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Research article

Banco de semillas del suelo bajo individuos aislados de especies arbóreas del Matorral Espinoso Tamaulipeco

Soil seed bank under isolated trees of the Tamaulipan Thorny Scrub

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Abstract

Studying the seed bank makes it possible to interpret the status of disturbed sites, the response to disturbance-driven changes, and the subsequent dynamics of a plant community. Heterogeneity in seed bank formation is influenced by seed dormancy, seed dispersal type, and such landscape components as topography or vegetation. The number of seeds in the soil depends, in part, on the vegetation present, however, in deforested and fragmented landscapes, isolated trees are the only potential reservoirs for vegetation regeneration. In this work, the spatial and temporal variation in abundance, density, and number of germinable seed species on the ground was explored during two years, under five common isolated tree species in open areas of the Tamaulipan Thorny Scrub. Seed bank characteristics were calculated for each isolated tree species and compared between species, seasons, and years of collection. The seed bank under the canopy of two zoochorous trees (*Neltuma laevigata* and *Diospyros texana*) was richer and denser than under the other three species (*Yucca filifera*, zoochorous; *Parkinsonia aculeata* and *Vachellia farnesiana*, unassisted dispersal). Also, more species and seeds germinated in Fall than in Spring, and more herbaceous than arboreal species were recorded.

Key words: *Diospyros texana* Scheele, *Neltuma laevigata* (Humb. & Bonpl. *ex* Willd.) Britton & Rose, regeneration, richness, dispersal syndrome, zoochory.

Resumen

Estudiar el banco de semillas permite interpretar el estado de sitios perturbados, la respuesta a cambios impulsados por disturbios y la consecuente dinámica de una comunidad vegetal. La heterogeneidad en la formación del banco de semillas está influida por la latencia de estas, su tipo de dispersión y componentes del paisaje como topografía o vegetación. El número de semillas en el suelo depende, en parte, de la vegetación presente, sin embargo, en paisajes deforestados y fragmentados, los árboles aislados representan los únicos reservorios potenciales para la regeneración de la vegetación. En este trabajo se exploró, durante dos años, la variación espacial y temporal en la abundancia, densidad y número de especies de semillas germinables en el suelo bajo cinco especies arbóreas aisladas comunes en áreas abiertas del Matorral Espinoso Tamaulipeco. Las características del banco de semillas se calcularon para cada especie de árbol aislado y se compararon entre ellas, estaciones y año de colecta. El banco de semillas bajo las copas de dos árboles zoócoros (*Neltuma laevigata* y *Diospyros texana*) fue más rico y denso que bajo otras tres especies (*Yucca filifera*, zoócora; *Parkinsonia aculeata y Vachellia farnesiana* dispersión no asistida). También se registraron más especies y semillas germinadas en otoño que en primavera, y más herbáceas que arbóreas.

Palabras clave: *Diospyros texana* Scheele, *Neltuma laevigata* (Humb. & Bonpl. *ex* Willd.) Britton & Rose, regeneración, riqueza, síndrome de dispersión, zoocoria.

Introduction

The soil seed bank plays an essential role in plant dynamics; it constitutes an important stage of regeneration, as it stores the plant species that will potentially become established in the soil (De Souza *et al*., 2006). Seed banks are dynamic in space and time (Fenner and Thompson, 2005); in space, fruits and seeds are dispersed when they fall to the ground or by several vectors such as wind, water or animals (Pijl, 1969). Over time, seeds may remain dormant in the soil, that is, they delay germination due to physical or physiological characteristics in their structures, or simply because the right environmental conditions for germination are not present (Baskin and Baskin, 2004). The seeds reach the soil through seed dispersal and rainfall, and they are eliminated from the soil through germination, predation, and death by pathogens (Fenner and Thompson, 2005).

Soil seed banks may contain species present in the vegetation or that were present before a disturbance and in nearby areas (Bossuyt and Honnay, 2008), and therefore are an important resource for the restoration and resilience of a damaged plant community (Shiferaw *et al*., 2018). Traditionally, in disturbed communities, degradation is assessed only by the status of the standing vegetation, often forgetting that the analysis of seeds stored in the soil provides crucial information for understanding plant dynamics, interpreting the conservation status, and determining the potential for plant recovery (Ma *et al.*, 2021).

Research on the temporal and spatial variations of the seed bank is approached by studying its basic characteristics such as density, diversity, or richness. An important aspect that influences the spatial distribution of seeds is their dispersal mechanism, since it is through this process that plant populations grow, exchange genes, and survive environmental changes (Levin and Muller-Landau, 2000). For example, seeds dispersed by animals are more frequently deposited near trees with similar means of dispersal than those with different dispersal mechanisms (Saatkamp *et al.*, 2013). This is due to the fact that plants with fruits attractive to animals tend to be visited by these for feeding, protection, nesting, or perching (in the case of birds), and while performing these activities, they defecate and thereby deposit the seeds under the tree canopy (DeMars *et al.*, 2010).

