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Research article

Abundance and diversity in reforestation and natural regeneration of the Tamaulipan Thornscrub under selective management practices

Abundancia y diversidad en reforestación y regeneración natural del Matorral Espinoso Tamaulipeco bajo manejo selectivo

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Abstract

The Tamaulipan Thornscrub (TTS) is distributed in Northeastern Mexico, especially in the states of *Nuevo León*, *Tamaulipas* and *Coahuila*. This subtropical ecosystem is highly fragmented due to land-use changes. To mitigate the associated impacts, active restoration projects are being promoted. The objective of this study was to compare species diversity and abundance between natural Regeneration and a Reforestation area in the TTS. The area was reforested with 25 native species and subjected to selective weeding, supplemental irrigation, pruning, and phytosanitary care. Five years after planting, individuals of shrub and tree species that had germinated in the area were counted, estimating abundance as well as alpha and beta diversity indexes. A total of 29 species were recorded in the Regeneration area, 21 of which were shared with the Reforestation. Abundance was higher in the Reforestation (4 875 individuals ha⁻¹) than in the Regeneration (2 286 individuals ha⁻¹). The Margalef Index showed a significant difference ($p=4.24e-05$), with greater richness in the Regeneration area. However, the Shannon Index ($p=0.2639$), true diversity ($p=0.2639$), Simpson Index ($p=0.7499$), and Simpson complement ($p=0.7499$) did not show significant differences. Among the beta diversity indexes, Sørensen Index indicated the highest similarity percentage, at 77 %. Although natural Regeneration presented higher species richness, both strata shared a similar abundance structure. Natural Regeneration, as a complement, could be a viable and cost-effective alternative for restoring the TTS, especially when surrounding vegetation fragments are preserved and the land-use history is considered.

Keywords: Alpha diversity, beta diversity, native species, ecological fragmentation, active restoration, species richness.

Resumen

El Matorral Espinoso Tamaulipeco (MET) se distribuye en el noreste de México, especialmente en Nuevo León, Tamaulipas y Coahuila. Este ecosistema subtropical presenta alta fragmentación debido al cambio de uso del suelo. Para mitigar los impactos asociados, se promueven proyectos de restauración activa. El presente estudio tuvo como objetivo comparar la diversidad y abundancia de especies entre la regeneración natural y una reforestación en el MET. El área se reforestó con 25 especies nativas y estuvo sujeta a deshierbe selectivo, riego complementario, podas y atención fitosanitaria. A cinco años de la plantación, se contabilizaron los individuos de especies arbustivas y arbóreas que germinaron en el área para estimar la abundancia y los índices de diversidad alfa y beta. Se registraron 29 especies en la regeneración, 21 compartidas con la reforestación. La abundancia fue mayor en la reforestación (4 875 ind. ha⁻¹) que en la regeneración (2 286 ind. ha⁻¹). El Índice de *Margalef* mostró diferencia significativa ($p=4.24e-05$), con mayor riqueza en la regeneración. Sin embargo, los índices de *Shannon* ($p=0.2639$), diversidad verdadera ($p=0.2639$), *Simpson* ($p=0.7499$) y su complemento ($p=0.7499$) no evidenciaron diferencias significativas. Entre los índices de diversidad beta, el de *Sørensen* indicó el mayor porcentaje de similitud con 77 %. Aunque la regeneración natural presentó mayor riqueza, ambas condiciones tuvieron abundancia similar. La regeneración natural como complemento podría ser una alternativa viable y económica para la restauración del MET, especialmente, si se conservan fragmentos de vegetación circundante y se considera el historial de uso del suelo.

Palabras clave: Diversidad alfa, diversidad beta, especies nativas, fragmentación ecológica, restauración activa, riqueza de especies.

Introduction

In Mexico, the Tamaulipas Thornscrub (TTS) covers approximately 3.3 million hectares and is distributed primarily in the states of *Nuevo León*, *Tamaulipas* and *Coahuila* (Comisión Nacional Forestal [Conafor], 2020). The vegetation is low, medium, and tall, primarily dense, with thorny and deciduous elements (NatureServe, 2009). The TTS provides food, nesting sites, and cover for many fauna species (Molina-Guerra et al., 2013). It is one of the most intensely impacted subtropical ecosystems in arid and semi-arid regions (NatureServe, 2009). It is experiencing decline and fragmentation due to, among other factors, land-use change (Torres-Barajas, 2018).

