of abandonment on vegetation structure*

189 To evaluate the differences among areas we used the analysis of variance and HSD posthoc
190 Tukey test when differences were found (both functions from "agricolae" R package; de
191 Mendiburu, 2020). ANOVA assumptions of normality and homoscedasticity were tested
192 graphically through residual plots and analytically with functions Shapiro test (for normality) and
193 Levene test (for homoscedasticity), both functions inside "car" R package (Fox & Weisberg,
194 2019). When the assumption of equal variances was not accomplished, we used the ANOVA test
195 assuming unequal variances (on the one-way function) and the Games-Howell posthoc test from
196 "userfriendlyscience" package (Peters, 2018) for the R software ver. 4.0.2 (R Core Team, 2020).

197

198 **Results**
199 We recorded 27 woody species, belonging to 23 genera and 15 families. The families with
200 highest species number were Fabaceae (11 species), Rubiaceae (2), and Rutaceae (2). While the
201 most representative genera were *Acacia* (3), *Parkinsonia,* and *Randia* (both with two species
202 each; see Table 1). We observed *Acacia farnesiana* as the unique plant species found in all
203 conditions of abandonment, while species like *Cordia boissieri*, *Celtis pallida*, *Prosopis*
204 *laevigata,* and *Sideroxylon celastrinum* were observed in areas ≥ 20 yr of abandonment. On the
205 other hand, we found that *Bernardia myricifolia*, *Condalia hookeri*, *Eysenhardtia polystachya,*
206 *Leucophyllum frutescens,* and *Yucca filifera* only occurring in > 30 yr site (Table 1).

207 Species richness and effective number of species. We found that the > 30 yr site showed the
208 highest species richness (21 taxa) and the number of species decreased as the disturbance became
209 more recent ($F_{3, 12} = 17.43$; $p < 0.001$). Likewise, for the effective number of species (^1D), we
210 found a similar pattern ($F_{3, 12} = 22.76$; $p < 0.001$), where the > 30 yr site had the highest number

211   of effective species (^1D = 9.3), followed by the 30 yr (^1D = 4.53), 20 yr (^1D = 2.39), and the
212   lowest was found in the 10 yr site (^1D = 1.28).

213   Species Height Profile Index (A-index). For this index, the residuals were normally distributed
214   (W = 0.98, p = 0.97) and the variance was not homogeneous (Levene's test: F = 4.58; p = 0.02).
215   The one-way analysis showed differences among the areas with times of abandonment ($F_{3,\ 6.25}$ =
216   21.135; p = 0.0011). The highest altitudinal floors were recorded in the > 30 yr area (A = 2.68 ±0
217   .18), while the lowest altitudinal floors were observed in the 10 yr area (A = 1.01 ± 0.37).

218   *Importance value Index*

219   Abundance. We found that the area > 30 yr showed the highest abundance of woody plants
220   (1828 ± 299 N·ha^{-1}; $F_{3,\ 12}$ = 4.824; p = 0.019), while the lowest abundance was observed in the
221   30 yr area (762 ± 336 N ha^{-1}) (Table 2). We observed that *Acacia farnesiana* was the most
222   abundant woody species in all successional stages except in the > 30 yr area. Nevertheless, the
223   abundance of *A. farnesiana* decreased as the time of abandonment increased (from 1426 to 156
224   individuals ha^{-1}) and became less abundant than *Havardia pallens*, *Diospyros texana*, *Acacia*
225   *amentacea*, and *Cordia boissieri* in the > 30 yr area (Table 2).

226   Dominance. The dominance showed differences among areas ($F_{3,\ 12}$ = 5.629; p = 0.012). The
227   highest values of dominance were recorded in the > 30 yr site with 8.86 ± 1.60 G ha^{-1}, however,
228   this site only showed differences from the 10yr site (2.19 ± 0.52 G ha^{-1}; Table 2). We observed
229   that *Acacia farnesiana* was the most dominant species in the three earliest successional stages.
230   While, in the > 30 yr area the species with highest dominance were *Diospyros texana*, *Cordia*
231   *boissieri,* and *Havardia pallens* (Table 2).

232   Volume. We found that the control area (> 30 yr) showed the highest wood volume (22.21 ± 3.61
233   m^3 ha^{-1}; $F_{3,\ 12}$ = 4.765; p = 0.0206), and the lowest was observed in the 10 yr area (4.13 ± 0.48
234   m^3 ha^{-1}). Wood volumes were 21.45 ± 13.55 for the 20 yr site and 19.58 ± 6.94 m^3 ha^{-1} for the 30
235   yr site.

