Acta Botanica Brasilica, 2024, 38: e20230130
doi: https://doi.org/10.1590/1677-941X-ABB-2023-0130

Original Article

Positive relationship between seedlings and saplings with adult trees at small scale influenced by dispersal vectors in semiarid thornscrub

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ABSTRACT

Seed dispersal is a process that can drive the spatial distribution of the community and subsequent plant-to-plant interaction and the study of these processes provides information for biodiversity management. Seed dispersal has been scarcely studied for Tamaulipan thornscrub, but dispersal syndromes based on fruit and seed characteristics are helpful to predict sites of seed deposition. In the present work, we determine the spatial relationships between seedlings and saplings around adult trees with different dispersal syndromes and infer the interactions through the community with spatial point pattern analysis using univariate and bivariate pair correlation functions, as well as multivariate Spatially explicit Simpson index $\beta(r)$ and Individual species-area relationship (ISAR). We found a clustered distribution pattern of animal-dispersed seedlings and saplings at 1 m around adult trees, regardless of the dispersal syndrome. We also observed a repulsion of these seedlings at 7-9 m from the stems. Non-animal dispersed adult trees, seedlings, and saplings exhibited a random distribution. Species with animal dispersal syndrome are clumped and have mainly interspecific interactions at a small scale. Using dispersal syndromes, our findings illustrate the influence that seed dispersion might have on the spatial organization and intra- and interspecific interactions of species of Tamaulipan thornscrub.

Keywords: *Acacia*, dispersal syndrome, point pattern analysis, *Prosopis,* seedling, thornscrub.

Introduction

Vegetation recovery following degradation is closely linked to the process of plant recruitment, therefore, seed dispersal toward degraded sites is particularly important for species that propagate by seeds (Schupp *et al.,* 2010). Seed dispersal can leave an imprint on plant distribution and, consequently, on their interactions with other plants (Schupp & Fuentes, 1995). For example, directed dispersal and limited dispersal can result in a clumped distribution of plants but lead to different interactions between seedlings (Lara-Romero *et al.,* 2016; Perea *et al.,* 2021).

The arrival of a substantial number of seeds to sites where they can successfully germinate and survive is known as directed dispersal (Schupp *et al.,* 2010). Directed dispersal studies mainly focus on zoochory, the process of seed transport by animals, as these vectors tend to deposit seeds on more predictable sites than abiotic vectors, such as

Received April 12, 2024; Accepted June 09, 2024
Editor-in-Chief: Thaís Elias Almeida; Associate Editor: Rodrigo F. Fadini

How to cite:
Valdes-Alameda R, Jurado E, Flores J, Estrada E *et al.* 2024. Positive relationship between seedlings and saplings with adult trees at small scale influenced by dispersal vectors in semiarid thornscrub. Acta Botanica Brasilica 38: e20230130. doi: 10.1590/1677-941X-ABB-2023-0130

wind and water runoff (Spiegel & Nathan, 2012). Research on various vegetation types indicates that particular mature tree species attract dispersers, which may transport seeds from other plant species. The attraction of dispersers by mature trees is achieved either by providing food sources, such as fleshy fruits, or by offering resting and sheltering sites (e.g., Herrera & García, 2009; Charles *et al.,* 2019; Miranda *et al.,* 2019). Zoochorous dispersal may enable plants to escape density-dependent mortality, such as that associated with pathogens or competition (Howe & Miriti, 2000). These processes of directed dispersal result in clumped distribution patterns in plants, where seedlings and saplings are clumped around adult trees and often have interspecific interactions (Arnell *et al.,* 2021; Perea *et al.,* 2021).

The production of fruits and structures for dispersal has energetic costs, especially for those with fleshy pericarps (Bolmgren & Eriksson, 2005). Consequently, some plants present fruits or seeds that lack any obvious adaptation for dispersal, which ultimately may limit their potential for dispersing in space, as their seeds tend to fall near the parent plant (Cheplick, 2022). However, plants without a clear dispersal strategy can still ensure their establishment if diaspores reach environmentally suitable microhabitats (Lord & Westoby, 2006; Cheplick, 2022). Limited dispersal results in a clumped distribution at the regeneration stage, often leading to intraspecific competition, which can eventually erase the clustered pattern and even induce segregation (Lara-Romero *et al.,* 2016).

Microhabitats beneath mature plants can provide a range of non-mutually exclusive advantages. These benefits include protection from herbivores; mitigation of heat, cold, or dry conditions; increased nutrient content in the soil; and a decrease in soil compaction and erosion. These facilitative associations between plants are recognized as nurse-protégé interactions and are prevalent in arid and semiarid environments (Flores & Jurado, 2003). Natural regeneration in arid and semiarid lands depends first on seed arrival under the canopies of potential nurse plants, and then on the nurse plant, providing the necessary conditions for the establishment and growth of juvenile plants (Kos & Poschlod, 2007).