Isolated trees that remain standing after a disturbance or are intentionally left in deforested areas are widely studied and utilized for their influence on the dynamics of regeneration and ecological restoration (Guevara *et al*., 2005). In addition, if these species attract frugivorous animals, they tend to act as seed reservoirs, increasing the interactions with other plants and animals and thereby maintaining high biodiversity (Camargo *et al*., 2020). This is likely to occur more frequently in forests and jungles because there are more zoochorous species there than in other ecosystems (Gentry, 1982; Willson *et al.*, 1990), however, in disturbed areas of arid zones, zoochorous dispersal and seed accumulation under isolated trees also occurs (Filazzola *et al*., 2019), and its study depends on whether it is a useful tool for the recovery of vegetation and the interactions that are lost with the continuous change of land use.

The Tamaulipan Thorny Scrub is located in a semi-arid zone in northeastern Mexico. It is a very fragmented vegetation type, composed of a matrix of induced vegetation (for livestock or agriculture) with small remnant patches of native vegetation, as well as isolated trees of different species (Molina-Guerra *et al*., 2013). In the thorny scrub, 37 species are recognized as having zoochorous dispersal, which represents a higher percentage of taxa with this type of dispersal compared to other semiarid zones (Jurado *et al.*, 2001a). However, the relationships between plants and dispersers, as well as the influence of the type of dispersal on regeneration, have been scarcely studied in this ecosystem.

Different methods have been used for seed bank research in the Tamaulipan Thorny Scrub (Pando-Moreno *et al*., 2010; Martínez-Adriano *et al*., 2021; Valdes-Alameda *et al.*, 2021); seed banks are known to occur within small undisturbed vegetation areas and at their edges, but there is no information on seed banks in cattle ranching sites, the most common land use in the region. On the other hand, due to the fragmentation of the scrubland, the role of isolated trees has been studied in the context of livestock production or agroforestry (Sarmiento-Muñoz *et al*., 2019), while in the ecological context, seed removal and fruit production were studied in order to compare them with those produced in the remaining continuous vegetation (Jurado *et al.*, 2006; Cuéllar-Rodríguez and Jurado, 2016).

The characteristics of the seed bank were determined in terms of richness and diversity, under isolated individuals of tree species with different dispersal syndromes (classified by the characteristics of their fruits). The soil seed bank was compared under the native species *Diospyros texana* Scheele and *Neltuma laevigata* (Humb. & Bonpl. *ex* Willd.) Britton & Rose (previously *Prosopis laevigata* (Humb. & Bonpl. *ex* Willd.) M. C. Johnst.), *Yucca filifera* Chabaud (of zoochorous dispersion), *Parkinsonia aculeata* L., and *Vachellia farnesiana* (L.) Wight & Arn. (previously *Acacia farnesiana* (L.) Willd.) (without apparent dispersion syndrome). The temporal variation of the seed bank studied was also explored. The hypotheses were: (1) Isolated individuals of zoochorously dispersed species have a greater richness and density of seeds under their canopies than species with other types of dispersal, due to a greater seed deposition generated by the visit of dispersers that are attracted to the zoochorous fruits, and (2) The composition of the banks is variable between seasons because the plants in the community do not all produce seeds in the same season.

Materials and Methods

Study area

The study area is located within the facilities of the Graduate School of Forest Sciences of the *Universidad Autónoma de Nuevo León*, in *Linares* municipality, state of *Nuevo León*. It lies between the 24°48'2.81" N and 99°31'54.51" W to the north, 24°47'50.17" N and 99°32'10.16" W to the south, 24°47'50.80" N and 99°31'39.01" W to the east, and 24°47'59.27" N and 99°32'18.12" W to the west, and has an average altitude of 379 m. The climate in the area is semi-warm sub-humid with summer rains, described as Bs hw(w) in Köppen's classification modified by García (2004). Rainfall is irregular from May to June and from September to October, with two dry periods: a short one in summer and a long one in winter (Foroughbakhch *et al.*, 2013). The average annual temperature is 23.7 °C and the average rainfall is 810 mm (Martínez-Adriano *et al.*, 2021). The area is 40 ha in size and consists of rotating cattle grazing plots, with isolated trees of different species that correspond to the vegetation prior to the clearing and that are present in the surrounding areas: the Tamaulipan Thorny Scrub.