As a measure to mitigate the environmental impact associated with land-use change, legislation promotes actions such as active restoration or reforestation, such as planting, weeding, burning, or cutting to achieve a desired structure (Rey-Benayas et

al., 2008). This restoration generally uses nursery plants and has as its main objective the manipulation of disturbance regimes to accelerate the process of ecological succession (Chazdon & Guariguata, 2016).

Relatively few robust restoration studies exist for the Tamaulipas Thornscrub. Between 2016 and 2024, eight restoration initiatives involving this type of action were recorded, all in the state of *Nuevo León* (Velázquez-Rincón *et al.*, 2025).

Natural or passive regeneration occurs after a disturbance and involves colonization by shrubs and trees followed by secondary succession (Rey-Benayas *et al.*, 2008). This type of regeneration can come from pre-existing plant material in the area, such as seeds, roots, and shoots (Siyag, 1998). Passive regeneration has been evaluated in TTS in abandoned areas and areas with a history of livestock farming (Alanís-Rodríguez *et al.*, 2023; Molina-Guerra *et al.*, 2013; Patiño-Flores *et al.*, 2021), following agricultural use (Mora-Donjuán *et al.*, 2013), and in sites that were subjected to controlled burning (Alanís-Rodríguez *et al.*, 2020). Regarding the specific analysis of regeneration as a result of or in combination with reforestation actions, it has been documented for plantations with native TTS species (Mata-Balderas *et al.*, 2023; Patiño-Flores *et al.*, 2022) and with exotic species (Martínez-Hernández *et al.*, 2014).

The control of exotic or aggressive plant species is an intervention method to promote natural succession (Ribeiro-Rodrigues *et al.*, 2011). In the TTS, ecological restoration initiatives through reforestation, using nursery-produced, rescued, or relocated plants, integrate maintenance activities such as supplemental irrigation and the removal of grasses and forbs (Velázquez-Rincón *et al.*, 2025). However, no initiative considered woody species germinating from seeds that could be present in the soil, such as selection or marking to avoid removing or damaging them with weeding.

To contribute to the ecological restoration of the TTS in the *Pesquería* municipality, *Nuevo León*, reforestation with native species was carried out in 2017 and received supplemental maintenance, which included the removal of forbs and grasses. During the last two years, woody species that germinated from pre-existing seeds in the

understory were not removed. In this context, the objective of this study was to compare the diversity and abundance of species from the natural regeneration of the TTS and from reforestation. It was hypothesized that both abundance and diversity would be greater in reforested areas.

Materials and Methods

The study area is located in the *Pesquería* municipality, East of the *Monterrey* metropolitan area, in the state of *Nuevo León*, between 25°43'00.31"-25°43'05.60" N and 99°58'11.03"-99°58'23.82" W, with an average altitude of 312 m. It consists of a 3.8 ha property located on the South side of the *Pesquería* Power Plant, owned by *Techgen S. A. de C. V.*

The climate is (A)C(w_o)x', which corresponds to the semi-warm sub-humid group of group C, with an average annual temperature above 18 °C (García, 2004).

The soil types in the area are Rendzinas and Xerosols with medium texture and petrocalcic physical phase, as well as pelic Vertisols and fine-textured calcic Xerosols (Instituto Nacional de Estadística, Geografía e Informática [INEGI], 1986).

Reforestation and selective management of herbaceous plants and grasses

In 2017, the property was reforested. Its original vegetation was TTS at the time of reforestation. The land was home to secondary vegetation and a significant presence of exotic grasses such as *Cenchrus ciliaris* L., which were clearly highly disturbed due

to its history of extensive livestock use. Before reforestation, the land had been abandoned for approximately five years.