Tamaulipan thornscrub is distributed in semiarid northeastern Mexico. Plant species within this ecosystem exhibit heights ranging from 0.5 to 12 meters (Leal-Elizondo *et al.,* 2018) and the spatial distribution of vegetation is described as following a clumped pattern, similar to other vegetation types found in arid and semiarid zones (Mora-Donjuán *et al.,* 2016). Although the influence of a more suitable microclimate under adult plants for germination and establishment is well understood, the dispersal process by which seeds arrive at these sites and the agents involved in dispersal have been scarcely studied for Tamaulipan thornscrub. Despite this, the existence of plant-disperser associations is recognized based on fruit traits, such as the presence of pulp and attractive colors that appeal to vertebrates (Jurado *et al.,* 2001). Furthermore, thornscrub is characterized by approximately 160 species (Foroughbakhch *et al.,* 2013), thirty-seven of which exhibit zoochorous dispersal traits, a higher number compared to other semiarid regions (Jurado *et al.,* 2001). The extensive clearing of this thornscrub for agricultural purposes has led to the fragmentation of remnant vegetation (Antonio-Némiga *et al.,* 2008). Hence, identifying species interactions sustaining the diversity and structure of a plant community helps improve the selection of key species in correct abundances that might boost vegetation regeneration and restoration (Genes & Dirzo, 2022; Ballarin *et al.,* 2024). Moreover, studying the influence of dispersal syndromes on plant distribution may provide information to infer hypotheses that are not as evident as those from animal-plant interactions (Tamme *et al.,* 2014).

In this study, our objective was to determine the spatial distribution of regenerating thornscrub plants and explore the relationships between woody species with different dispersal syndromes using point pattern analyses. We hypothesized that zoochorous seedlings and saplings species are clustered around any adult tree, with a higher concentration around zoochorous adult trees due to an attraction effect. Additionally, we expected that non-zoochorous seedlings and saplings may also exhibit a clustered distribution of fruits beneath trees due to the natural falling of fruits, rather than being consumed, contributing to the observed clustering pattern. To gain further insight into the possible intra- or interspecific interactions within each plant assemblage, we conducted a multivariate analysis using diversity metrics.

Materials and methods

Study site

The study was carried out in 30 ha of regenerating Tamaulipan thornscrub in Linares, Nuevo León, northeastern Mexico, at the university campus of the School of Forest Sciences (24° 47’ 02.6” N; 99° 31’ 38.5” W at 350 m above sea level). The field of study has a low tree cover and has been in a regeneration process for the past 33 years. The land was previously cleared for grazing but is currently protected. The climate is dry sub-humid with summer rains (García, 2004). The mean annual temperature is 23,7 °C, mean maximum 30,8 °C, mean minimum 16,5 °C, absolute max 48,0 °C, and absolute min -4 °C, with rainfall ranging from 500 mm and rarely up to 800 mm in years with high hurricane activity (INEGI, 2010).

Tamaulipan thornscrub is distributed in semiarid northeastern Mexico, half of its plant species are thorny trees and shrubs that can be very dense in areas with little disturbance. Tree heights ranged from 0.5 to 12 m (Leal-

Elizondo *et al.*, 2018). It has high species richness (S = 32) and density (> 16,983 ind./ha) values compared with other scrub vegetation in the region (Mora-Donjuán *et al.*, 2013). The most abundant woody species are *Vachellia rigidula* (Benth.) Seigler & Ebinger, *Vachellia farnesiana* (L.) Willd. Arn. (formerly *Acacia farnesiana*), *Diospyros texana* Scheele, *Neltuma laevigata* (Humb. & Bonpl. ex Willd.) Britton & Rose (formerly *Prosopis laevigata*), *Zanthoxylum fagara* (L.) Sarg. and *Condalia hookeri* M.C.Johnst (Leal-Elizondo *et al.*, 2018).

Data collection

We collected data from May to September 2021 in a 1 ha block in which every woody seedlings and adult plants were located and measured. For each plant, we recorded species and coordinates in 5×5 m subplots and represented them on paper sheets with a 1×1 mm grid (Fig. 1). Every plant with a height of less than 10 cm was considered a seedling, while plants taller than 10 cm, lacking flowers or fruits, were classified as juveniles or saplings. Those showing signs of a reproductive stage (i.e., flowers or fruits) were considered adults. The distribution patterns of seedling and sapling stages, among other aspects, depend on the distribution of adult plants. The former patterns are subsequent to the latter, and since they are not yet contributing to the next generation, no discernible patterns arise from their distribution. Therefore, to analyze only two categories of plants as required by the selected analysis, we combined seedlings and juvenile plants, while adult plants were treated as a distinct category. The sampling plot was selected based on the following criteria: 1) similar topographic conditions in the entire area, 2) lack of evidence of recent disturbances, such as machinery and logging activities, 3) absence of fences within a 50-meter radius, and 4) presence of native species similar to those found in the region. A dispersal syndrome classification was assigned to the plants found and identified, following the proposal of Jurado *et al.* (2001) for native tamaulipan thornscrub plants. We worked with two categories of dispersal, 1) zoochorous and 2) non-zoochorous.

Analysis

We selected point pattern analysis because it is a valuable tool for examining the spatial distribution of plants in relation to various biotic and abiotic factors, providing insights into their influences (Illian *et al.*, 2008). This analysis works with point (i.e., plant) distribution in space and describes the types of patterns that the points follow, such as random, clumped, regular, or segregated distributions.

