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Review / Revisión

Association between cacti and nurse plants: a quantitative literature review

Jessica Snell Cordero and Héctor Godínez-Alvarez*

Unidad de Biología, Tecnología y Prototipos, Facultad de Estudios Superiores Iztacala, Universidad Nacional Autónoma de México, Tlalnepantla, Estado de México, Mexico
*Corresponding author: hgodinez@unam.mx

Abstract
The association between cacti and nurse plants has been reviewed by different authors. These reviews however were qualitative because only evaluated aspects such as species identity of cacti and nurse plants, probable explanatory causes of their association, and location of study sites. To our knowledge, there are no quantitative reviews that have evaluated the association between cacti and nurse plants for different subfamilies, tribes, and growth forms of cacti and nurse plants, and different plant communities and soil properties. To address these issues, we performed a quantitative review of the studies on the association between cacti and nurse plants. The studies were searched in the ISI Web of Knowledge from 1986 to 2021. Data obtained from studies were analyzed with the relative risk ratio and ratio of medians. Most studies on the association between cacti and nurse plants were performed mainly in Mexico and the USA. Globose, cylindrical, and columnar cacti of the subfamily Cactoideae, and tribes Cacteae, Cereeae, and Echinocereeae were associated to nurse plants of Asteraceae, Euphorbiaceae, and Fabaceae. However, other subfamilies (Opuntioideae) and tribes (Notocacteae) of cacti, and families (Asparagaceae) of nurse plants were not associated. Nurse plants ameliorated temperature, moisture, and nitrogen of soil. The association between cacti and nurse plants occurred in desert shrubland and tropical dry forest. Further studies are needed on the association between cacti and nurse plants that consider more cactus subfamilies and tribes in countries with high cactus diversity in Central and South America.
Keywords: Cactaceae, desert shrubland, Fabaceae, plant facilitation, nurse plants, tropical dry forest.

Resumen
La asociación entre cactáceas y plantas nodriza ha sido revisada por diferentes autores. Sin embargo, estas revisiones fueron cualitativas porque solo evaluaron las especies de cactáceas y plantas nodriza, las probables causas de su asociación y los sitios de estudio. Hasta donde sabemos, no existen revisiones cuantitativas que hayan evaluado la asociación entre cactáceas y plantas nodriza para distintas subfamilias, tribus y formas de crecimiento de cactáceas y plantas nodriza, y distintas comunidades de plantas y propiedades del suelo. Para abordar estos aspectos, realizamos una revisión cuantitativa de los estudios sobre la asociación entre cactáceas y plantas nodriza. Los estudios fueron buscados en el ISI Web of Knowledge de 1986 a 2021. Los datos fueron analizados con la razón de riesgo relativo y la razón de medianas. Los estudios sobre la asociación entre cactáceas y plantas nodriza fueron realizados en México y EUA. Las cactáceas globosas, cilíndricas y columnares de la subfamilia Cactoideae y las tribus Cacteae, Cereeae y Echinocereeae estuvieron asociadas a plantas nodriza de Asteraceae, Euphorbiaceae y Fabaceae. Sin embargo, otras subfamilias (Opuntioideae) y tribus (Notocacteae) de cactáceas, y familias (Asparagaceae) de plantas nodriza no estuvieron asociadas. Las plantas nodriza mejoraron la temperatura, humedad y nitrógeno del suelo. La asociación entre cactáceas y plantas nodriza ocurrió en matorral desértico y selva baja caducifolia. Es necesario realizar estudios adicionales sobre la asociación entre cactáceas y plantas nodriza que consideren otras subfamilias y tribus de cactáceas, en países con alta diversidad de cactáceas en Centro y Sudamérica.
Palabras clave: Cactaceae, Fabaceae, facilitación, matorral desértico, planta nodriza, selva baja caducifolia.

Arid and semiarid regions have harsh environmental conditions, and thus several plant species grow associated to nurse plants that ameliorate the physical and biological conditions under their canopies (Withgott 2000). This spatial association has been reported for 429 plant species belonging to 84 plant families such as Euphorbiaceae (18 species), Fabaceae (24 species), Poaceae (43 species), Asteraceae (45 species), and Cactaceae (63 species, Flores & Jurado 2003).