236   IVI. We observed that *Acacia farnesiana* was the most important species in all successional
237   stages, except in the control area (> 30 yr). Nevertheless, as the time after perturbation increased
238   other species appear to be more important, especially those with tree-like characteristics (tall
239   trees with wide canopy) such as *D. texana, C. boissieri,* and *H. pallens* (Table 2).

240   *Similarity among areas with different years of abandonment*

241   We found the highest similarity between areas with closer years of abandonment and decreased
242   with the temporal distance of abandonment. The most similar areas were 10 yr and 20 yr,
243   followed by 20 yr and 30 yr (Table 3). The cluster analysis showed three well-defined groups
244   (Cophenetic correlation = 0.95), one formed by 10 yr and 20 yr sites, and the 30 yr and > 30 yr
245   sites in solitary branch each (Table 3; Figure 2).

246

Discussion

248 In this study, we simultaneously explored the changes in species richness, diversity, and
249 importance value index among four sites with different times of abandonment in the Tamaulipan
250 thornscrub.

251   We found 27 woody species in this study which represents the same number of plant
252 species reported by Jiménez-Pérez et al. (2009) and similar to the species recorded by Alanís-
253 Rodríguez et al. (2013; 2015b) (30 plant species) in the Tamaulipan thornscrub. While
254 Canizales-Velázquez et al. (2009) reported 52 plant species in a piedmont scrub (a value almost
255 two times higher than our results). This means that our study represents at least more than half of
256 the plant species of these previous studies. Additionally, we observed that Fabaceae was the
257 family with the highest number of species. These results agree with previous floristic studies in
258 remnants of Tamaulipan thornscrub, where Fabaceae was the family with a higher number of
259 species (Alanís-Rodríguez et al., 2015b; González-Rodríguez et al., 2010; Jiménez-Pérez et al.,
260 2009; Molina-Guerra et al., 2013). This indicates that the family possibly has species with the
261 potential to adapt to the conditions that occur at sites with different successional stages (e.g.
262 humidity, exposure, radiation).

263   Our first hypothesis said that the early successional sites would have lower values of
264 species richness, diversity, and A index than sites with earlier-time of abandonment. This
265 prediction is supported by our results since our findings showed that species richness, effective
266 species index, and A index were higher in the >30yr site, while the number of species decreased
267 when the successional stage was more recent. These results are similar to the general pattern for
268 scrubs found in previous studies where the oldest plant communities have higher plant species
269 richness and diversity (Abella, 2010; Alanís-Rodríguez et al., 2018; Connell, 1978; Ugalde,
270 Granados-Sánchez & Sánchez-González, 2008). Similarly, several studies highlight an increase
271 in species richness and diversity of tree communities from early to late successional stages in
272 tropical deciduous forests (Quesada et al., 2009). However, previous studies found that certain
273 attributes of plant communities (as basal area) are predicted adequately from chronosequences
274 (Chadzon et al., 2007; Pascarella et al., 2004) whereas differences are found concerning species
275 richness and species composition (Chazdon et al., 2007; Johnson & Miyanishi, 2008; Pascarella
276 et al., 2004; Sheil, 2001). Regarding abundance and biomass (volume) we found similar patterns
277 that a study on the Sonoran thornscrub, which also found that older-growth forests have a more
278 complex structure, higher biomass, and individual densities than younger ones (Álvarez-Yépiz et
279 al., 2008). Thus, we corroborated that plant communities that occur in later successional stages
280 within Tamaulipan thornscrub, also could have more complex structure (in both horizontal and
281 vertical stratification), than those that occur in early successional stages. This makes us notice
282 the importance of ecological succession in the dynamics and structure of Tamaulipan thornscrub
283 ecosystems.

284   Our second hypothesis said that species similarities among sites will be related to the
285   time of abandonment; therefore, we would find the lowest species similarity between the sites
286   with early and late years of abandonment. Our results supported this prediction and were similar
287   to the findings of Alanís-Rodríguez et al. (2018) since the highest similarity occurred among
288   areas with a similar time of abandonment. Additionally, we found the same pattern of similarity
289   to the findings reported by Sánchez-Reyes et al. (2021), where the lowest similarity was
290   observed between the two sites with an extreme time of abandonment (10 yr and 30 yr in our
291   study, and 4 yr and conserved areas in the study of Sánchez-Reyes et al. (2021). Kalacska et al.
292   (2004) also found a lower similarity between the early and late stages of successional stages.
293   However, we found the highest similarity among 10 and 20 yr sites, but Connell (1978) attributes
294   this pattern to the possible coexistence of typical species of early, intermediate, and late-
295   successional stages (Connell, 1978). Thus our results suggest that the Tamaulipan thornscrub
296   also follows a similar trend to dry forests in tropical regions.