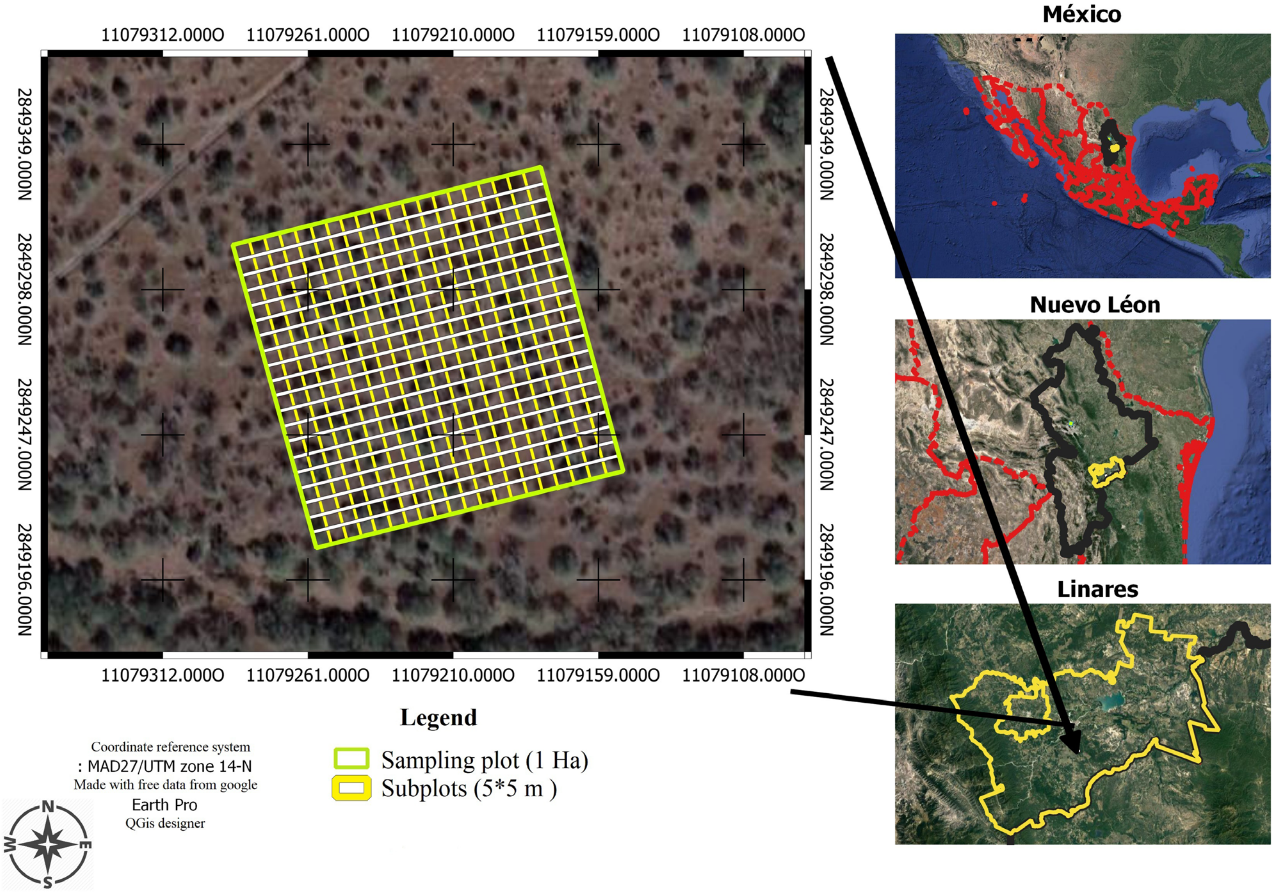

Figure 1. Location map of the sampling plot.

(Illian *et al.,* 2008; Velázquez *et al.,* 2016). Pattern analysis can incorporate both quantitative and qualitative information about studied objects, such as survival, life stage, size, and condition. Thus, point pattern analysis serves as an ecological archive containing information on the processes that impact ecosystem structure and function (Velázquez *et al.,* 2016). This analytical approach has been applied to several ecosystems and enables the exploration of different questions about the interactions that support diversity, species richness and diversity indices, temporal and spatial species distribution, environmental factors, intra or interspecific interactions, or the role of specific species within the community (Ben-Said, 2021). repulsed

Identification of environmental heterogeneity in point patterns

All analyses of spatial point patterns were performed using the Programita software (Wiegand & Moloney, 2014). The heterogeneous environment created by the canopies of adult trees could affect the distribution of seedlings and saplings in tamaulipan thornscrub. Since our focus was only on the direct interaction between plant distributions, we needed to eliminate the influence of the environment. To achieve this, we first indirectly assessed the potential influence of environmental heterogeneity by examining the shapes of the pair correlation function g(r) and L-function (Supplementary Material). As we found evidence of possible environmental heterogeneity affecting the spatial pattern (Figure S1), we selected the null model of the heterogeneous Poisson process with a bandwidth of R = 10 m for comparison with the observed patterns in the analysis. The bandwidth of 10 m was based on the maximum distance between the stem and the limit of the tree canopy.