Cattle ranching significantly reduces the abundance, dominance and diversity of tree and shrub communities in this scrubland (Mora *et al*., 2013) in which around 160 species have been counted (Foroughbakhch *et al.*, 2013); although not all have been classified by dispersal syndrome, there are six taxa with explosive fruits (autochorous), 37 with adaptations for animal dispersal (zoochorous), 31 with wind dispersal characteristics (anemochorous), and 43 species with no characteristics clearly associated with any dispersal vector (unassisted) (Jurado *et al.*, 2001a).

The phenology of the species has been studied in a limited number, but the tendency is for the dispersal season to occur around June and July (early summer), or October-November (late fall and early winter), with some taxa bearing fruit in both seasons (García, 1997). In this region, the seeds of some species can germinate above their current distribution range, so they may have the capacity to move to higher altitudes due to climate change (Pérez-Domínguez *et al.*, 2013).

Species selection and sampling

The selected species were mesquite (*Neltuma laevigata*), white *chapote* (*Diospyros texana*), and *yuca* (*Yucca filifera*), all of which have zoochorous dispersion, as well as *huizache* (*Vachellia farnesiana*) and mexican *palo verde* (*Parkinsonia aculeata*), whose fruit characteristics classify them as unassisted because they lack apparent traits related to a dispersal syndrome (Jurado *et al.*, 2001a). The criteria for selecting 10 individuals of each species were as follows: (1) Not having any other adult or fruiting tree within a 10 m radius around it; (2) An average canopy size of 6 m (±1.0), with the exception of cassava which was selected with a canopy size of 10 (±1.0) m, and (3) Being located at less than 90 m (±10) away from the closest continuous fragment of scrubland.

Four samples per tree (40 per species) were collected during the two years of study to evaluate the seed bank under the canopy of each selected tree. The collection period was twice a year, in March and September (early spring and fall), 2021 and 2022, which correspond to the seasons after the dispersal of most of the shrubs and before the germination season.

The collection site was determined at an average distance between the trunk and the top of each individual. The soil sample size was 30×30 cm and 3 cm deep (approximately 1 600±132 g).

Emergence and species identification

The seed bank was estimated using the seedling-emergence method, which is the most useful method for describing the reserves of the entire plant community (Piudo and Cavero, 2005). Soil samples were placed in trays for germination in the greenhouse of the School of Forestry Sciences of the *Universidad Autónoma de Nuevo León*; they were kept under natural light with a 50 % shade net and at a temperature of 20 to 25 °C. Irrigation was applied every other day in order to maintain constant humidity. Every day, the number and species of all seedlings that emerged during the experiment over a four-month period (when no new seedlings germinated for 15 days) was recorded, and their identification was carried out according to the Texas vascular plant manual (Correll and Johnston, 1970). The identified seedlings were removed from the containers, and the unrecognized seedlings were transplanted into nursery bags in order to allow their growth and subsequent identification. When it was not possible to assign the name of the species, the seedlings were identified at genus level. The emergence of a seedling was regarded as indicative of a viable seed. Once the seedlings were identified, information on the origin, habit, and type of dispersal of the species was obtained (Table 1). The number of emerged seedlings was recorded, without knowing how much time the seeds had spent in the soil.

Table 1 Seed bank species composition, growth habit, origin, and assigned dispersal syndrome.

Species		**Habit**	**Origin**	**Dispersal syndrome**
Scientific name	**Common name**			
Acanthaceae				
Ruellia nudiflora (Engelm. & A. Gray) Urb.	*Ruellia*	Herbaceous	Native	Explosive fruit (Vargas-Mendoza *et al.*, 2015)
Amaranthaceae				
Amaranthus palmeri S. Watson		Herbaceous	Native	Unassisted (Jurado *et al.*, 2001a)
Amaranthus viridis L.		Herbaceous	Exotic	Anemochorous/ Hydrochorous (SER and RBGK, 2023)
Chenopodium album L.	*Quelite*	Herbaceous		Unassisted (Williams, 1963)
Apiaceae				
Cyclospermum leptophyllum (Pers.) Sprague *ex* Britton & P. Wilson	*Apio silvestre*	Herbaceous	Native	Anemochorous (Ogle, 2023)
Asparagaceae				
Yucca filifera Chabaud	*Yuca*	Tree	Native	Zoochorous (Waitman *et al.*, 2012)*
Asteraceae				
Calyptocarpus vialis Less.	*Hierba de caballo*	Herbaceous	Native	Unassisted (Valerio and Moreira, 1986)
Cirsium texanum Buckley	*Cardo*	Herbaceous	Native	Anemochorous (SER and RBGK, 2023)
Conyza canadensis (L.) Cronquist		Herbaceous	Prob. native	Anemochorous (SER and RBGK, 2023)
Erigeron L. sp.		Herbaceous		Anemochorous (Pijl, 1969)*
Helianthus annuus L.	*Girasol*	Herbaceous	Native	Unassisted
Parthenium confertum A. Gray		Herbaceous	Native	Anemochorous (Mao *et al.*, 2019)
Sanvitalia ocymoides DC.		Herbaceous	Native	Anemochorous (Jurado *et al.*, 2001a)
Sonchus oleraceus L.	*Lechuguilla común*	Herbaceous	Exotic	Anemochorous (SER and RBGK, 2023)