Studies on the spatial association between cacti and nurse plants have shown that cacti can grow associated to different types of nurse plants such as herbs, shrubs, trees, rosettes, and even cacti (McAuliffe 1984, Hutto *et al*. 1986, Valiente-Banuet *et al*. 1991, Arriaga *et al*. 1993, Mandujano *et al*. 1998). These types of nurse plants can decrease direct solar radiation (Franco & Nobel 1989, Cares *et al*. 2013), soil surface temperature (Franco & Nobel 1989, Valiente-Banuet *et al*. 1991, Arriaga *et al*. 1993, Cares *et al*. 2013), and evapotranspiration (Cares *et al*. 2013). Moreover, they can attract animals that deposit seeds under their canopies (Sosa & Fleming 2002), increase soil nutrient content (Valiente-Banuet *et al*. 1991, Arriaga *et al*. 1993), and protect cactus seeds and seedlings from predators (McAuliffe 1984, Valiente-Banuet & Ezcurra 1991, Sosa & Fleming 2002, Holland & Molina-Freaner 2013, Ortíz-Martínez *et al.* 2021). Although nurse plants can provide diverse benefits to cacti, most of the empirical evidence about these benefits is restricted to the amelioration of physical conditions under the canopy of nurse plants; hence, in this study, we focus our analysis to the soil properties under nurse plants and in open spaces between plants (hereafter open spaces).

The spatial association between cacti and nurse plants has been reviewed by Callaway (1995), Flores & Jurado (2003), and Godínez-Alvarez *et al*. (2003). Callaway (1995) found several cacti associated to nurse plants, although he only reported five cactus species and six nurse plant species. The reviewed studies were performed in the USA and Mexico, and most of them only evaluated the spatial patterns of association (Callaway 1995). Flores & Jurado (2003) found 63 cactus species growing beneath 62 nurse plant species, which belonged to 23 plant families. The Mimosaceae and Asteraceae families had the highest number of nurse plant species (Flores & Jurado 2003). Godínez-Alvarez *et al*. (2003) found eight cactus species with different growth forms (*i.e.,* columnar cacti, barrel cacti, globose cacti, platyopuntias, and cylindropuntias) associated to 41 nurse plant species. The seedlings and juveniles of cacti were the life cycle stages most commonly associated to nurse plants. Lastly, the protection from direct solar radiation was the most probable cause of the association between cacti and nurse plants (Godínez-Alvarez *et al*. 2003).

These literature reviews made a significant contribution to the understanding of the spatial association between cacti and nurse plants (Callaway 1995, Flores & Jurado 2003, Godínez-Alvarez *et al*. 2003). However, these reviews were qualitative because only evaluated data such as species identity of cacti and nurse plants, probable causes of their association, and location of study sites. To our knowledge, there are no quantitative reviews that have used the observed and expected number of cacti under nurse plants and in open spaces, obtained through area sampling methods, to evaluate the spatial association between cacti and nurse plants for different subfamilies, tribes, and growth forms of cacti and nurse plants. Moreover, there are no quantitative reviews of this spatial association for plant communities different from those in arid and semiarid regions. Lastly, there are also no quantitative reviews about the amelioration of soil properties under the canopy of nurse plants compared to open spaces.

In this study, we performed a quantitative review of the studies on the spatial association between cacti and nurse plants to determine if this association differs between subfamilies, tribes, and growth forms of cacti and nurse plants, if it varies with plant communities, and if nurse plants ameliorate the soil properties under their canopies. To do this, we performed a literature review from 1986 to 2021 to find studies on the spatial association between cacti and nurse plants that used area sampling methods. We only considered this kind of studies because area sampling methods are most commonly used to evaluate this spatial association than distance sampling methods. Data obtained from studies were analyzed with the relative risk ratio and ratio of medians.

The quantitative review performed in this study however might be biased because we established the criteria to include the studies in our review, and we only included studies cited in indexed journals. Studies often published in indexed journals are those that found significant differences. In contrast, studies that did not find significant differences are seldom published or published in non-indexed journals, thus it is probable that several of these studies were not included in the review.

Material and methods

Data compilation. The studies on the spatial association between cacti and nurse plants were searched in the ISI Web of Knowledge from 1986 to 2021 using the terms "cact*" or "spatial distribution" or "nurse". We chose this time period because we did not find studies on the spatial association between cacti and nurse plants that used area sampling methods before 1986, and our study was performed in 2021. We found 1,023 studies that included at least one of the search terms. Of these 1,023 studies, only 58 studies had titles directly related to the topic. The examination of the abstract of these 58 studies showed that 28 studies had data relevant to the topic. Lastly, the examination of the full text of these 28 studies showed that 16 studies provided useful data on the association between cacti and nurse plants (Figure 1, Suppl. Mat.). These studies provided data on 39 cactus species, 76 nurse plant species, and 316 associations between cacti and nurse plants that were analyzed with the relative risk ratio (see below). The studies were performed in Mexico (6), USA (2), Mexico and USA (2), Argentina (2), Venezuela (2), Bolivia (1), and Chile (1). Figure 2.