297   Our third hypothesis said that species with a high ecological importance value in early
298   successional stages will not have high importance values in fragments with vegetation in the late-
299   successional stage. In this sense, we found that Fabaceae species have high representativeness in
300   all stages of abandonment, like recent studies findings at Tamaulipan thornscrub (Alanís-
301   Rodríguez et al., 2018; Pequeño-Ledezma et al., 2018). It has been documented that Fabaceae
302   species play an important role as pioneer species and can be found in the initial stages of
303   ecological succession due to their capacity to fix atmospheric nitrogen and resistance to drought
304   (Jia et al., 2020; Zhou et al., 2019).. These adaptations could give to this plant family the ability
305   to maintain high abundances in disturbed areas, mainly in the early successional stages.
306   Contrary, in late-successional stages, Fabaceae species are generally less important, because
307   these species require open sites with abundant light.

308   At the species level, we found that *Acacia farnesiana* was the woody species with the
309   highest abundance and IVI values in the first three successional stages (10, 20, and 30 years of
310   abandonment), but in the >30 yr area *Havardia pallens* and *Diospyros texana* become the species
311   with highest IVI values. These results are similar to the findings reported in several studies from
312   Tamaulipan thornscrub (Alanís-Rodríguez et al., 2018; González-Rodríguez et al., 2010;
313   Pequeño-Ledezma et al., 2017; Pequeño-Ledezma et al., 2018), where *A. farnesiana* (along with
314   other native species of Tamaulipan thornscrub) was recorded as species with higher dominance
315   in the four areas of Tamaulipan thornscrub. This could indicate that *A. farnesiana* could play an
316   important role in the early stages of the successional process at Tamaulipan thornscrub
317   vegetation. Thus, *A. farnesiana* could have an essential function in the regeneration of
318   ecosystems that have disturbance such as grazing.

319   In addition to all aforementioned, we highlight that Tamaulipan thornscrub areas have a
320   relatively fast successional recovery (~30 years). However, Quesada et al. (2009) said that
321   regeneration rates in dry forests show relatively lower regeneration rates than we think because
322   in almost secondary forests the coppicing from remainings (stumps and roots) after disturbance

323   theoretically allows these forests to reach maturity faster than the other forests (Ewel, 1977;
324   Murphy and Lugo, 1986). In the case of this study, the areas have a well-defined history of use
325   for cattle grazing (according to owners), therefore their rapid recovery is basically due to the
326   introduction of pioneer species by some seed vector of surrounding matrix of vegetation. Then,
327   we recommend that future studies also explore the distance of the seed sources from the
328   surrounding matrix to the studied sites and the intensity of use before abandonment (Guariguata
329   and Osterag, 2001); services of seed vectors, which are variables that have an important role in
330   plant dynamics in degraded sites (Ramos-Robles et al., 2018); and changes in the functional
331   characteristics of woody species within fragments (Guariguata and Osterag, 2001). Thus we
332   highlight the importance of secondary forests for Tamaulipan thornscrub, as they harbor a higher
333   woody plant diversity, which in turn could have the capacity to support the associated fauna that
334   occurs in places with intact vegetation.

335

Conclusions

337   With the resulting data, we observed the successional trajectory of the Tamaulipan thornscrub
338   fragments. We highlighted that the advance of the successional stages in post-grazing sites of
339   Tamaulipan thornscrub (latest successional stages) generates communities with higher species
340   richness and a higher complex structure than those communities with earliest time of
341   abandonment. The highest similarity among sites with different time of abandonment was
342   observed between sites with closer time of abandonment. On the other hand, a lower similarity
343   was shown between the sites with extremes time of abandonment. *Acacia farnesiana* was the
344   most important and abundant species in the first three successional stages, so we propose it as
345   good pioneer species for restoration programs on Tamaulipan thornscrub ecosystems. We
346   conclude that Tamaulipan thornscrub shows a similar trend of ecological succession to other dry
347   forests and the time of abandonment has a high mediation on plant dynamics in the Tamaulipan
348   thornscrub. Also, we stand out the importance of secondary forests for Tamaulipan thornscrub
349   communities, as they harbor a higher woody plant diversity, which in turn could have the
350   capacity to support the associated fauna that occurs in sites with intact vegetation. Finally, we
351   recommended for future successional studies include aspects of regeneration speed, the
352   proximity of mature vegetation within the matrix where these studied fragments are found, and
353   the interactions of plants with their seed dispersers.