Taraxacum officinale F. H. Wigg.	*Diente de león*	Herbaceous		Anemochorous (SER and RBGK, 2023)
Boraginaceae				
Lithospermum matamorense DC.		Herbaceous	Native	Unassisted (Pijl, 1969)*
Brassicaceae				
Lepidium virginicum L.	*Lenteja de campo*	Herbaceous	Native	Anemochorous (Díaz and Ríos, 2017)
Cactaceae				
Opuntia Mill. sp.	Tree	Tree	Native	Zoochorous (SER and RBGK, 2023)
Campanulaceae				
Lobelia L. sp.		Herbaceous		Anemochorous (SER and RBGK, 2023)
Cannabaceae				
Celtis laevigata Willd.	*Palo blanco*	Tree	Native	Zoochorous (Jurado *et al.*, 2001a)
Celtis pallida Torr.	*Granjeno*	Tree	Native	Zoochorous (Jurado *et al.*, 2001a)
Convolvulaceae				
Convolvulus arvensis L.		Herbaceous	Exotic	Unassisted (SER and RBGK, 2023)
Ipomoea L. sp.		Herbaceous		Unassisted (SER and RBGK, 2023)
Cordiaceae				
Cordia boissieri A. DC.	*Anacahuita*	Tree	Native	Zoochorous (Jurado *et al.*, 2001a)
Ebenaceae				
Diospyros texana Scheele	*Chapote blanco*	Tree	Native	Zoochorous (Jurado *et al.*, 2001a)
Euphorbiaceae				
Argythamnia humilis (Engelm. & A. Gray) Müll. Arg.		Herbaceous	Native	Unassisted (SER and RBGK, 2023)
Croton ciliatoglandulifer Ortega	*Croton*	Shrub	Native	Zoochorous (Jurado *et al.*, 2001a)
Croton cortesianus Kunth	*Croton*	Herbaceous	Native	Zoochorous (Jurado *et al.*, 2001a)
Croton fruticulosus Engelm. *ex* Torr.	*Croton*	Shrub	Native	Zoochorous (Jurado *et al.*, 2001a)
Croton incanus Kunth	*Croton*	Shrub	Native	Zoochorous (Jurado *et al.*, 2001a)
Euphorbia prostrata Aiton	*Hierba de la golondrina*	Herbaceous	Native	Unassisted (Baiges *et al.*, 1991)
Tragia ramosa Torr.	*Ortiguilla*	Herbaceous	Native	Unassisted (Everitt *et al*, 1999; SER and RBGK, 2023)
Fabaceae				
Desmanthus virgatus (L.) Willd.		Herbaceous	Native	Unassisted (Jurado *et al.*,

				2001a)
Galactia texana (Scheele) A. Gray		Herbaceous	Native	Explosive fruit (Jurado *et al.*, 2001a)
Mimosa monancistra Benth.	*Uña de gato*	Shrub	Native	Unassisted (Jurado *et al.*, 2001a)
Neltuma laevigata (Humb. & Bonpl. *ex* Willd.) Britton & Rose	Mesquite	Tree	Native	Zoochorous (Jurado *et al.*, 2001a)
Parkinsonia aculeata L.	Mexican *palo verde*	Tree	Native	Hydrochorous (SER and RBGK, 2023)
Vachellia farnesiana (L.) Wight & Arn.	*Huizache*	Tree	Native	Unassisted (Jurado *et al.*, 2001a)
Lamiaceae				
Teucrium cubense Jacq.		Herbaceous	Native	Unassisted (Jurado *et al.*, 2001a)
Malvaceae				
Malvastrum coromandelianum (L.) Garcke	Malva	Herbaceous	Prob. native	Unassisted (Jurado *et al.*, 2001a)
Sida rhombifolia L.		Herbaceous		Zoochorous (Mori and Brown, 1998)
Namaceae				
Nama jamaicensis L.		Herbaceous	Native	Unassisted (Pijl, 1969)*
Onagraceae				
Oenothera speciosa Nutt.	*Hierba del golpe*	Herbaceous	Native	Anemochorous (SER and RBGK, 2023)
Oxalidaceae				
Oxalis L. sp.		Herbaceous	Native	Explosive fruit (Unison and ASU, 2023)
Plantaginaceae				
Plantago lanceolata L.	*Plantago*	Herbaceous	Exotic	Anemochorous (SER and RBGK, 2023)
Portulacaceae				
Portulaca L. sp.	*Verdolaga*	Herbaceous	Exotic	Unassisted (SER and RBGK, 2023)
Rhamnaceae				
Condalia hookeri M. C. Johnst.	*Brasil*	Tree	Native	Zoochorous (Jurado *et al.*, 2001a)
Rubiaceae				
Diodia teres Walter		Herbaceous	Native	Unassisted (SER and RBGK, 2023)
Randia rhagocarpa Standl.	*Cruceto*	Tree	Native	Zoochorous (Jurado *et al.*, 2001a)
Rutaceae				
Zanthoxylum fagara (L.) Sarg.	*Colima*	Tree	Native	Zoochorous (Jurado *et al.*, 2001a)
Sapotaceae				