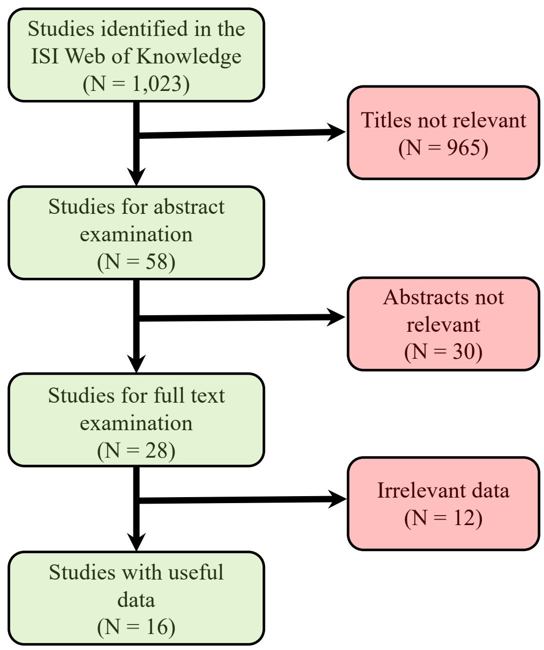

Figure 1. Flow diagram of the literature search.

For each study, we recorded author and year; plant community (*i.e.*, arid tropical shrubland, desert shrubland, *Larrea* shrubland, semiarid shrubland, thorn scrubland, tropical dry forest, xeric shrubland); subfamily, tribe, species, and growth form of cacti (*i.e.*, shrub cactus, columnar cactus, cylindrical cactus, globose cactus, flattened globose cactus *sensu* Vázquez-Sánchez *et al*. 2012); family, species, and growth form of nurse plants (*i.e.*, grass, herb, shrub, tree, rosette). When cacti acted as nurse plants, we used the growth forms previously mentioned for cacti. In addition to these data, we recorded the observed number of cacti under nurse plants and in open spaces, and the expected number of cacti under nurse plants and in open spaces. When the number of cacti under nurse plants and in open spaces was reported graphically, we used the program WebPlotDigitizer version 4.6 (Rohatgi 2022) to extract the numerical values.

For those studies that evaluated soil properties under nurse plants and in open spaces, we recorded family, species, and growth form of nurse plants as previously described, and numerical values of the soil properties under nurse plants and in open spaces. The numerical values of the soil properties obtained from the studies were expressed in the same units of measurement to compare them.

Data analysis. Data on the spatial association between cacti and nurse plants were analyzed with the relative risk ratio because it allowed us to compare the probability of cacti growing under shrubs *versus* the probability of cacti growing in open spaces. The relative risk ratio was calculated as: Relative risk ratio = ln [(observed number of cacti under nurse plants / expected number of cacti under nurse plants) / (observed number of cacti in open spaces / expected number of cacti in open spaces)], where ln is the natural logarithm. If the relative risk ratio = 0 the probability of cacti growing under nurse plants and the probability of cacti growing in open spaces were similar, if the relative risk ratio > 0 the probability of cacti growing under nurse plants was higher than the probability of cacti growing in open spaces, and if the relative risk ratio < 0 the probability of cacti growing under nurse plants was lower than the probability of cacti growing in open spaces. This ratio was used to evaluate the effect of subfamily, tribe, and growth form of cacti, the effect of family and growth form of nurse plants, and the effect of plant community on the association between cacti and nurse plants.