The preparation of the 38 000 m² site consisted of the manual and mechanical removal of grasses and secondary vegetation. A plan was designed for 11 reforestation areas with variable dimensions and shapes, bordered by paths between each area. Within the areas, the planting was staggered with a density of around 4 874 individuals per ha⁻¹. Native plants from regional nurseries were used, specifically 25 species belonging to 22 genera and 15 families. The species with the highest number of introduced plants were *Havardia pallens* (Benth.) Britton & Rose and *Leucophyllum frutescens* (Berland.) I. M. Johnst. During the first three years of monitoring, dead specimens were replaced with the same species.

Plantation maintenance activities included supplemental irrigation (monthly) of 20 liters per individual, formative pruning, and the removal of herbaceous plants and grasses to reduce competition for space and water. Starting in 2020, weeding was selective, which consisted of identifying and marking woody seedlings in the understory with brightly colored plastic tape to prevent them from being removed by machinery or hand tools during herbaceous clearing. Furthermore, operating staff were thoroughly trained to perform this task.

Data collection and analysis

Data collection was carried out during 2022. All plantation individuals were censused (38 000 m²), and the plantation areas were used as sampling units. The number of planted individuals per species (reforestation) and those that regenerated naturally in the understory (regeneration) were recorded in each area. Reforestation specimens of all species were producing seeds at the time of the assessment; therefore, the

regeneration seed may be the product of these individuals or of the area's preexisting seed bank. A plant identification guide for the region (Mora-Olivo & Martínez-Ávalos, 2012) was used to identify the species. Furthermore, the taxa were verified using Mexico's National Biodiversity Information System (Sistema Nacional de Información sobre Biodiversidad [SNIB], 2024). Abundance values (Magurran, 2004) per species for reforestation and regeneration were estimated per hectare. The abundance of species shared between the two strata was analyzed using the Mann-Whitney U test, as the data did not present a normal distribution ($p=6.03e-05$, $p=2.76e-06$) according to the Shapiro-Wilk test, and there was no homogeneity of variance (Levene's test).

Alpha diversity indices were also determined: Margalef's richness index (D_{Mg}) (Margalef, 1951), Shannon's diversity (H') (Shannon, 1948), Shannon's true diversity ($1D$), Simpson's diversity (D), and Simpson's complement ($1-D$) (Magurran, 2004), as well as beta diversity indices: Sørensen and Jaccard's (Magurran, 1988) and the Morisita-Horn index (Magurran, 2004). The normality of the indices was determined using the Shapiro-Wilk test (Table 1).

Table 1. p values for data normality tests (Shapiro-Wilk).

Stratum	Index				
	D_{Mg}	H'	$1D$	D	$1-D$
Reforestation	0.7337	0.9894	0.9865	0.5456	0.5456
Regeneration	0.5915	0.0022	0.0060	0.0002	0.0002

D_{Mg} = Margalef's richness index; H' = Shannon's diversity; $1D$ = Shannon's true diversity; D = Simpson's diversity; $1-D$ = Simpson's complement.

The homogeneity of variances of the indexes between the two strata was verified using Levene's test, with the following results: D_{Mg} ($p=0.0211$), H' ($p=0.8490$), $1D$ ($p=0.8040$), D ($p=0.5700$) and $1-D$ ($p=0.5700$).

The Margaleff index was analyzed using Welch's t test for normal distribution and unequal variances. The remaining indicators were analyzed using the Mann-Whitney U test with Holm's adjustment for false positives. All statistical analyses were performed using R software version 4.5.0 (R Core Team, 2025).

Results and Discussion

A total of 18 families, 29 genera, and 33 plant species were recorded in both strata. Reforestation represented 15 families, 22 genera, and 25 species (Table 2). Regeneration represented 15 families, 26 genera, and 29 species, of which 21 were shared with reforestation. The most highly represented families were Fabaceae, which contributed ten taxa in reforestation and 11 in regeneration; Rhamnaceae with four in regeneration and one in reforestation, and Euphorbiaceae and Cannabaceae, with two in each stratum (Table 2).

Table 2. Abundance of species recorded for reforestation (Ref) and regeneration (Reg).