Sideroxylon celastrinum (Kunth) T. D. Penn.	*Coma*	Tree	Native	Zoochorous (Jurado *et al.*, 2001a)
Solanaceae				
Capsicum annuum L. var. *glabriusculum* (Dunal) Heiser & Pickersgill	*Chile piquín*	Shrub	Native	Zoochorous (Jurado *et al.*, 2001a)
Physalis viscosa L.	*Tomatillo*	Shrub	Native	Zoochorous (Jurado *et al.*, 2001a)
Urticaceae				
Urtica chamaedryoides Pursh	*Ortiguilla*	Herbaceous	Native	Unassisted (Pijl, 1969)*
Verbenaceae				
Glandularia bipinnatifida (Nutt.) Nutt.	*Alfombrilla*	Herbaceous	Native	Anemochorous (Pijl, 1969)*
Lantana L. sp.	*Lantana*	Shrub	Native	Zoochorous (SER and RBGK, 2023)
Verbena canescens Kunth	*Verbena*	Herbaceous	Native	Anemochorous (Jurado *et al.*, 2001a)
Violaceae				
Hybanthus verticillatus (Ortega) Baill.		Shrub		Unassisted (Pijl, 1969)*

* Personal observation based on the reference; Prob. native = Probably native.

Statistical analysis

The data obtained were used to calculate the richness and density of seedlings per square meter (seedlings m^2), as well as the richness and density of herbaceous and tree species. The density is given in square meters in order to facilitate its contrast with other works. Each parameter was compared between the two study years, the seasons of collection (spring vs fall), and isolated tree species.

Given that the data did not meet the assumption of normality ($P<0.01$), a comparison of medians of richness and density was made with the nonparametric Kruskall-Wallis test and the Bonferroni correction method (for comparison between species), and the Mann-Whitney U test (for comparison between seasons and years)

(Zar, 1999). Analyses were performed with SPSS statistics (version 25.0) (IBM, 2022).

Results

A total of 57 species belonging to 29 families were identified in the seed bank (Table 1): 21 were arboreal or shrubby, and 36 were herbaceous (Figure 1). Of the total number of species, 21 were classified as having unassisted dispersal, 19 as zoochorous, 14 as anemochorous, three as having explosive dispersal or autochorous, and one species as hydrochorous or water-dispersed (Jurado *et al*., 2001a). Most taxa (45) were considered native or probably native, and five were exotic; the most abundant taxa during the two years of study were *Malvastrum coromandelianum* (L.) Garcke (754 seedlings total) and *Nama jamaicensis* L. (616 seedlings total), both herbaceous. The most abundant tree species were *Neltuma laevigata* (54 seedlings total) and *Yucca filifera* (49 seedlings total), mostly under the parent plant, and the most abundant seedlings found under a different species were *Opuntia* Mill. sp. (44 seedlings) and *Zanthoxylum fagara* (L.) Sarg. (39 seedlings). The best represented families were Asteraceae (9) and Euphorbiaceae (7), followed by Fabaceae (6).