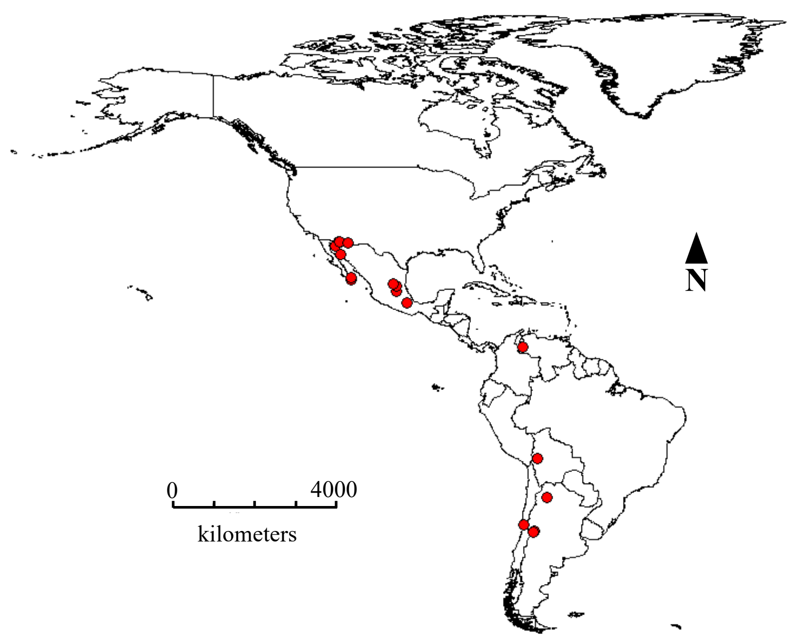

Figure 2. Distribution of the studies on the spatial association between cacti and nurse plants. Each point can represent more than one study.

Data on the soil properties were analyzed with the ratio of medians because it allowed us to compare the soil properties under shrubs *versus* the soil properties in open spaces. We calculated the ratio of medians because several soil properties such as moisture, organic matter, nitrogen, and calcium carbonate content were estimated in percentage. The ratio of medians was calculated as: Ratio of medians = ln (numerical value of the soil property under nurse plants / numerical value of the soil property in open spaces), where ln is the natural logarithm. If the ratio of medians = 0 the soil property was similar under nurse plants and in open spaces, if the ratio of medians > 0 the soil property was higher under nurse plants than in open spaces, and if the ratio of medians < 0 the soil property was lower under nurse plants than in open spaces.

The relative risk ratio and ratio of medians were analyzed with the Wilcoxon one-sample signed-rank test to evaluate whether they differ from zero. We used this non-parametric test because the number of cacti under nurse plants and in open spaces are discrete variables that do not have a normal distribution. Moreover, several studies did not report the dispersion measures of the soil properties, nor the sample size, thus we could not use parametric tests. The non-parametric tests have been used in quantitative reviews of ecological aspects such as ecological restoration with ants (Casimiro *et al*. 2019, Ríos-Casanova & Godínez-Alvarez 2023), and biodiversity and ecosystem services (Rey-Benayas *et al*. 2009). The statistical tests were performed in the software PAST version 4.11 (Hammer *et al*. 2001).

Results

Cacti: subfamilies, tribes, and growth forms. We obtained data for the subfamilies Opuntioideae and Cactoideae. For the subfamily Opuntioideae, the probability of cacti growing under nurse plants was lower than the probability of cacti growing in open spaces (Z = 2.49, P = 0.013). In contrast, for the subfamily Cactoideae, the probability of cacti growing under nurse plants was higher than the probability of cacti growing in open spaces (Z = 7.88, P < 0.000; Figure 3A).

As for the tribes, we obtained data for the tribes Cacteae, Cereeae, Notocacteae, Echinocereeae , and Trichocereeae. For the tribes Notocacteae and Trichocereeae, the probability of cacti growing under nurse plants and the probability of cacti growing in open spaces were similar (Notocacteae: Z = 1.60, P = 0.109, Trichocereeae: Z = 0.28, P = 0.779). For the tribes Cacteae, Cereeae, and Echinocereeae , the probability of cacti growing under nurse plants was higher than the probability of cacti growing in open spaces (Cacteae: Z = 3.67, P < 0.000, Cereeae: Z = 3.90, P < 0.000, Echinocereeae : Z = 5.88, P < 0.000; Figure 3B).

As for the growth forms, we obtained data for shrub cacti, columnar cacti, cylindrical cacti, and globose cacti. The probability of cylindrical, columnar, and globose cacti growing under nurse plants was higher than the probability of growing in open spaces (cylindrical cactus: Z = 3.06, P = 0.002, columnar cactus: Z = 6.78, P < 0.000, globose cactus: Z = 3.20, P = 0.001). Conversely, the probability of shrub cacti growing under nurse plants was lower than the probability of growing in open spaces (Z = 2.49, P = 0.013; Figure 3C).

Nurse plants: families and growth forms. We obtained data for 22 plant families. However, the Anacardiaceae, Bignoniaceae, Capparaceae, Celastraceae, Oleaceae, Rubiaceae, and Turneraceae were not analyzed because they had only one datum each (Figure 4A).