Families	Species	Biological form	Abundance (individuals ha ⁻¹)	
			Ref	Reg
Asparagaceae	<i>Yucca filifera</i> Chabaud*	Tree	22.37	0.00
Berberidaceae	<i>Berberis trifoliolata</i> Moric.	Scrub	0.00	0.26
Cannabaceae	<i>Celtis laevigata</i> Willd.*	Tree	2.63	0.00
Cannabaceae	<i>Celtis pallida</i> Torr.*	Scrub	1.58	0.53
Celastraceae	<i>Schaefferia cuneifolia</i> A. Gray	Scrub	0.00	26.58

Cordiaceae	<i>Cordia boissieri</i> A. DC.*	Tree	203.42	31.84
Ebenaceae	<i>Diospyros texana</i> Scheele*	Tree	1.05	3.16
Ehretiaceae	<i>Ehretia anacua</i> (Terán & Berland.) I. M. Johnst.*	Tree	0.26	0.00
Euphorbiaceae	<i>Bernardia myricifolia</i> (Scheele) S. Watson	Scrub	0.00	1.05
Euphorbiaceae	<i>Croton incanus</i> Kunth*	Scrub	148.42	156.05
Fabaceae	<i>Ebenopsis ebano</i> (Berland.) Barneby & J. W. Grimes*	Tree	16.84	0.26
Fabaceae	<i>Erythrostemon mexicanus</i> (A. Gray) Gagnon & G. P. Lewis*	Tree	329.74	30.53
Fabaceae	<i>Eysenhardtia texana</i> Scheele*	Scrub	206.05	73.42
Fabaceae	<i>Havardia pallens</i> (Benth.) Britton & Rose*	Tree	1 339.74	61.58
Fabaceae	<i>Neltuma glandulosa</i> (Torr.) Britton & Rose*	Tree	310.26	4.47
Fabaceae	<i>Parkinsonia aculeata</i> L.*	Tree	535.79	0.26
Fabaceae	<i>Parkinsonia texana</i> (A. Gray) S. Watson*	Tree	9.74	240.26
Fabaceae	<i>Senegalia greggii</i> (A. Gray) Britton & Rose*	Scrub	0.26	5.26
Fabaceae	<i>Vachellia farnesiana</i> (L.) Wight & Arn.*	Tree	577.37	7.11
Fabaceae	<i>Vachellia rigidula</i> (Benth.) Seigler & Ebinger*	Scrub	196.84	535.79
Fabaceae	<i>Vachellia schaffneri</i> (S. Watson) Seigler & Ebinger	Tree	0.00	110.53
Fagaceae	<i>Quercus virginiana</i> Mill.*	Tree	2.11	0.00
Oleaceae	<i>Forestiera angustifolia</i> Torr.*	Scrub	3.16	1.05
Rhamnaceae	<i>Colubrina texensis</i> (Torr. & A. Gray) A. Gray	Scrub	0.00	122.11
Rhamnaceae	<i>Condalia hookeri</i> M. C. Johnst.*	Scrub	1.58	5.53
Rhamnaceae	<i>Karwinskia humboldtiana</i> (Schult.) Zucc.	Scrub	0.00	97.37
Rhamnaceae	<i>Condaliopsis obtusifolia</i> (Hook. ex Torr. & A. Gray) Suess.	Scrub	0.00	33.95

Rubiaceae	<i>Randia obcordata</i> S. Watson*	Scrub	0.53	1.58
Rutaceae	<i>Zanthoxylum fagara</i> (L.) Sarg.*	Scrub	241.32	471.84
Sapotaceae	<i>Sideroxylon lanuginosum</i> Michx.*	Scrub	5.26	6.32
Scrophulariaceae	<i>Leucophyllum frutescens</i> (Berland.) I. M. Johnst.*	Scrub	716.32	65.00
Simaroubaceae	<i>Castela texana</i> (Torr. & A. Gray) Rose*	Scrub	2.11	91.84
Zygophyllaceae	<i>Guaiaacum angustifolium</i> Engelm.	Scrub	0.00	100.00
Total			4 874.75	² 285.50

*Species used in initial reforestation. Ref = Reforestation; Reg = Regeneration.