354

Acknowledgments

356   We thank R. Domínguez who helped with plant species identification. N. Leal helped with map
357   elaboration.

358

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Figure 1

Study area location.

A) Mexico state division. B) Nuevo Leon State municipalities. B) Studied areas localization within Linares municipality.

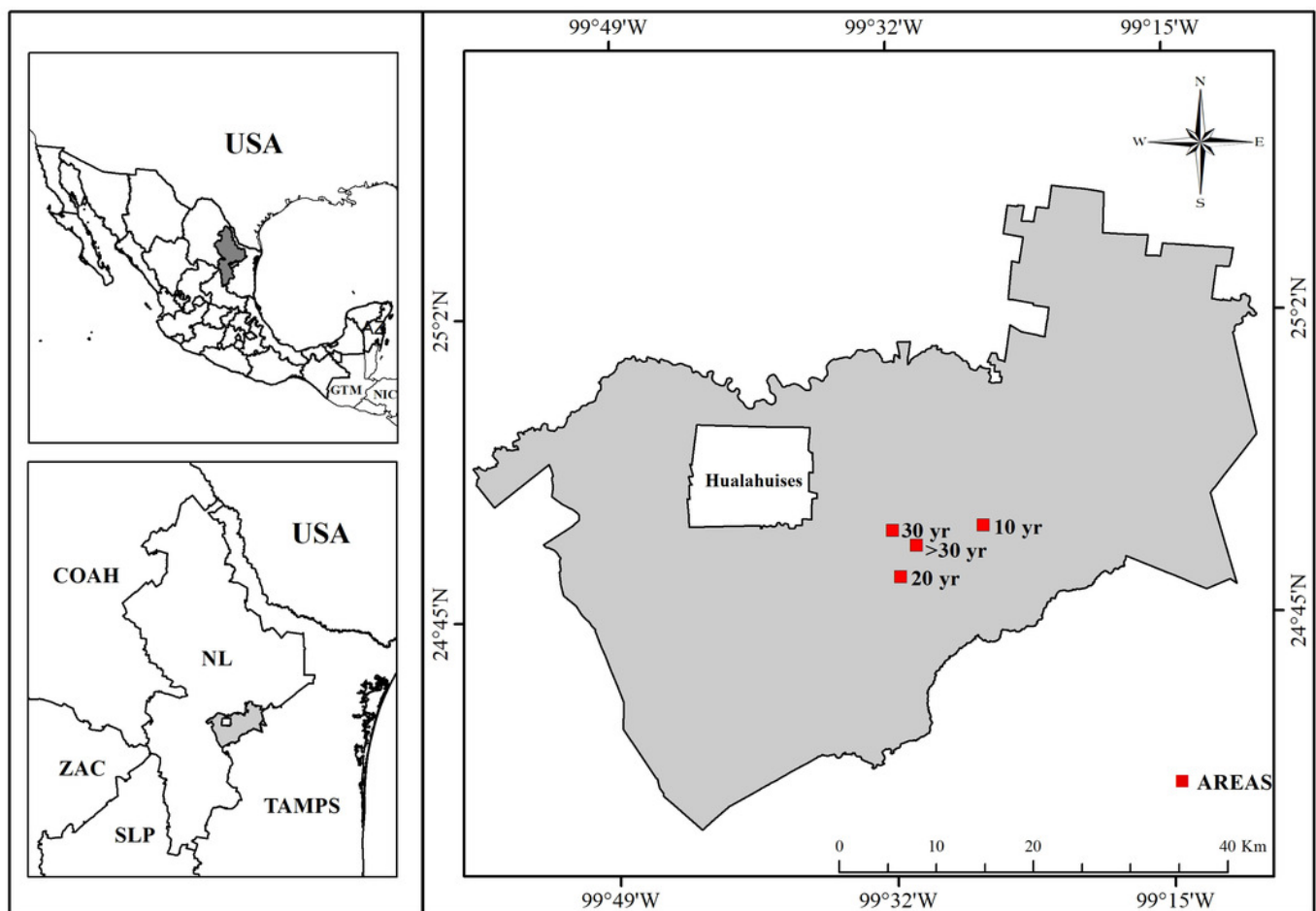
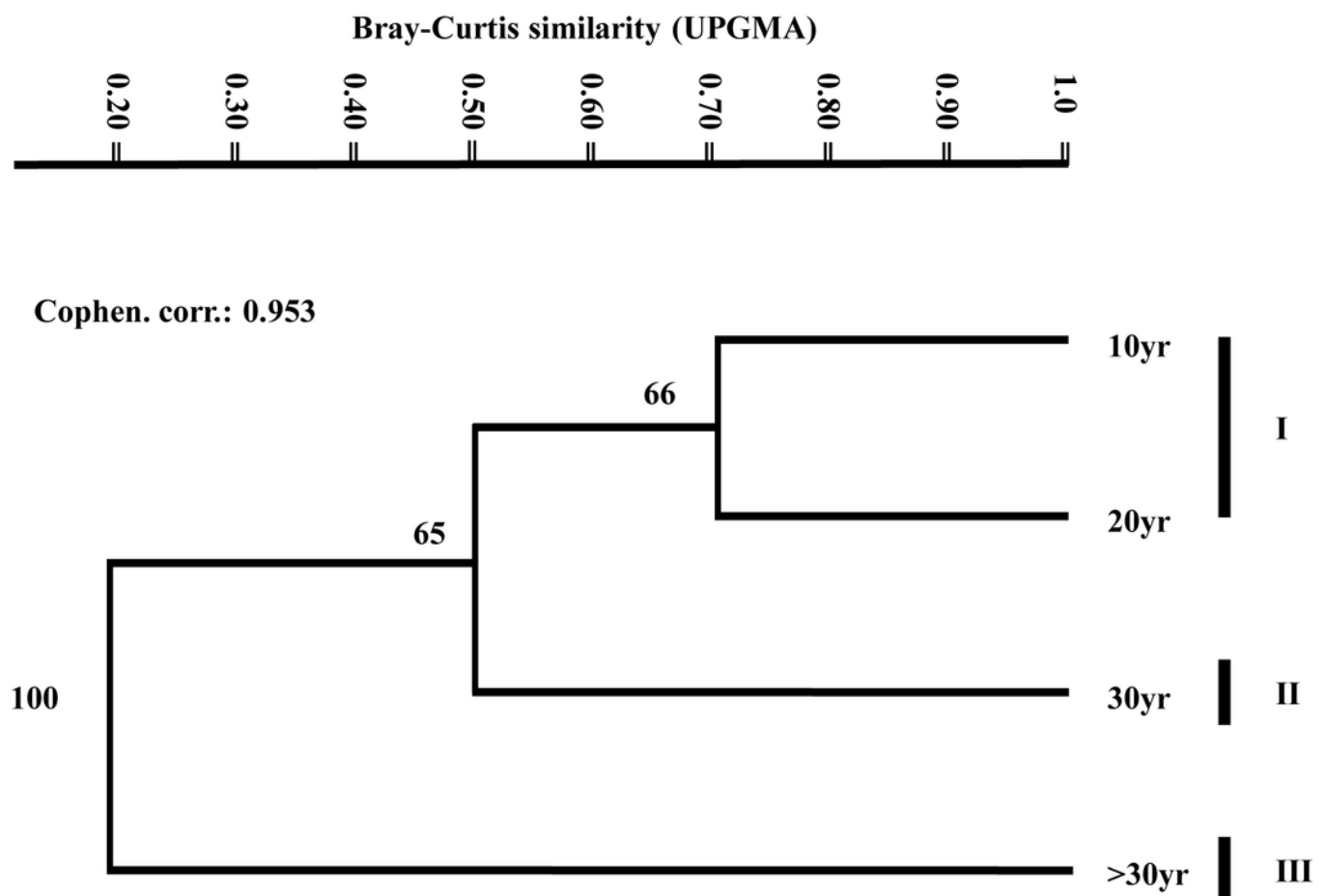



