

Topography drives tree-habitat association and functional and phylogenetic structure in the Northernmost tropical dry forest of the Americas

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Abstract

Environmental conditions of a habitat that determine species distributions are strongly influenced by physiographic characteristics of the landscape. The tropical dry forest (TDF) of northern Mexico, defined by drought season and rugged topography, is an excellent system to study the topographic effect on tree-habitat association. Some studies have documented the effects of slope orientation (SO: north-facing/south-facing) and topographic position (TP: ridge/valley) on species distribution patterns in TDF; however, most have been conducted at low latitudes. In this study, we explore how the taxonomic, functional, and phylogenetic composition of tree communities of TDF are correlated with two topographic aspects in juveniles and adults in the northernmost TDF of the Americas. Our results (PCA) based on abundance showed segregation of two species groups (north-facing or south-facing) driven by SO in both life stages. Regarding the strength of habitat association of species, we found significant association in 71% of the species in juveniles or adult stages, with habitat (north-facing or south-facing slopes), and two thirds of these species (68%) were similarly associated to the same habitat in both juveniles and adults. The SO also influenced taxonomic, functional and phylogenetic structure, but differently in life stages. TP did not show any significant effects on the community structure or species habitat-association patterns. In both life stages, communities on north-facing slopes were evolutionarily similar to each other, whereas they were distantly related to those on south-facing slopes. The consistent functional and evolutionary segregation of species between the two habitats indicates a mechanism of topographic habitat specialization.

Introduction

The environmental heterogeneity in tropical systems has allowed researchers to study the association and distribution patterns of tree species and infer the possible mechanisms that drive these patterns (Chesson 2000; Harms et al. 2001; Engelbrecht et al. 2007; Comita and Engelbrecht 2009; Balvanera et al. 2011; Krishnadas et al. 2016; Muscarella et al. 2019; Mendez-Toribio et al. 2020). Tree-habitat associations have been widely studied in tropical humid ecosystems' however, in tropical dry forests (TDF) these associations have been inadequately studied and are poorly understood. Highly seasonal ecosystems, such as TDFs, are characterized by their wide variability of abiotic conditions and particularly availability of water, even at small spatial gradients (Engelbrecht et al. 2007; Maass and Burgos 2011; Méndez-Toribio et al. 2017). In these ecosystems, water availability at local scale is considered one of the main factors influencing habitat association patterns, niche partitioning and spatial distribution of trees and functional traits (Segura et al. 2003; Borchert et al. 2004; Comita and Engelbrecht 2009; Balvanera et al. 2011; Bhaskar et al. 2014; Pineda-Garcia et al. 2015). Particularly in Mexico, TDFs are characterized by their long dry season, with up to 6–8 months of drought, and the rugged topography in which these ecosystems occur (e.g. canyons and steep ravines) (Martínez-Yrizar et al. 2000; Dirzo et al. 2011).

Studies have also shown, however, that topography does not always affect the vegetation in the same way, especially across sites from different latitudes (Gallardo-Cruz et al. 2009). For example, in the

Northern Hemisphere south-facing slopes are usually characterized as drier, with greater insolation and lower water availability than north-facing slopes (Galicia et al. 1999). These differences have led to questioning the relative importance of the topographic position and the slope exposure in driving the species association and distribution patterns and/or the dominance of their adaptive strategies for water use (Webb and Peart 2000; Valencia et al. 2004; Balvanera et al. 2011; Méndez-Toribio et al. 2017). Sites at lower latitudes (near to Equator) are expected to have a lower environment-vegetation interaction effect than those at higher latitudes, due to the marked difference in solar radiation incidence and other environmental variables related, such as water availability (Galicia et al. 1999). Existing studies of the topography and drought related effect on TDF have been conducted mainly at low latitudes (Gallardo-Cruz et al 2009; Markesteijn et al. 2011; Balvanera et al. 2011; Méndez-Toribio et al. 2017); while in areas where TDF reaches its latitudinal range limits, there are no studies on this subject. These limit our understanding of the main physiographic factors that drive the assembly of species in these species-rich ecosystems.

The effects of marked seasonality, high variability in soil water availability and the high levels of solar radiation are manifest in a large number of structural, phenological and functional adaptations (e.g. pubescence, leaf retention time, xylem water content) which enable species of the TDF to tolerate or avoid water shortages and to take advantage of water available only for short periods of time (Borchert 1994; Markesteijn et al. 2011; Mendez-Alonzo et al. 2012; Pineda-García et al. 2015). Drought-tolerant species are generally slow-growing, with dense tissue on leaves, roots, and stems. Its leaf blades are small and durable. They have a xylem resistant to hydraulic failure, but with a restricted efficiency in conducting water. This limits the ability of the species to take advantage of water when it is available and grow rapidly (Mendez-Alonso et al. 2012; Pineda-Garcia et al. 2015). On the other hand, drought-avoiding species have soft stems with high water storage capacity. They have a highly efficient xylem but vulnerable to embolism. Its leaves are large and short-lived (Mendez-Toribio et al. 2017). Such traits might enable species to thrive under a broader range of spatial and temporal variability in water availability.