The preeminence of the Fabaceae family in the natural regeneration processes of the TTS has been supported by multiple studies conducted in the state of *Nuevo León* on the structure and composition of vegetation in areas with a history of varied use (Alanís-Rodríguez *et al.*, 2020, 2023; Jiménez-Pérez *et al.*, 2013; Mata-Balderas *et al.*, 2023; Molina-Guerra *et al.*, 2013; Mora-Donjuán *et al.*, 2013; Patiño-Flores *et al.*, 2021, 2022).

In terms of abundance, reforestation gathered a total of 4 875 individuals per hectare (ind. ha⁻¹), higher than the 2 286 ind. ha⁻¹ in regeneration. This latter value was similar to the 2 055 ind. ha⁻¹ in a ten-year regeneration without selective management, although with 23 fewer species than in the present study (Patiño-Flores *et al.*, 2022). In contrast, in an 11-year regeneration that included hunting use, a higher abundance of 27 species was described (3 256 ind. ha⁻¹) (Mata-Balderas *et al.*, 2023). Likewise, the corresponding (4 766 ind ha⁻¹) regeneration of 26 species from the TTS in a 27-year-old *Eucalyptus* spp. plantation (Martínez-Hernández *et al.*, 2014) was more than double that of the present study, a mass that was greater than that recorded (735 ind. ha⁻¹) in an area with three years of post-fire regeneration (Alanís-Rodríguez *et al.*, 2020).

Regarding time, abundance was lowest (1 828 ind. ha⁻¹) in areas abandoned for more than 30 years (Alanís-Rodríguez et al., 2023); whereas, in the regeneration of areas with 20 years of abandonment, abundance was highest (16 983 ind. ha⁻¹) (Jiménez-Pérez et al., 2013).

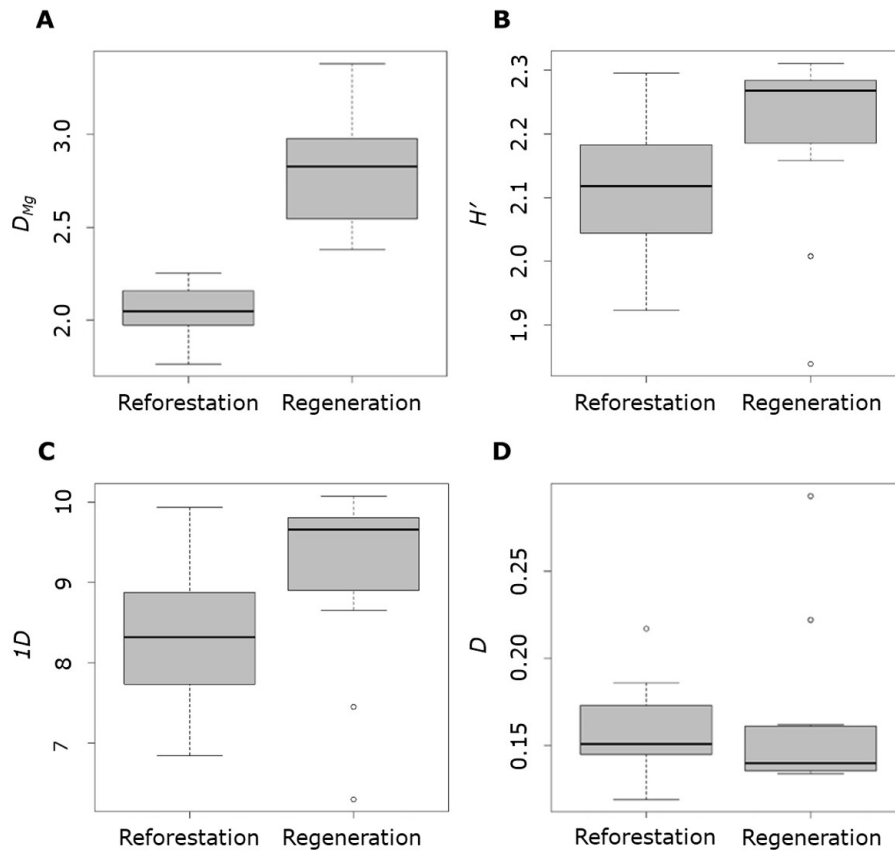
The higher abundance values obtained in the study described here suggest that this parameter could be affected by land use history and the time elapsed since the start of reforestation, in addition to the inherent environmental factors of each site. Furthermore, reforestation management actions such as marking and caring for woody species (which are not removed with weeding) could favor short-term abundance in the regenerating stratum.