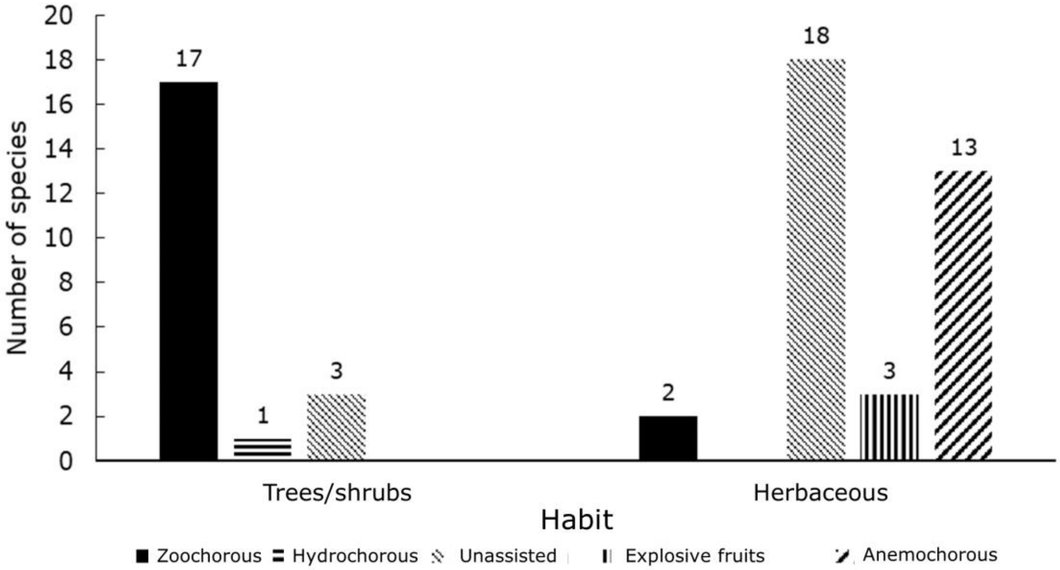


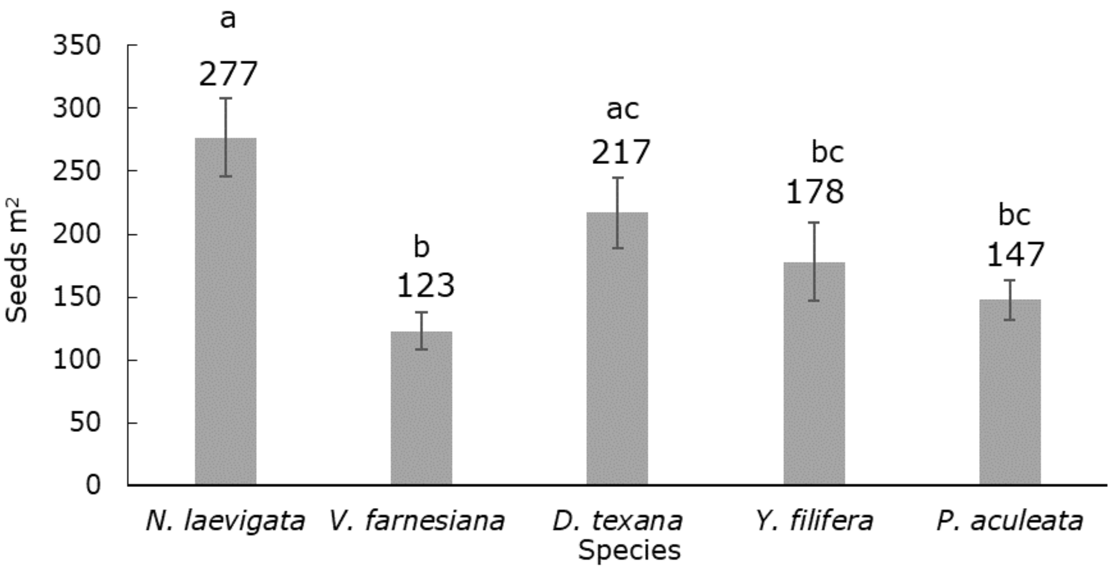
Figure 1. Habit of the species and their dispersal type.

Based on the analysis of the soil seed bank under each isolated tree species, it was determined that seedling richness and density were similar between the two study years (Richness *N. laevigata*: *U*=186, *Z*=-0.38, *P*=0.71; *V. farnesiana*: *U*=194, *Z*=-0.79, *P*=0.88; *D. texana*: *U*=134, *Z*=-1.79, *P*=0.76; *Y. filifera*: *U*=135, *Z*=-1.78, *P*=0.81; *P. aculeata*: *U*=192, *Z*=0.22, *P*=0.84; Density *N. laevigata*: *U*=197, *Z*=-0.08, *P*=0.97; *V. farnesiana*: *U*=180, *Z*=-0.58, *P*=0.60; *D. texana*: *U*=147, *Z*=-1.43, *P*=0.15; *Y. filifera*: *U*=184, *Z*=-0.42, *P*=0.67, *P. aculeata*: *U*=147, *Z*=-1.43, *P*=0.15).

The comparison between collecting seasons resulted in a higher richness and density of seedlings in the autumn bank under all species (Richness *N. laevigata*: *U*=49, *Z*=-4.12, *P*<0.01; *V. farnesiana*: *U*=86, *Z*=-3.10, *P*=0.002; *D. texana*: *U*=80, *Z*=-3.27, *P*=0.001; *Y. filifera*: *U*=60, *Z*=-3.82, *P*<0.01; *P. aculeata*: *U*=64, *Z*=-3.77, *P*<0.01; Density *N. laevigata*: *U*=40, *Z*=-4.13, *P*<0.01; *V. farnesiana*: *U*=80, *Z*=-3.24,

P=0.001; *D. texana*: U=132, Z=-1.82, P=0.06; *Y. filifera*: U=74, Z=-3.42, P<0.01; *P. aculeata*: U=63, Z=-3.71, P<0.01).