We used a bivariate pair correlation function to analyze the spatial relationships of 1) all seedlings around trees in the community, 2) zoochorous seedlings and saplings around adult trees with similar dispersion, 3) zoochorous seedlings and saplings around non-zoochorous adult plants, 4) non-zoochorous seedlings and saplings around zoochorous adult plants, and 5) non-zoochorous seedlings and saplings around adult plants with similar dispersion. Bivariate analyses were chosen because they counted the points of pattern two (seedlings and saplings) around a random point of pattern one (adult trees). All analyses were performed individually. The initial width (dr) was 1 m. Additionally, the univariate pair correlation function g(r) was used to describe the observed patterns of the adult trees. We employed a null model with antecedent conditions for comparison with observed patterns. In this null model, the positions of the adult trees were kept fixed, while the seedlings and saplings were randomly relocated. The points of pattern two were redistributed within a 10 m bandwidth, therefore we only interpreted the deviation results up to 10 m. Negative deviations (values $g(r) < 1$) from the null model indicated repulsion and that woody seedlings and saplings were not associated with or are less likely to develop where adult trees occur. While a positive deviation (values of $g(r) > 1$) would reflect attraction, a scenery in which seeds are deposited under adult trees and seedlings develop under or close to the crowns (Wiegand & Moloney, 2004; Ben-Said, 2021).

To infer intra- and interspecific interactions in both zoochorous and non-zoochorous plant assemblages, we conducted a multivariate analysis using null communities. Multivariate data were conformed with several types of points, in this case, there were all found species. We used two multivariate datasets for each community; pattern one was zoochorous and non-zoochorous adult trees each separately, and pattern two was all seedlings and saplings. With the previous data arrangement, the calculated functions provided the probability that two randomly selected points (a large tree and a seedling or sapling at any distance apart) were from two different species (Wiegand, 2018). We used the local toroidal shift null community to evaluate the spatially explicit Simpson index β(r) and the individual species-area relationship ISAR. We selected this null community because it maintains the aggregated pattern of individual species but not the spatial association between species and the association of species with habitat (Wiegand, 2018). Deviations from the null model indicate interspecific interactions or environmental factors not considered by the model (Wiegand & Moloney, 2014).

To test whether each empirical function (observed pattern) is compatible with the selected null model or the scales at which significant deviations may occur, we used goodness of fit tests, carried out with 199 Monte Carlo simulations selecting the fifth highest and lowest values of the simulated patterns to obtain $P = 0.05$ (Wiegand *et al.,* 2016). The null models and summary functions used to respond to questions regarding community and plant associations in Tamaulipan thornscrub are presented in Tab. 1.

Results

Coordinates for the database came from 1,266 plants (981 seedlings and saplings, 285 adults) from 25 species, with a density of 0.12 individuals/m^2. The most abundant species was *Mimosa monancistra* (336). There was only one individual of *Havardia pallens. Diospyros texana*, *Lycium berlandieri*, *Vachellia berlandieri*, *Cercidium macrum,* and *V. wrightii* had five or fewer individuals (Tab. 2 includes species and authors). More abundant adult plants were from *M. monancistra*, *Neltuma laevigata*, *V. farnesiana*, and *V. schaffneri*, and more abundant seedlings and saplings were from *Condalia hookeri*, *Forestiera angustifolia*, and *Zanthoxylum fagara* (Tab. 2). The number of zoochorous species (16) was larger than the non-zoochorous ones (9) and there were not any wind or ballistic dispersed species.

Table 1. Selected functions with the compared null model for each question.

Question	Hypothesis	Function	Null model
What is the spatial relationship between seedlings and saplings and adult tress in the tamaulipan thornscrub community?	Seedlings and saplings are surrounding adult trees	Bivariate pair correlation function $g_{12}(r)$	Antecedent conditions with heterogeneous Poisson pattern
What is the spatial pattern of adult trees?	Adult trees are randomly distributed	Univariate pair correlation function g(r)	Homogeneous Poisson process
What is the spatial relationship between animal-dispersed seedling and sapling around adult trees with similar dispersion? What is the spatial relationship between animal-dispersed seedlings and saplings and non-animal dispersal adult tress?	There are more animal-dispersed seedlings and saplings surrounding animal-dispersed adult trees than those with other dispersal syndromes. Animal dispersed seedlings and saplings have a positive relationship with all adult trees.	Bivariate pair correlation function $g_{12}(r)$	Antecedent conditions with heterogeneous Poisson pattern
What is the spatial relationship between non-animal seedlings and saplings and zoochorous adult tress? What is the spatial relationship between non-animal dispersed seedlings and saplings and adult trees?	Non-animal-dispersed seedlings and saplings are grouped with adult trees of similar dispersal, having a positive relationship with them and none with adult zoochorous trees	Bivariate pair correlation function $g_{12}(r)$	Antecedent conditions with heterogeneous Poisson pattern
Are the distribution of seedlings and saplings around adult trees imposed by environmental heterogeneity and intraspecific interactions?	Seedlings surrounding a zoochorous adult tree are more likely to be heterospecific. Seedlings surrounding a non-animal dispersed adult tree are more likely to be conspecific.	Spatially explicit Simpson index β(*r*) Individual species-area relationship (ISAR)	Local toroidal shift

In the analysis of all plant community, adult trees of all species showed a random distribution. In addition, the observed pattern of seedlings and saplings revealed a clumped distribution up to 1 m from the stem of any adult plant. There were three more individuals than expected with a random distribution, while at larger scales (7-9 m), seedlings and saplings showed repulsion from adult trees (Fig. 2).