In the present study, at the time of the assessment, the most abundant species in the reforestation were *Havardia pallens* and *Leucophyllum frutescens*, which is logical because they are considered typical of arid sites with high and low productivity, respectively (Navar et al., 2014). *Vachellia farnesiana* (L.) Wight & Arn., classified as a pioneer species, also stood out (Alanís-Rodríguez et al., 2023).

For regeneration, *Vachellia rigidula* (Benth.) Seigler & Ebinger, *Zanthoxylum fagara* (L.) Sarg. and *Parkinsonia texana* (A. Gray) S. Watson, along with *Cordia boissieri* A. DC. were the most important in an undisturbed TTS fragment in the same municipality (Alanís-Rodríguez et al., 2021). The abundance of *Vachellia rigidula* is consistent with the abundance (516 ind. ha⁻¹) in *Linares* municipality, *Nuevo León* (Martínez-Hernández et al., 2014). In contrast, the species with the lowest abundance in regeneration were *Parkinsonia aculeata* L., *Ebenopsis ebano* (Berland.) Barneby & J. W. Grimes and *Berberis trifoliolata* Moric. In another nearby area of *Pesquería* municipality, *Nuevo León*, *Vachellia farnesiana* was the most abundant and *Parkinsonia aculeata* and *Ebenopsis ebano* were recorded with abundances of 80 and 75 ind. ha⁻¹ respectively (Patiño-Flores et al., 2022).

No significant differences ($p=0.1209$) were found in the abundance of shared species between reforestation and regeneration.

The Margalef index showed a significant difference ($p=4.24e-05$) between reforestation and regeneration, and species richness was higher in the latter; values ranged from 1.76 to 2.25 for reforestation, and from 2.38 to 3.38 for regeneration (Figure 1A). These data indicate medium richness, but were higher than the values ($D_{Mg}=0.69$) for TTS regeneration in abandoned areas with a history of livestock (Mora-Donjuán *et al.*, 2013), and the values for natural regeneration ($D_{Mg}=1.91$) in an active restoration context (Patiño-Flores *et al.*, 2022). The richness values from the present study were closer to those estimated ($D_{Mg}=3.87$) in the *Cadereyta* municipality, *Nuevo León*, for a reforestation in TTS (Mata-Balderas *et al.*, 2023); this may be attributed to the fact that management actions such as herbaceous removal were carried out in both studies. Martínez-Hernández *et al.* (2014) reported a higher value ($D_{Mg}=4.3$) for a regenerated community without management actions, but with a longer history for the *Linares* municipality. This demonstrates that richness varies depending on the state of ecological succession.



A = Margalef; B = Shannon; C = Shannon's true diversity; D = Simpson.

Figure 1. Indexes for reforestation and regeneration.

The Shannon index did not show a significant difference ($p=0.2639$) between reforestation and regeneration. H' values ranged from 1.92 to 2.27 for reforestation and from 1.84 to 2.30 for regeneration (Figure 1B), indicating low levels of diversity (Magurran, 2004). Both ranges were higher than the results ($H'=0.21, 1.31$) found in other studies (Mora-Donjuán et al., 2013; Patiño-Flores et al., 2022). The diversity obtained in this study was similar ($H'=2.22$ to 2.11, 2.13) to that documented in livestock systems in TTS and reforestation with *Eucalyptus* spp. in the same vegetation type (Martínez-Hernández et al., 2014; Molina-Guerra et al., 2013);

however, they were lower than the diversity ($H'=2.63$) of a reforestation site in TTS (Mata-Balderas *et al.*, 2023).