The probability of cacti growing under nurse plants belonging to Acanthaceae, Asparagaceae, Boraginaceae, Bromeliaceae, Cactaceae, Capparidaceae, Fouquieriaceae, Rhamnaceae, Simaroubaceae, Solanaceae, Verbenaceae, and Zygophyllaceae was similar to the probability of cacti growing in open spaces (Acanthaceae: Z = 1.34, P = 0.18, Asparagaceae: Z = 1.99, P = 0.06, Boraginaceae: Z = 2.02, P = 0.06, Bromeliaceae: Z = 1.60, P = 0.11, Cactaceae: Z = 1.21, P = 0.23, Capparidaceae: Z = 0.53, P = 0.59, Fouquieriaceae: Z = 0.53, P = 0.59, Rhamnaceae: Z = 0.40, P = 0.69, Simaroubaceae: Z = 1.83, P = 0.07, Solanaceae: Z = 1.83, P = 0.07, Verbenaceae: Z = 1.78, P = 0.08, Zygophyllaceae: Z = 0.63, P = 0.53; Figure 4A). In contrast, the probability of cacti growing under nurse plants belonging to Asteraceae, Euphorbiaceae, and Fabaceae was higher than the probability of cacti growing in open spaces (Asteraceae: Z = 2.52, P = 0.01, Euphorbiaceae: Z = 2.16, P = 0.03, Fabaceae: Z = 5.63, P < 0.00; Figure 4A).

As for the growth forms, we obtained data for the herbs, shrubs, trees, rosettes, and cylindrical cacti. The probability of cacti growing under nurse plants such as trees, shrubs, and rosettes was higher than the probability of growing in open spaces (tree: Z = 3.78, P < 0.000, shrub: Z = 4.97, P < 0.000, rosette: Z = 2.43, P = 0.015; Figure 4B). In contrast, the probability of cacti growing under nurse plants such as herbs and cylindrical cacti was similar to the probability of growing in open spaces (herbs: Z = 0.45, P = 0.655, cylindrical cactus: Z = 1.60, P = 0.109; Figure 4B).

Plant communities. We obtained data for 10 plant communities. However, eight plant communities were comparable to the desert shrubland, thus we only considered the desert shrubland and tropical dry forest. In both plant communities, the probability of cacti growing under nurse plants was higher than the probability of cacti growing in open spaces (desert shrubland: Z = 6.66, P < 0.000, tropical dry forest: Z = 2.76, P < 0.006; Figure 5A).