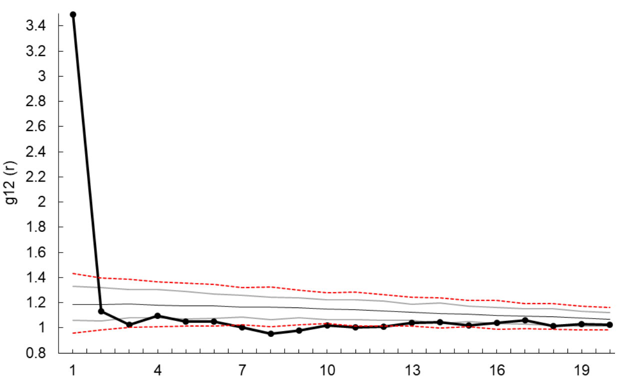

Figure 2. Spatial association between all seedlings and saplings around all adult trees at the study site. The black line and filled circles show pair correlation function $g_{12}(r)$ from the observed data. Gray lines show expected values of $g_{12}(r)$ under a heterogeneous Poisson process with a bandwidth = 10 m. Red dashed lines represent values of global simulations and goodness of fit ($P < 0.05$).

In the analysis of each assemblage of species, data from zoochorous seedlings and saplings (392) were used as pattern two and were analyzed first in relation to zoochorous adult plants (35 individuals) as pattern one (Fig. 3). For the later analysis, all non-zoochorous adult trees (250 individuals) were used as pattern one, and the same previous pattern two (Fig. 4). Seedlings and saplings were clustered around all adult trees, regardless of dispersal syndrome, but in different quantities. There were 13 and 6 more zoochorous individuals immediately after (0-1 m) mature zoochorous and non-zoochorous trees, respectively (Fig. 3 and 4). This positive relationship between individuals of different sizes ceases 1 m from the stems of the adult plants. Additionally, weak repulsion was observed at 7-9 m in both bivariate analyses. The non-zoochorous seedlings and saplings (590) were randomly distributed in relation to zoochorous adult trees ($P = 0.100$; Figure S2) and to adults with the same dispersal syndromes ($P = 0.415$; Figure S3).

The Spatially explicit Simpson index β(r) shows that there was a 79–97% probability that a seedling or sapling near a zoochorous tree was not of the same species within 10 m from its stem. For a non-zoochorous adult, there was 69–89 % chance that a close recruit was heterospecific. However, zoochorous seedlings were clustered only at 1 m from the stem of any adult tree (Fig. 3 and 4) and at this scale, there was a slight deviation of the Simpson index from the null model around 1 m, so the range of probability o form heterospecific clusters under a zoochorous tree

Table 2. Species found in the study site, common name, number of individuals, and dispersal syndrome.

Family / species	Common name	Number of seedlings	Number of adults	Dispersal syndrome
Boraginaceae				
Cordia boissieri A.DC. 1845	Anacahuita	3	4	Zoochory
Ehretia anacua (Terán & Berland.) I.M.Johnst. 1924	Anacua	6	0	Zoochory
Cannabaceae				
Celtis laevigata Willd.	Palo blanco	6	1	Zoochory
Celtis pallida Torrey	Granjeno	23	0	Zoochory
Ebenaceae				
Diospyros texana Scheele	Chapote blanco	5	0	Zoochory
Fabaceae				
Cercidium macrum I.M. Johnst.	Palo verde	4	0	Unassisted
Havardia pallens (Benth.) Britton & Rose	Tenaza	1	0	Unassisted
Mimosa monancistra Benth.	Mimosa	285	51	Unassisted
Parkinsonia aculeata L., SP. PL.	Retama	18	7	Unassisted
Neltuma laevigata (Humb. & Bonpl. ex Willd.) Britton & Rose	Mesquite	43	16	Zoochory
Vachellia berlandieri Benth.	Guajillo	1	1	Unassisted
Vachellia farnesiana (L.) Willd. & Arn.	Huizache	182	130	Unassisted
Vachellia rigidula (Benth.) Seigler & Ebinger	Chaparro Prieto	80	9	Unassisted
Vachellia schaffneri (S. Watson) F.J. Herm., 1948	Huizache chino	19	52	Unassisted
Vachellia wrightii Benth. ex A.Gray	Uña de gato	1	1	Unassisted
Oleaceae				
Forestiera angustifolia Torr.	Panalero	79	3	Zoochory
Rhamnaceae				
Condalia hookeri M.C.Johnst	Brasil	63	3	Zoochory
Karwinskia humboldtiana (Schult.) Zucc.	Coyotillo	6	1	Zoochory
Rubiaceae				
Randia rhagocarpa H.B.K.	Cruceto	7	0	Zoochory
Rutaceae				
Zanthoxylum fagara (L.) Sarg.	Colima	113	5	Zoochory
Sapotaceae				
Sideroxylon celastrinum (Kunth) T.D.Penn	Coma	6	0	Zoochory
Simaroubaceae				
Castela erecta (Torr. & A.Gray) Cronquist	Chaparro amargoso	5	1	Zoochory
Solanaceae				
Capsicum annuum (Dunal) Heiser and Pickersgill	Chile piquín	13	1	Zoochory
Lycium berlandieri Dunal	Cilindrillo	3	0	Zoochory
Verbenaceae				
Citharexylum berlandieri B.L.Rob.	Árbol del pollo	7	1	Zoochory
Total	**25 species**	**981**	**285**	**1266 individuals**