True Shannon diversity was not significantly different ($p=0.2639$) between reforestation and regeneration. Values for this index ranged from 6.84 to 9.93 in reforestation, and from 6.29 to 10.08 in regeneration (Figure 1C). In both cases, diversity values were higher than the diversity (1.28) of a site that had been abandoned for 10 years (Alanís-Rodríguez *et al.*, 2023). True diversity values in regeneration may increase in the future if no disturbances occur, since in some TTS sites this index increases with the time of abandonment, from 1.28 (10 years) to 9.3 (more than 30 years) (Alanís-Rodríguez *et al.*, 2023); in contrast, for another site with the same vegetation with 36 years of abandonment, the value was low (5.91) (Patiño-Flores *et al.*, 2021).

In the early successional stage of the TTS, true Shannon diversity is higher than in the present study; for example, three years after a controlled burn and without active restoration intervention, the value was 16.44 (Alanís-Rodríguez *et al.*, 2020), possibly because the fire created conditions conducive to germination, which did not occur at the sites in the present study.

The Simpson index ($p=0.7499$) and its complement ($p=0.7499$) did not show significant differences between reforestation and regeneration. In reforestation, the index ranged from 0.12 to 0.22 (Figure 1D), and its complement ranged from 0.78 to 0.88. For regeneration, the Simpson index ranged from 0.13 to 0.29, and its complement ranged from 0.71 to 0.87.

In total, 21 species were shared between reforestation and regeneration, a similar number (21 and 23 species) to the total number of species in communities reported in other TTS studies (Alanís-Rodríguez *et al.*, 2020; Mora-Donjuán *et al.*, 2013). *Havardia pallens* stood out for its high abundance in reforestation, but very low in regeneration, the latter slightly higher than the abundance (32 ind. ha⁻¹) in the TTS regeneration in *Cadereyta Jiménez, Nuevo León* (Mata-Balderas *et al.*, 2023). In

contrast, *Vachellia rigidula* presented high and low abundance in regeneration and reforestation, respectively; this species is one of the most important due to its abundance (196.84 ind. ha⁻¹) in other areas (Mata-Balderas et al., 2023).

According to the Margalef index, species richness differs between reforestation and regeneration, but according to the other indices (which also consider evenness or dominance) (Magurran & McGill, 2011), there is insufficient evidence to affirm that there is a significant difference in the diversity structure between strata. The Margalef index measures richness, that is, the number of species regardless of their abundance (Magurran, 2004); therefore, the result of this index in the present study may reflect species differences between strata, although they could have similar abundance distributions. Meanwhile, the Shannon and Simpson indices include both richness and evenness (Magurran & McGill, 2011); therefore, the fact that they do not show differences could be due to the fact that, although the number of species changes, the abundance structure is similar.

Therefore, since the objective of the present study is to compare both strata of the community in terms of diversity and abundance, the use of the estimated indicators is complementary. The Margalef index is appropriate for the number of species, while the Shannon and Simpson indexes provide a more complete view of community structure (Alanís-Rodríguez et al., 2020). For the purposes of our results, both reforestation and regeneration have a similar abundance structure.

In terms of beta diversity, the Sørensen index was 77.8 %, higher than that of two regenerated communities (48 %) with a history of livestock (Pequeño-Ledezma et al., 2018). The Jaccard index suggests similarity of 63.64 %, while the Morisita-Horn index estimated similarity of 27 %.

The floristic composition of areas under restoration is a product of natural regeneration combined with the reproduction of planted species (Molina-Guerra et al., 2023).

In this study, the species recorded in the understory as part of the regeneration were not only those used in reforestation and in the process of replacing dead plants, but also eight additional species native to the TTS: *Condaliopsis obtusifolia* (Hook. ex Torr. & A. Gray) Suess., *Colubrina texensis* (Torr. & A. Gray) A. Gray, *Berberis trifoliolata*, *Bernardia myricifolia* (Scheele) S. Watson, *Guaiaacum angustifolium* Engelm., *Karwinskia humboldtiana* (Schult.) Zucc., *Schaefferia cuneifolia* A. Gray and *Vachellia schaffneri* (S. Watson) Seigler & Ebinger (Table 2). Some of them are recorded in early successional stages (Alanís-Rodríguez *et al.*, 2020); while others appear in more advanced successional stages (Martínez-Hernández *et al.*, 2014; Mata-Balderas *et al.*, 2023; Patiño-Flores *et al.*, 2021). Among these species, *Bernardia myricifolia* had very low abundance in this study; however, it was reported to be more important in a regenerated area with a history of livestock use (Jiménez-Pérez *et al.*, 2013).