This prior research highlights the importance of addressing the processes of niche differentiation, habitat specialization and environmental filtering to understand the association patterns and coexistence of TDF's species. In theory, the physiographic characteristics (i.e., slope exposure and topographic position) can be seen as underlying factors of the environmental filtering, which may delimit tree species distribution to a specific habitat (Webb 2000; Cavender-Bares et al. 2009). Few studies, mainly from humid forests, have directly evaluated the tree-habitat association patterns and have considered the habitat specialization as a mechanism operating from early stages of development (Webb & Peart 2000; Comita et al. 2007; Metz et al. 2012); in the case of dry forests these patterns are poorly understood. Taking into account that the requirements to assimilate the same resource change through the ontogeny of a species (Donovan and Ehleringer 1992; Poorter 2007; Comita et al. 2007; Hietz et al. 2017), we believe that addressing the study of diversity in its different facets and between different life stages adds important value to understanding the mechanisms that drive the structuring patterns of these ecosystems. To our knowledge, there are no precedents for studies that jointly evaluate the habitat

association and the functional and phylogenetic structure of communities of dry forest tree species in different life stages.

In this article, we explore how the taxonomic, functional, and phylogenetic patterns of woody species of a Northwestern Mexican TDF are correlated with two physiographic factors, slope compass orientation and topographic position (high or low on slopes). By studying these patterns in two life-stages (juveniles and adults) of trees and shrubs, we could infer the mechanisms driving the distribution and co-occurrence of species in this TDF's community.

Comparison between juvenile and adult life-stages can be very informative to elucidate the importance of habitat on the association and coexistence patterns of species in different stages of development. In a scenario where juvenile and adult species share the same habitat, it is possible to observe three possible association patterns (Webb and Peart 2000): (i) Juvenile stages are less strongly associated with a habitat than adults; (ii) adult stages are less strongly associated with a habitat than juveniles; and (iii) adults and juveniles have a similar habitat association. The observation of any of these patterns could be the result of underlying mechanisms such as density-dependence, limited dispersal and/or habitat specialization, promoting the association and coexistence of species at a local scale (Webb and Peart 2000; Valencia et al. 2004; Comita et al. 2007; Metz 2012). The first pattern may occur when there is wide seed dispersal to the preferred habitat of adults, but seeds establish in low proportions due to harsh habitat conditions. Thus, large seed dispersal may generate random association patterns in early stages, but with marked association patterns through larger stages. The second pattern may be found when the habitat is initially suitable for establishment, but not for survival through larger stages. That is, seedlings establish in large quantities, but negative density-dependence prevents adults not associated to a specific habitat. The last pattern may occur in an scenario of preferential habitat of species of limited dispersal, where seeds are dispersed in the same habitat of adults. In this scenario we assume that habitat is optimal for survival of earlier stages and adaptation of topographic habitat precede their establishment. A last scenario which could produce this third pattern may be the seed dispersal by disperser agents, with high habitat fidelity (Zwolak and Sih 2020).

Specifically, we address the following questions: (i) is the distribution of juvenile and adult trees associated with any physiographic factor, such as slope orientation and topographic position, and if we find this evidence, at what taxonomic level does this association occur?; (ii) are the habitat association patterns of juvenile trees conserved in adults?; (iii) what can we infer about the functional and phylogenetic structure of TDF communities among two different life-stages?; and (iv) what are the possible mechanisms that drive habitat association in the northernmost tropical dry forest of the Americas in the northwest of Mexico?

Methods

Study site

This study was conducted in the ~ 93,000 ha Flora and Fauna Protected Area “Sierra de Álamos-Rio Cuchujaqui” (APFF-SARC, for its Spanish acronym) in the state of Sonora, Mexico (López-Toledo *et al.* 2011). The APFF-SARC forms part of a network of Protected Areas recognized by UNESCO. This Protected Area contains a large extension of TDF and has a very pronounced dry season (November - June). During the dry season TDFs receive only 25–35 % of the total annual precipitation and annual temperatures are on average 21.5 °C and range between 10–41 °C.