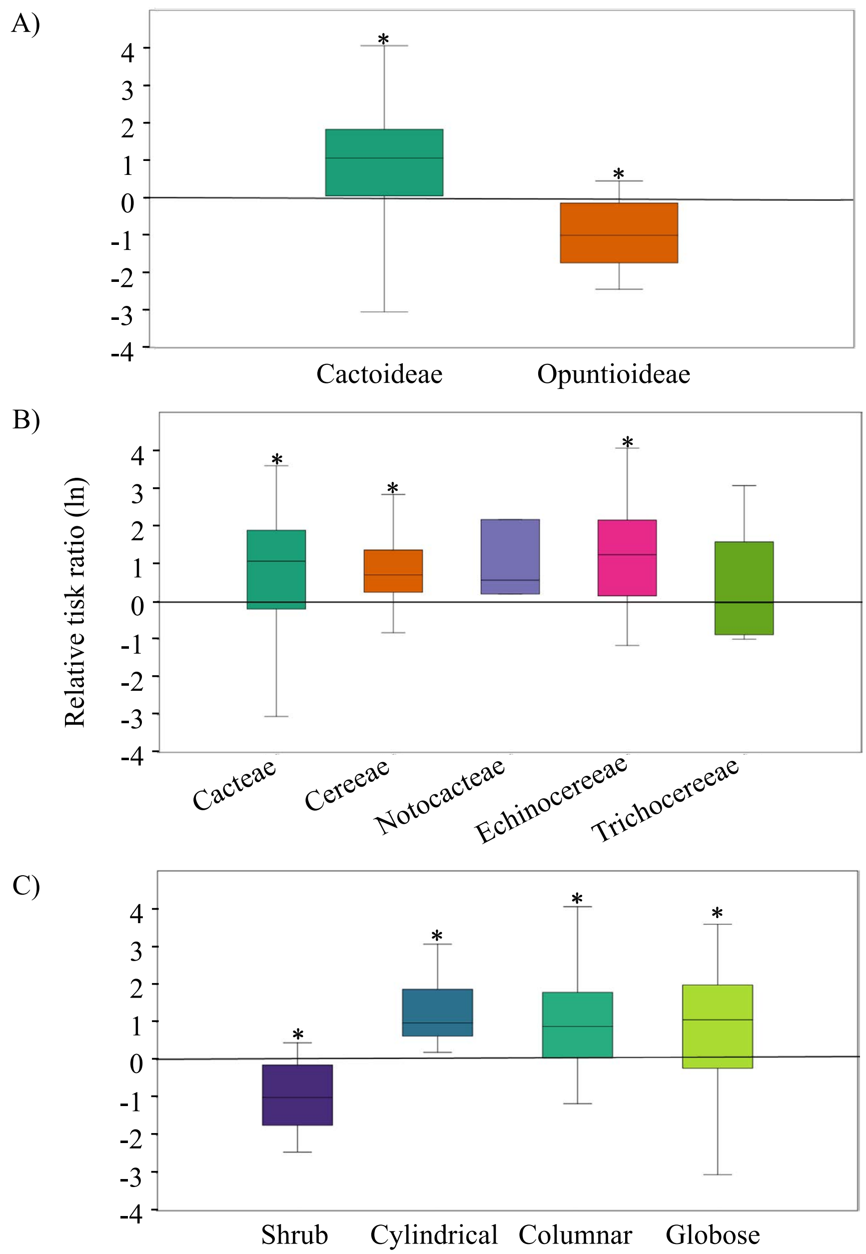

Figure 3. Relative risk ratio for A) subfamilies, B) tribes, and C) growth forms of cacti. The ratios marked with * significantly differed from zero.

Soil properties. We obtained data for 13 soil properties. Of these soil properties, the soil surface temperature was higher in open spaces than under nurse plants (Z = 2.20, P = 0.028; Figure 5B).

The soil electrical conductivity, soil moisture, nitrogen, phosphorus, calcium, and magnesium were higher under nurse plants than in open spaces (electrical conductivity: Z = 2.52, P = 0.012, moisture: Z = 2.37, P = 0.018, nitrogen: Z = 2.19, P = 0.028, phosphorus: Z = 2.37, P = 0.018, calcium: Z = 2.50, P = 0.013, magnesium: Z = 2.40, P = 0.017; Figure 5B).

The soil organic matter, pH, calcium carbonate, potassium, sodium, and sulfates were similar under nurse plants and in open spaces (organic matter: Z = 1.57, P = 0.12, pH: Z = 0.65, P = 0.515, calcium carbonate: Z = 0.45, P = 0.655, potassium: Z = 1.35, P = 0.176, sodium: Z = 1.69, P = 0.109, sulfates: Z = 0.32, P = 0.753; Figure 5B).

Discussion

The results showed that cacti were associated to nurse plants. However, this association did not occur in all subfamilies, tribes, and growth forms of cacti, nor in families and growth forms of nurse plants. Moreover, nurse plants only ameliorated some soil properties. These results suggest that the association between cacti and nurse plants could be due to the amelioration of soil properties such as the soil surface temperature under the canopy of nurse plants. However, our review only considered studies that evaluated the spatial pattern of cactus association with area sampling methods by calculating the observed and expected number of cacti under nurse plants and in open spaces. Studies on the spatial pattern of cactus association with distance sampling methods, the association of cacti with nurse objects, and the experimental studies on seed germination and seedling survival under nurse plants and in open spaces were not considered in the review. Despite this limitation, as far as we know, this is the first review that quantitatively analyzed the association between cacti and nurse plants.