to form heterospecific clusters under a zoochorous tree was 79–88 % (Fig. 5A), while the Simpson index for non-zoochorous species did not show a significant deviation (Fig. 6A). The ISAR function of zoochorous trees confirmed that there was higher richness than expected at small-scale (< 3 m), although it barely reached one species on average more than expected (Fig. 5B). There were more species richness beneath mature non-zoochorous trees than expected by chance (Fig. 6B). The observed Simpson index and ISAR functions for the two groups of adult trees with different

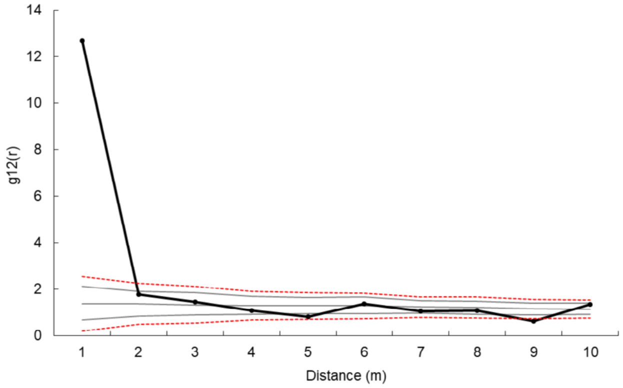

Figure 3. Spatial relationship between zoochorous seedlings and saplings around adult trees with similar dispersion. Black line and filled circles show pair correlation function $g_{12}(r)$ from the observed data. Open circles show a positive deviation from the function with respect to the null model. Gray lines show expected values of $g_{12}(r)$ under a heterogeneous Poisson process with a bandwidth = 10 m. Red dashed lines represent values of global simulations and goodness of fit ($P = 0.01$).

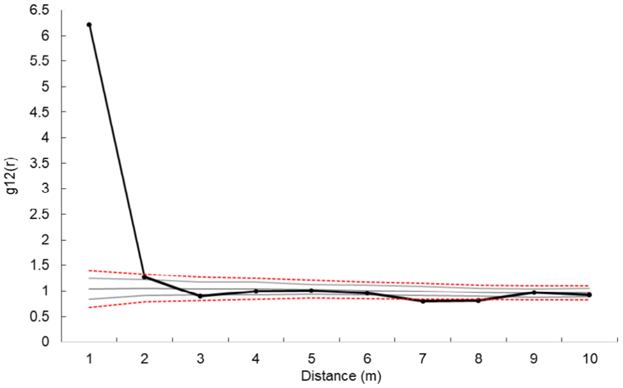

Figure 4. Spatial association between non-zoochorous adult trees and zoochorous seedlings. The black line and filled circles show pair correlation function $g_{12}(r)$ from the observed data. Open circles show a positive deviation from the function with respect to the null model. Gray lines show expected values of $g_{12}(r)$ under a heterogeneous Poisson process with a bandwidth = 10 m. Red dashed lines represent values of global simulations and goodness of fit ($P < 0.01$).

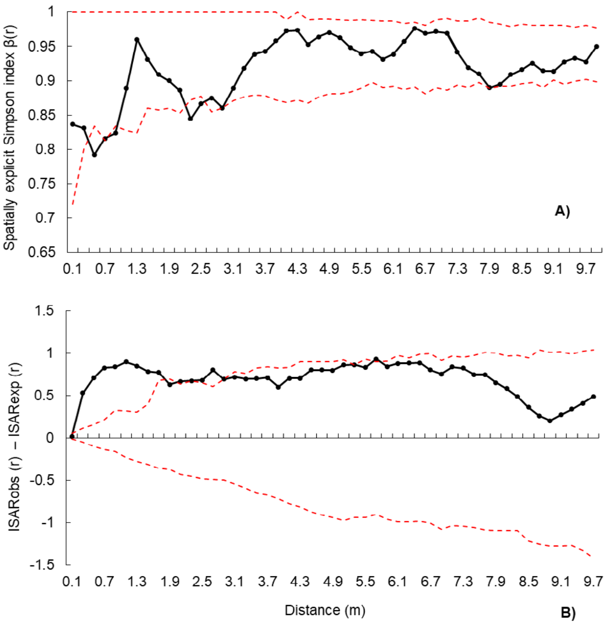

Figure 5. Diversity metrics for all saplings around zoochorous adult trees. A) Spatially explicit Simpson index β(r) and B) individual species-area relationship calculated. Multivariate analysis with two patterns, 1) zoochorous adult trees and 2) all seedlings and saplings. The null model was a local toroidal shift with R = 10 m. Black lines show the summary functions. Red dashed lines represent values of goodness of fit.