The zoochorous dispersal taxa (*N. laevigata* and *D. texana*), had a higher average canopy richness than the rest of the species (H=21.14; d. f.=4; P<0.001). In addition, the seedling density was higher under *N. laevigata* than under *V. farnesiana* and *P. aculeata*; the number of species with unassisted seeds was even larger under *N. laevigata* with respect to *Y. filifera*, which is also zoochorous (H=23.44; d. f.=4; P<0.001.) (Figure 2).

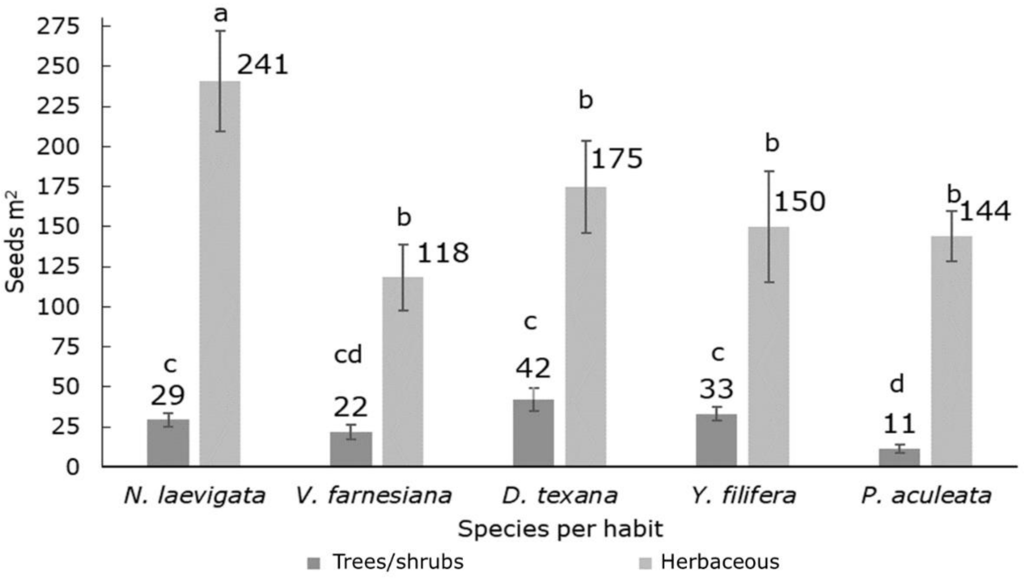


Density data are rounded to the nearest whole number. The error bars represent the standard deviation.

Figure 2. Average seedling density under each species.

In general, more richness and density of herbaceous than of arboreal species was obtained under all species (Richness U=3 765, Z=-3.11; P=0.002; Density U=4

075, Z=-2.31, P=0.02). More tree seedlings emerged on average under *D. texana* and *Y. filifera* (two species, H=29.93, d. f.=4, P<0.001), and more herbaceous species under *N. laevigata* (five species, H=13.96, d. f.=4, P=0.007). The highest density of arboreal species seedlings was found to occur under *N. laevigata*, *D. texana*, and *Y. filifera*, while the density of herbaceous plants was highest under N*. laevigata* (H=22.47, d. f.=4, P<0.001; H=16.97, d. f.=4, P=0.002, respectively) (Figure 3).



Density data are rounded to the nearest whole number. The error bars represent the standard deviation.

Figure 3. Average density of tree and herbaceous seedlings under each species.

Discussion

The results of this study showed a higher species richness in the seed bank than in any other study conducted in the Tamaulipan Thorny Scrub; 27 more species were identified than those recorded by Martínez-Adriano *et al.* (2021), who cite 30 species in seed banks present in remnant fragments of the Tamaulipan Thorny Scrub. Likewise, the richness was higher than that estimated in an area of dense scrub (33 species) (Pando-Moreno *et al.*, 2010). On the other hand, the average densities of seedlings m^2 under *N. laevigata* and *V. farnesiana* are between those recorded in the dense area (1 900 seeds m^2) and in an eroded area (62 seeds m^2), both with Tamaulipan Thorny Scrub (Pando-Moreno *et al*., 2010).