Figure 2

Bray-Curtis similarity among species diversity of the studied communities.

The numbers close to each branch are the percentage of permutations that each node is still supported on the final grouping dendrogram (see Hammer, Harper & Ryan, 2001). The cophenetic correlation (Cophen. corr.) obtained, showed a good measure of degree of fit for the classification of our data set (Saraçli, Doğan & Doğan, 2013).

List of woody plant species recorded in the study area.

The scientific names of woody plants were obtained from The Plant List web page (TLP 2013).

Family	Plant species
Boraginaceae	*Cordia boissieri* A. DC.
Cannabaceae	*Celtis pallida* Torr.
Koeberliniaceae	*Koeberlinia spinosa* Zucc.
Ebenaceae	*Diospyros texana* Scheele
Euphorbiaceae	*Bernardia myricifolia* (Scheele) S.Watson
Fabaceae	*Acacia amentacea* DC.
Fabaceae	*Acacia farnesiana* (L) Willd.
Fabaceae	*Acacia rigidula* Benth.
Fabaceae	*Caesalpinia mexicana* A. Gray
Fabaceae	*Ebenopsis ebano* (Berland.) Barneby & J.W.Grimes
Fabaceae	*Eysenhardtia polystachya* (Ortega) Sarg.
Fabaceae	*Havardia pallens* (Benth.) Britton & Rose
Fabaceae	*Mimosa monancistra* Benth.
Fabaceae	*Parkinsonia aculeata* L.
Fabaceae	*Cercidium texanum* A.Gray
Fabaceae	*Prosopis laevigata* (Willd.) M.C.Johnst.
Asparagaceae	*Yucca filifera* Chabaud
Oleaceae	*Forestiera angustifolia* Torr.
Rhamnaceae	*Condalia hookeri* M.C.Johnst.
Rubiaceae	*Randia obcordata* S.Watson
Rutaceae	*Helietta parvifolia* (A. Gray) Benth.
Rutaceae	*Zanthoxylum fagara* (L.) Sarg.
Sapotaceae	*Sideroxylon celastrinum* (Kunth) T.D.Penn.
Scrophulariaceae	*Leucophyllum frutescens* (Berland.) I.M. Johnst.
Simaroubaceae	*Castela erecta* Turpin
Zygophyllaceae	*Porlieria angustifolia* (Engelm.) A. Gray

Woody plant species recorded in the study area.

The absolute abundance (Nha), dominance (Gha), and importance value index (IVI) of each plant species per condition of abandonment. In bold, we highlight the highest values for each site.

Species	10 years			20 years			30 years			> 30 years		
	Nha	Gha	IVI	Nha	Gha	IVI	Nha	Gha	IVI	Nha	Gha	IVI
A. amentacea	70.31	0.20	15.73							215.63	0.49	8.17
A. farnesiana	**1415.63**	**1.97**	**76.16**	**931.25**	**5.88**	**60.56**	**459.38**	**6.02**	**49.49**	156.25	0.53	7.24
A. rigidula							7.81	0.05	1.64			
B. myricifolia										1.56	<0.01	0.64
C. boissieri				20.31	0.19	4.66	4.69	0.02	2.53	185.94	1.77	12.45
C. erecta							26.56	0.13	5.03	4.69	0.01	0.72
C. hookeri										51.56	0.38	4.76
C. mexicana				23.44	0.13	2.87						
C. pallida				29.69	0.04	2.62	17.19	0.06	5.45	28.13	0.09	2.06
D. texana							45.31	0.14	5.90	**429.69**	**2.34**	**19.01**
E. ebano				4.69	0.07	2.03				31.25	0.08	1.47
E. polystachya										54.69	0.19	4.08
F. angustifolia				15.63	0.02	2.13				4.69	0.03	0.78
G. angustifolium				1.56	0.00	1.64				6.25	0.02	1.99
H. pallens	9.38	0.02	4.16	28.13	0.13	4.58				434.38	1.30	15.18
H. parvifolia				3.13	0.01	1.71				31.25	0.11	2.77
K. spinosa							9.38	0.02	1.60			
L. frutescens										1.56	0.01	0.65
M. monancistra				1.56	0.00	1.64						
P. aculeata							20.31	0.18	2.74			
P. laevigata				85.94	0.67	11.95	90.63	0.99	12.53	20.31	0.07	1.21
P. texana							31.25	0.24	4.59	31.25	0.18	3.05
R. obcordata				4.69	0.00	1.73				3.13	0.01	0.68
S. celastrinum				7.81	0.02	1.88	28.13	0.09	3.83	78.13	0.51	5.72
Y. filifera										4.69	0.55	3.35
Z. fagara	4.69	0.01	3.95				21.88	0.09	4.66	53.13	0.18	4.04
Add	1500.00	2.20	100.00	1157.81	7.15	100.00	762.50	8.03	100.00	1828.13	8.86	100.00

Bray-Curtis similarity matrix.

In bold letters, we show the highest values of similarity between paired areas.

	10	20	30	>30
10	1.000	**0.708**	0.410	0.145
20		1.000	**0.599**	0.186
30			1.000	0.255
>30				1.000