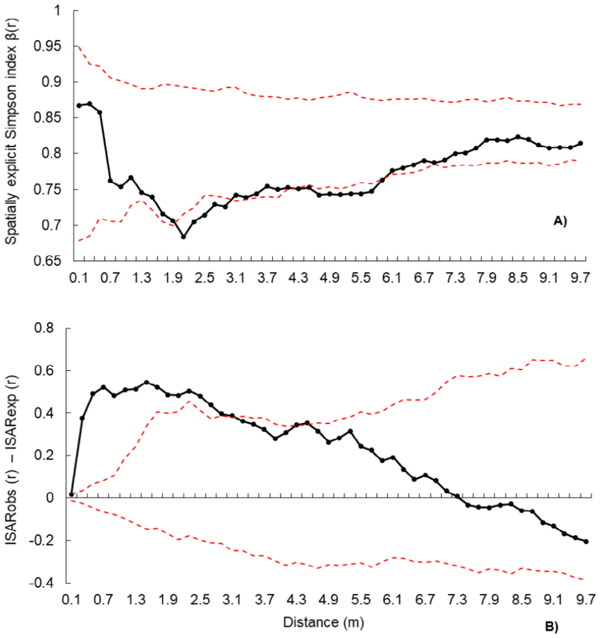

Figure 6. Diversity metrics for all saplings around non-zoochorous adult trees. A) Spatially explicit Simpson index β(r) and B) individual species-area relationship calculated. Multivariate analysis with two patterns, 1) non-zoochorous adult trees and 2) all seedlings and saplings. The null model was a local toroidal shift with R = 10 m. Black lines show the summary functions. Red dashed lines represent values of goodness of fit.

was 79–88 % (Fig. 5A), while the Simpson index for non-zoochorous species did not show a significant deviation (Fig. 6A). The ISAR function of zoochorous trees confirmed that there was higher richness than expected at small-scale (< 3 m), although it barely reached one species on average more than expected (Fig. 5B). There were more species richness beneath mature non-zoochorous trees than expected by chance (Fig. 6B). The observed Simpson index and ISAR functions for the two groups of adult trees with different dispersal syndromes showed a null model fit at scales of 5–10 m.

Discussion

In Tamaulipan thornscrub, adult trees had a random spatial distribution pattern, while seedlings and saplings had a clumped distribution pattern near adult plants. The zoochorous species assemblage was clustered and exhibited higher richness than the non-zoochorous species, which, in addition, showed a random distribution pattern.

The observed clumped pattern of seedlings and saplings throughout the community indicated a positive relationship with adult plants on a small scale. Communities of Tamaulipan thornscrub with different land use had similar patterns (Mora-Donjuán *et al.,* 2016). Canizales-Velázquez (2016) also found a clumped plant community but at larger scales ranging from 1 to 12 m. However, despite the differences in scale, our results are consistent with our initial hypothesis and align with the findings of previous studies. Various ecological processes can influence the observed aggregated spatial pattern, for example, seed dispersal limitation (Nguyen *et al.,* 2018), directed seed dispersal (Spiegel & Nathan, 2012), herbivory (Wang *et al.,* 2020), as well as intra- and interspecific facilitation or nurse effects resulting from environmental heterogeneity (Schleicher *et al.,* 2011). In arid and semiarid ecosystems, the nurse effect is one of the key drivers of vegetation structure (Flores & Jurado, 2003). For this vegetation, Jurado *et al.* (2006a) suggested that adult trees might generate microclimatic conditions suitable for seedling establishment of other species. However, we used heterogeneous Poisson processes as null models, which allowed the identification of small-scale spatial structures (Carrer *et al.,* 2018). Considering this, the observed spatial pattern suggests that biological processes, such as directed dispersal and seed dispersal limitation, besides environmental factors, influence the distribution in this community. Other studies in arid and semiarid communities have found aggregated patterns potentially influenced by environmental heterogeneity and identified additional interactions between different species or plant sizes (Wiegand *et al.,* 2006; Lara-Romero *et al.,* 2016; Pozo Inofuentes & Säumel, 2022).

In addition to the clustered assemblage of zoochorous seedlings and saplings around adults, we found that the most abundant seedlings and saplings were from other species and not from the most abundant adult trees. Notably, within the study plot, six zoochorous species were present as seedlings without any surrounding adult trees. Although dispersal processes in Tamaulipan thornscrub remain relatively understudied, there is evidence suggesting that dispersal vectors play a crucial role in facilitating the arrival of zoochorous seeds beneath nurse plants (Valdes-Alameda *et al.,* 2021).

In the study area, the isolated trees may function as 'stepping stones', connecting remnant shrub fragments for species that require specific conditions for their germination and growth (Loehle, 2007). This confirms that the zoochorous dispersal process is important for the arrival of seeds into disturbed areas, making a noticeable difference, at least during the early stages of regeneration. While the relationship between early-stage plants and adult trees with zoochorous dispersal syndromes has been observed in many ecosystems (Zucaratto & Pires, 2015; Mason *et al.,* 2022; Pozo Inofuentes & Säumel, 2022), it is less commonly studied in semiarid lands. This may be because arid and semiarid regions are understudied from a spatial perspective (Huenneke *et al.,* 2001), and these areas have fewer zoochorous species than tropical regions (Gentry, 1982; Willson *et al.,* 1990). Additionally, we observed lower conspecific species abundance and higher species richness than expected under zoochorous trees. Probably, as in other ecosystems, the movement of dispersers between different species during the fruiting season could explain these findings. However, to further strengthen our understanding of this process and its role in the regeneration of the zoochorous community in tamaulipan thornscrub, it would be beneficial to conduct a direct analysis of seed rain composition, as well as investigate subsequent stages such as seed bank and seedling emergence. These additional investigations could provide valuable insights into the mechanisms driving the observed patterns of plant composition and shed light on the dynamics of trees' entry and exit from an environment, as they reflect the different processes plant individuals undergo before successfully establishing (Quintero *et al.,* 2024).