There was no annual variability in seed bank density and richness, but there was seasonal variation, as there were more species and density in the seed bank collected in autumn. In other semi-arid regions, variations in species richness, abundance, and seed density in the soil are recorded in different years, due to variations caused by extreme climatic conditions (Quevedo-Robledo *et al.*, 2010; Dreber and Esler, 2011; da Silva *et al.*, 2013). Fruit production can change depending on environmental factors and on the resources that are variable over time, consequently, temporal changes are observed in seed banks (Quevedo-Robledo *et al.*, 2010); although some plants are very constant and maintain their phenological patterns or respond to the variability of resources with a shift of a few days in their phenological stages (Gordo and Sanz, 2009). Slight variation in fruit production may not be sufficient to be reflected in the seed bank composition in short-term studies.

On the other hand, in zoochorous plants, the abundance of fruit consumers may increase or reduce the density of deposited seeds (García and Martínez, 2012), however, there is little or no information on these interactions in the region. Furthermore, the various species in a community usually have different germination strategies, and with the method used in this research, these strategies directly influence the results, so that the recorded seasonal variation may depend on whether the necessary germination conditions are met or not. For the plants of the thorny scrub, Jurado *et al.* (2001b) indicated that some of the studied species germinated more in autumn, consistently with the results documented herein. Seed bank research using other methods such as sieving, may help to confirm whether there are differences in seed numbers or whether the seasonal variations detected are caused by the germination adaptations of the community. The analysis of the seed bank must take into account this seasonal variation, since sampling in a single season would provide incomplete information for the proper evaluation of disturbed areas or the determination of the potential plant richness.

The results show that zoochorous plants had more species and seed density under their canopies, consistently with the stated hypothesis. Similar results have been described for other arid, semi-arid, and dry forests (Warnock *et al.*, 2007; Hadinezhad *et al.*, 2021), as well as for tropical (Camargo *et al.*, 2020), Mediterranean (González-Varo *et al.*, 2017), and temperate ecosystems (Rodríguez-Pérez *et al.*, 2014).

Most of the seeds of the identified tree species have zoochorous dispersal characteristics and are found under a zoochorous tree species (*D. texana*); thus, the dispersing fauna, among other factors, may shape the tree community as is the case in other ecosystems (Warnock *et al.*, 2007; Hadinezhad *et al.*, 2021). Moreover, seed removal is slower under isolated trees than in the dense thornscrub (Jurado *et al.*, 2006), which may also influence the number of species identified. According to Jurado *et al.* (2006), the removal was slower, especially in isolated *N. laevigata* trees, this is one of the species with the highest richness and density of seeds in the studied Tamaulipan Thorny Scrub. The same removal process may determine the seed composition of isolated *chapote* individuals, which was similar to that of mesquite. The above seems to indicate that in this semi-arid region, the choice of tree species to leave standing or for reforesting influences the ability of the seeds to reach disturbed sites and remain in the seed bank.

The largest number of herbaceous species was obtained in the seed bank under *N. laevigata*, with a high density and anemochorous or unassisted dispersal. Likewise, the herbaceous species outnumbered the tree species under all species. This is related to the fact that herbaceous plants tend to produce many small seeds, whereas trees produce fewer but larger seeds (Moles *et al*., 2004; Moles *et al.*, 2005), also, they are selected more often by predators (Dylewski *et al.*, 2020), a fact which may have influenced the recorded lower density. Another factor is that in general, more herbaceous than woody species are dormant in ecosystems with extreme conditions such as those with frost or drought, as is the case of the Tamaulipan Thorny Scrub. The ratio of dormant to non-dormant species does not differ significantly (Jurado and Flores, 2005).

All this information is important because it represents the potential richness that would be obtained in a natural regeneration trajectory. With the evaluation of seed banks and standing vegetation, it is possible to interpret whether areas that appear degraded will recover the pre-disturbance vegetation structure and diversity or have an alternative status (Ma *et al.*, 2021). In the present study, a high density and richness of native species was determined, in addition, it is inferred that there is an influx of seeds from nearby areas, which suggests that the studied area is in a suitable condition to recover its vegetation through natural regeneration, once disturbances cease to occur.

Conclusions

Isolated trees of the native species *Diospyros texana*, *Neltuma laevigata*, *Yucca filifera*, *Parkinsonia aculeata* and *Vachellia farnesiana* of the Tamaulipan Thorny Scrub, are reservoirs of a high richness and diversity of seeds. Seed banks composed under species with zoochorous dispersal maintain a higher seed richness and density than those consisting under taxa with other dispersal syndromes. The number of species and the density of germinable seeds undergo a seasonal variation, as the assessed parameters are higher in autumn than in spring.

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Conflict of interest

The authors declare that they have no conflict of interest.

Contribution by author

Renata Valdes–Alameda: conceptualization, methodology, writing of the original manuscript, and formal analysis; Enrique Jurado: conceptualization, methodology and writing and manuscript review; Joel Flores: methodology and manuscript review; Eduardo Estrada: species identification, analysis supervision, manuscript review

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