The presence of these additional species can be explained by the presence of seeds in the soil and by the surrounding vegetation, which acts as a potential source of propagules (Molina-Guerra *et al.*, 2023). Some fruits and seeds have greater potential for dispersal by fauna based on their physical characteristics, as is the case with *Karwinskia humboldtiana* and *Vachellia schaffneri* (Valdes-Alameda *et al.*, 2024). In contrast, although seed production has been documented for all reforested species in the study area, *Celtis laevigata* Willd., *Ehretia anacua* (Terán & Berland.) I. M. Johnst., *Quercus virginiana* Mill. y *Yucca filifera* Chabaud were not recorded during regeneration, which is attributed to their low densities during reforestation. In the case of *Yucca filifera*, its maturity stage was the factor that perhaps negatively influenced the availability and establishment of its propagules.

The observed diversity and abundance values are comparable to those found in the TTS with different use histories and longer periods since disturbance, suggesting that the lack of active restoration actions limits the development of more advanced successional stages. Five years after reforestation actions, the understory has created conditions conducive to the germination of native species other than those

planted, highlighting the importance of land use history in the formation of a seed bank and the existence of fragments of original vegetation in the surrounding area as sources of propagules.

The former results suggest that land-use history (grazing, abandonment, disturbance, etc.) influences the abundance and composition of the plant community. Therefore, it is important to develop restoration strategies that adapt to the historical context of each site, conducting a thorough assessment of previous land use before selecting the appropriate species and techniques for restoration projects.

Because regeneration showed greater species richness (Margalef index), it is important to promote it as a complementary or even alternative strategy to active reforestation. In this sense, passive restoration schemes should be encouraged where conditions permit, reducing costs and favoring well-adapted native species.

The Shannon and Simpson indexes indicate that the similar diversity structure between reforestation and regeneration implies structural convergence in the medium term. Thus, active restoration can be used as an initial accelerator of vegetation structure, without discounting the role that regeneration plays in ecological succession. On a large scale, this could have the effect of increasing connections between TTS fragments.

Since some reforested species failed to establish themselves in regeneration, perhaps due to their density, maturity, or limited dispersal, species with good dispersal capacity and field viability should be prioritized, in addition to implementing management practices such as post-planting protection, as has been done in some projects (Mata-Balderas et al., 2023; Molina-Guerra et al., 2023).

Conclusions

The results show that natural regeneration of the Tamaulipan Thornscrub presented greater species richness compared to active reforestation, although both strategies shared a similar abundance structure, according to the Shannon and Simpson diversity indices. This structural convergence suggests that, in the medium term, both regeneration and reforestation can contribute to the functional restoration of the ecosystem.

The fact that regeneration included non-planted species and characteristics of different successional stages highlights its ecological value and its potential as a complementary strategy to active restoration in contexts where viable seed banks and surrounding vegetation are well preserved.

Together, these findings highlight the importance of integrating context-adapted management practices, prioritizing species with a high capacity for establishment, conserving natural vegetation fragments, and maintaining long-term ecological monitoring to assess the progress and success of restoration efforts in the TTS.

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Conflict of interest

The authors declare that there is no conflict of interest.

Contribution by author

Ramiro Velázquez Rincón and Eduardo Alanís Rodríguez: conducted the fieldwork, data analysis and manuscript preparation; Luis Gerardo Cuéllar Rodríguez and Oscar A. Aguirre Calderón: participated in the data analysis and writing and reviewing the manuscript; Javier Jiménez Pérez and Arturo Mora Olivo: participated in fieldwork, taxonomic identification and review and correction of the manuscript. All authors participated in the conception of the research and approval of the final version.

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