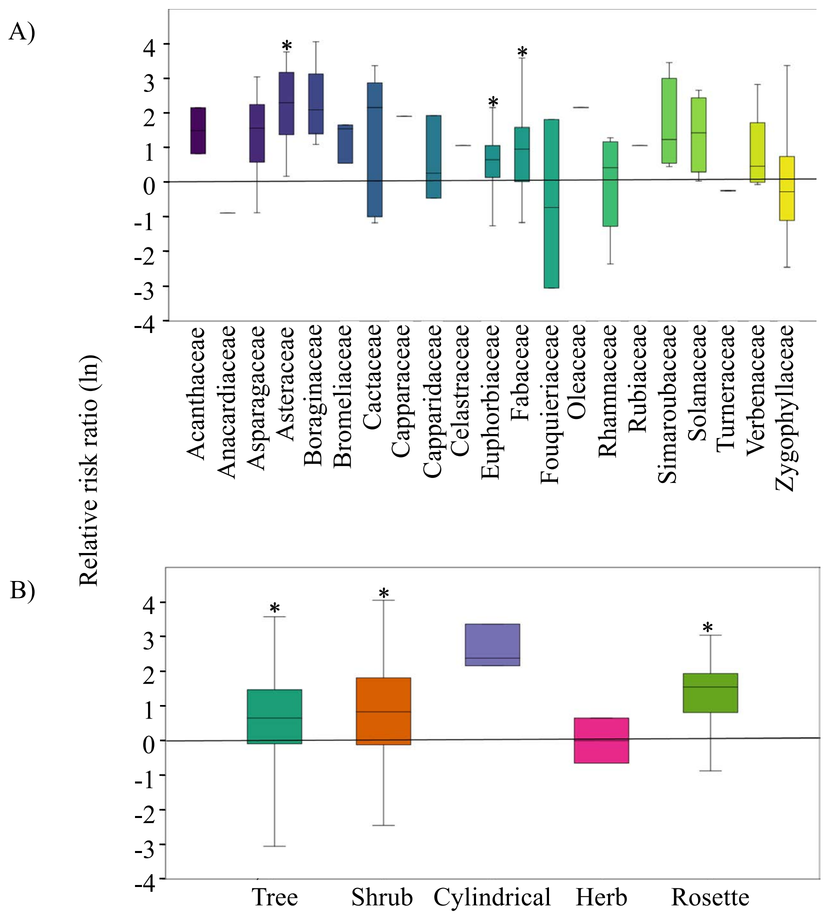

Figure 4. Relative risk ratio for A) families and B) growth forms of nurse plants. The ratios marked with * significantly differed from zero.

The shrub cacti of the subfamily Opuntioideae had a relatively low probability of being associated to nurse plants whereas the globose, cylindrical, and columnar cacti of the tribes Cacteae, Cereeae, and Echinocereeae , belonging to the subfamily Cactoideae, had a relatively high probability of being associated to nurse plants. These results suggest that some genera of the subfamily Opuntioideae such as *Opuntia* and *Cylindropuntia* can establish in open spaces probably due to their ability to propagate vegetatively (Evans *et al*. 2004). The areoles of cladodes or terminal stem segments that fall to the ground can produce new roots and stems that originate new individuals. In fact, some species such as *Opuntia rastrera*, *Opuntia macrocentra*, and *Cylindropuntia imbricata* can propagate vegetatively in stressful environments like open spaces (Allen *et al*. 1991, Mandujano *et al*. 1998), although this ability to propagate is seemingly higher in *Opuntia* than in *Cylindropuntia* due to the larger volume of cladodes to storage water and carbohydrates (Flores-Torres & Montaña 2012).

In addition to the vegetative propagation, some species of *Opuntia* such as *Opuntia pilifera* can grow in open spaces because its cladodes are facing east and west. This orientation increases the absorption of photosynthetically active radiation, and decreases cladode temperature, thus allowing photosynthesis (Cano Santana *et al*. 1992).

The probability of cacti growing under perennials and the probability of cacti growing in open spaces were similar in the Acanthaceae, Asparagaceae, Boraginaceae, Bromeliaceae, Cactaceae, Capparidaceae, Fouqueriaceae, Rhamnaceae, Simaroubaceae, Solanaceae, Verbenaceae, and Zygophyllaceae. In contrast, the probability of cacti growing under nurse plants was higher than the probability of cacti growing in open spaces in the Asteraceae, Euphorbiaceae, and Fabaceae. These results suggests that these two groups of plant families differ in the amelioration of soil properties under their canopies and thus, in the provision of an adequate microclimate for seed germination and seedling growth of cacti. Other studies (Flores & Jurado 2003, Godínez-Alvarez *et al*. 2003) also found that the Fabaceae and Asteraceae had high numbers of species acting as nurse plants.

The nurse plants of some families such as Asparagaceae (*Agave*), Bromeliaceae (*Hecthia*), and Cactaceae (*Echinocactus*) can be rosettes or cylindrical cacti that do not provide enough shade, nor produce enough soil organic matter to facilitate cactus establishment. Moreover, the nurse plants of other families such as Solanaceae (*Capsicum*) are shrubs with sparse crowns and relatively superficial root systems unable to decrease the direct solar radiation and