In our study, we observed an abrupt decline in zoochorous seedlings and saplings around the stems of adult trees. We also found a random distribution pattern of non-zoochorous seedlings and saplings. Changes from clustered to less aggregated or regular patterns on temporal and spatial scales are frequently related to density-dependent mortality such as competition (Meyer *et al.,* 2008). Furthermore, the spatially explicit Simpson index and the individual species-area relationship suggest the presence of intraspecific interactions, probably due to dispersal limitation, which usually carries intraspecific competition (Cheplick, 2022). However, there was no evidence of competition in germination or survival of seedlings growing together for 24 months in Tamaulipan thornscrub (Jurado *et al.,* 2020; Jurado *et al.,* 2022). Nevertheless, these experiments were conducted under controlled conditions and the stress might be different in natural conditions. Alternatively, in this thornscrub, there is evidence of seed removal of all seed types, but especially for fleshy fruits (Jurado *et al.,* 2006b), and predators typically visit sites with high food abundance which could result in a reduction of seedlings (Ballarin *et al.,* 2022). However, given the evidence of grazing in the sample plot, the potential effect of herbivory cannot be discarded. Probably, a combination of both processes caused a decline in seedlings under the canopies of adult trees in this community.

The distribution of adult trees in a random pattern, coupled with a clustering pattern of juvenile plants, also suggests a negative interaction between different life stages, such as increased competition as plants mature (Meyer *et al.,* 2008) or mortality due to the Janzen-Connell effect, e.g., specialized natural enemies cause distance- or density-dependent mortality among host plants (Janzen, 1970; Connell, 1971). However, it is important to consider that the study area has a history of grazing, and approximately half of the adult trees observed were intentionally left standing to provide shade for livestock. Therefore, caution is advised when interpreting these results. Nonetheless, this information has been valuable in characterizing the region and gaining a better understanding of its impact on regeneration dynamics. To further enhance our understanding, it would be beneficial to conduct studies in areas with more mature or less disturbed vegetation, such studies could help elucidate the underlying process responsible for the shift from clustering patterns in young plants to the random distribution of adult trees.

The number of points used in spatial point analysis is a significant consideration. While many studies prefer a large number of points to minimize the risk of misinterpreting random or independent patterns, it is worth noting that meaningful patterns can still be identified with a small number of points (Cordero *et al.,* 2016). In our study, although we acknowledge the limitations of a relatively small number of points and the potential interference from grazing activities, we have collected the largest dataset of vegetation positions in the region. We believe that our results are valuable in inferring the processes occurring during the regeneration stage, as emphasized by Ben-Said (2021) in exploratory studies of spatial patterns in previously uninvestigated sites. Our findings contribute to the understanding of these processes and serve as a foundation for further investigations in this ecosystem.

The Tamaulipan thornscrub plant community has zoochorous and non-zoochorous plant assemblages in accordance with our hypothesis. Additionally, we identified the presence of environmental heterogeneity in the region and its influence on the observed patterns. These findings, along with the diversity metrics, provide initial insights into the role of dispersal dynamics in shaping spatial patterns and subsequent interactions among species in thornscrub. For restoration purposes, the choice of plant species at an adequate abundance for promoting effective seed movement and deposition of various plant species would be useful (Ballarin *et al.,* 2024). The information presented here highlights the influence of dispersal processes on plant regeneration dynamics and emphasizes the need for further investigation to understand the extent to which these processes drive the composition of mature communities. To fully confirm the role of dispersal agents in regeneration, direct studies focusing on the agents themselves and their seed deposition rates are necessary. Obtaining this information would not only confirm their importance but also provide valuable insights for making informed decisions and improving restoration strategies; therefore, we strongly recommend that future research efforts concentrate on addressing this knowledge gap, as it remains a critical aspect that warrants further exploration.

Acknowledgments

We acknowledge PAICYT-UANL and a doctorate scholarship to R.VA, CONACYT (694733) for supplying the funding. We also thank the personnel from the School of Forestry for their assistance in this research. J.A. López assisted with fieldwork.

Authors’ Contributions

RVA: Conceptualization, Formal analysis, Methodology, Writing – original draft. EJ: Conceptualization, Supervision, Writing – review & editing. JF: Conceptualization, Writing – review & editing. EEC: Methodology and Writing – review & editing.

Conflict of Interest

We declare that there are no conflicts of interest (personal, scientific, commercial, political, or financial) in this manuscript.

Supplementary Material

The following online material is available for this article.

S1 – Identification of environmental heterogeneity in point patterns.

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