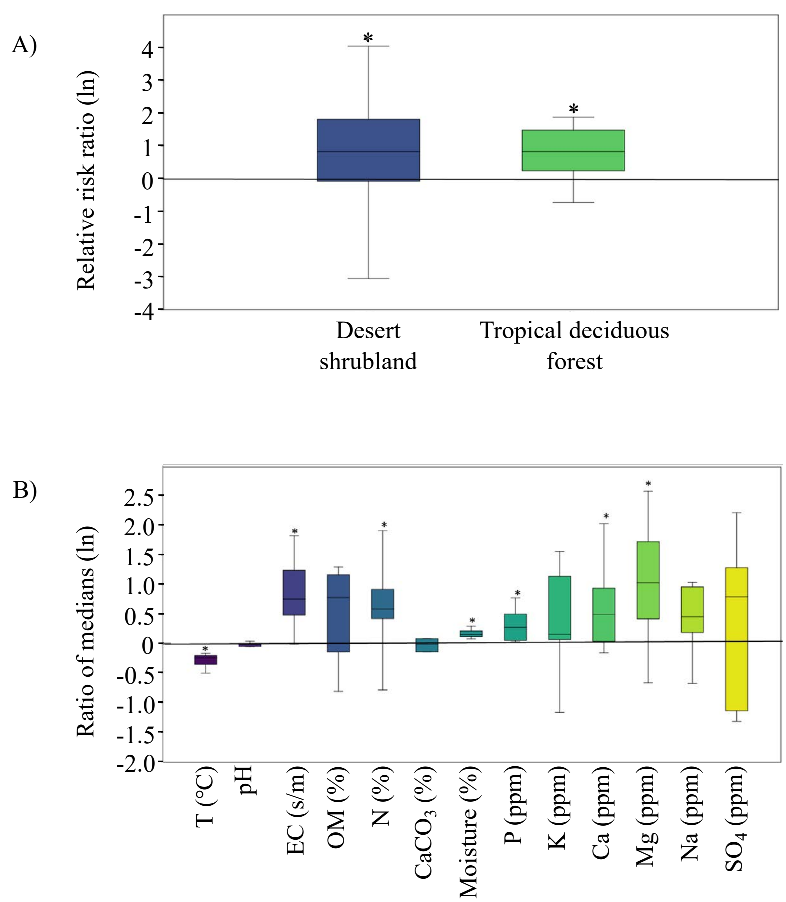

Figure 5. Relative risk ratio and ratio of medians for A) plant communities, and B) soil physical and chemical properties, respectively. The ratios marked with * significantly differed from zero. EC = soil electrical conductivity, OM = soil organic matter, T = soil surface temperature.

transport water from the deep, moist soil layers to the superficial and dry layers of soil. In contrast, the nurse plants of some families such as Asteraceae (*Ambrosia*), Euphorbiaceae (*Jatropha*), and Fabaceae (*Prosopis*) are trees and shrubs with dense crowns and deep root systems, particularly nurse plants in the Fabaceae family, that can decrease the direct solar radiation and soil surface temperature, and increase the soil moisture through hydraulic lift (Muñoz *et al*. 2008). Moreover, these trees and shrubs can produce enough leaf litter to increase the organic matter and nutrient content of the soil (Cares *et al*. 2013). In fact, our results showed that nurse plants increased the electrical conductivity, moisture, nitrogen, phosphorus, calcium, and magnesium content of soil. However, nurse plants did not increase the organic matter, pH, calcium carbonate, potassium sodium, and sulfate content of soil. Flores & Jurado (2003) also found that soil nitrogen content and litter are higher under nurse plants than in open spaces.

The association between cacti and nurse plants occurred in the desert shrubland and tropical dry forest. These results suggest that both plant communities have harsh conditions of temperature and rainfall that can limit cactus establishment. For instance, the desert shrubland has low mean annual rainfall (< 50 mm to < 700 mm) that occurs mainly in the summer when the solar radiation, soil surface temperature, and evapotranspiration are high (Challenger 1998). In contrast, the tropical dry forest has a mean annual temperature of 20-29 °C and a mean annual rainfall of 600-1,200 mm (Challenger 1998). However, the rainfall is seasonal with a dry season that can last 5-8 months (Challenger 1998). Because of these climatic conditions, the successful establishment of cacti in the desert shrubland and tropical dry forest can occur only under the canopy of nurse plants.

This quantitative review showed that several studies have evaluated the spatial association between cacti and nurse plants. However, this plant association does not include all the members of the cactus family because some subfamilies, tribes, and growth forms were not associated to nurse plants. Also, the nurse plants only modified some soil properties. Lastly, this plant association has been evaluated only in the desert shrubland and tropical dry forest. Therefore, further studies are needed on a greater number of subfamilies, tribes, and growth forms of cacti in different plant communities. Moreover, further studies are needed on the amelioration of soil properties under the canopy of nurse plants and their influence on cactus establishment. Finally, most studies on the association between cacti and nurse plants have been performed in Mexico and the USA, thus more research is needed in other countries with a high cactus diversity in Central and South America.

Supplementary material

Supplemental data for this article can be accessed here: https://doi.org/10.17129/botsci.3520

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