In 2018 through a collaboration among scientists from Universidad Michoacana de San Nicolás de Hidalgo, University of California-Los Angeles and Monte Mojino Reserve the Alamos Forest Dynamics Plot (AFDP), a 50 ha permanent plot was established within the APFF-SARC to study the forest dynamics in the northernmost limit of the tropical dry forest (TDF) in the Americas. The total area (500 × 1000 m) was gridded by iron stakes every 20 m. After the 50-ha plot was gridded and with the help of a digital elevation model, 16 subplots (20 × 40 m each) were selected that had different slope compass orientations that we could group into two classes: slope orientation (SO: North-facing and South-facing) and topographic position (TP: High and Low), which refer to a subplots at high or low position in the slope of hills with short differences in elevation (< 80 m). These subplots reflected the different environmental/topographic conditions present in the 50 ha plot. For example, the high and low subplots are far and near, respectively, to intermittent streams. The four treatments were: (i) north-facing low, (ii) north-facing high; (iii) south-facing low and (iv) south-facing high. Each of these treatments was replicated 4-fold (Fig. 1).

Data collection

We used the standardized methodology developed by the Center for Tropical Forest Science (now ForestGeo) for long-term and large-scale census of plots in tropical ecosystems (Condit 1998) to census individuals of woody species (trees, shrubs and arborescent cacti). In each of the 16 subplots, we recorded the structure and species composition of woody stems in a total area of 1.28 ha. All woody stems ≥ 1 cm diameter at breast height, 1.3 m (DBH) were mapped and identified and their height and DBH measured. We collected vouchers for every stem recorded in each plot. Stems were identified to species following Felger *et al.* (2001) and Van Devender *et al.* (2000) and we consulted four regional and national Herbaria: Universidad Autónoma de Sonora (USON), Universidad Michoacana de San Nicolás de Hidalgo (EBUM), Centro Regional del Bajío (IE-Bajío) and National Herbarium of Mexico (MEXU). From the inventory, we obtained the following six measures of vegetation structure: density of individuals, number of stems, density and diversity of species (Fisher’s alpha index), basal area and above ground biomass.

To characterize and differentiate the distribution of the species and their water use strategies we measure functional traits of branches, which provide important information on the performance of tree species in extreme drought conditions (Chave *et al.* 2014; Muscarella and Uriarte 2016; Mendez-Toribio *et al.* 2017). Specifically, during the 2018 dry season within the AFDP, we randomly selected five individuals of each species and measured the following five functional traits: (i) Wood density (WD), (ii) Bark water content (Bwc), (iii) Bark thickness (Bt), (iv) Xylem water content (Xwc) and Maximum height (H_{max}). From each of these five individuals, we collected three second order branches with a diameter of ~ 2.5 to 3 cm and at

least a length of 16 cm. Individuals were of similar height and all the collected branches had similar sun exposure and no apparent signs of herbivores and/or pathogens. All samples were transported and processed at the Plant Ecology Lab at Universidad Michoacana. Bark thickness was measured with a digital caliper to 0.01 mm. Wood density was calculated as the ratio of dry weight of a sample wood without bark (oven dried at 90°C for 72 h) and the fresh volume, following the water displacement method (Williamson and Wiemann 2010). The X_{wc} and B_{wc} were estimated as $X_{wc}/B_{wc} = ([\text{fresh weight} - \text{dry weight}] / \text{dry weight}) \times 100$. The fresh weight of the branches was obtained after a hydration period of 24 h in distilled water (Mendez-Toribio et al. 2017). We calculated the community-weighted means (CWM) for each trait t and each community (plot) p as:

$$CWM_{tp} = \sum_{i=1}^S a_{ip} \times t_i;$$

where a_{ip} is the relative basal area of species i in plot p and t_i is the mean trait value of species i (Muscarella and Uriarte 2016). We used these CWMs for all functional analysis.

Phylogenetic construction

We built a species pool using the list of sites sampled and previous studies in the Alamos region in Sonora (Martin et al. 1998; Van Devender et al. 2000; Martínez-Yrizar et al. 2000; Quisehuatl-Medina et al. 2020). The final list consisted of 106 tree shrubs and arborescent cacti species: 105 angiosperms and 1 outgroup (*Cycas revoluta*). For all species, we obtained three nuclear markers from GenBank (ITS, containing ITS1, *5.8s* and ITS2). Given data for 8 out of the 53 species on the local list (Table S1) were not available, we added sequences from congeneric taxa that occur in tropical forest habitats of the Americas.

The sequences were aligned with MUSCLE (Edgar 2004) and the best-fit model of nucleotide substitution based on the Akaike Information Criterion (AIC) was performed with the jModelTest (Posada 2008). We generated a phylogeny based on Bayesian posterior probability using *Mr. Bayes* 3.2.1 (Ronquist et al. 2012). The parameters were estimated by Markov Chain Monte Carlo (MCMC) simulation for 30 million generations. We used a nucleotide substitution model GTR + I + Γ and an unrestricted exponential molecular-clock model for each analyzed sequence. We sampled the runs every 1000 generations and the first 50000 trees were discarded as burn-in. Tracer version 1.5 was used to confirm an acceptable mixture, a stationary verisimilitude, an appropriate burn-in and an effective sample size. The *bladj* algorithm of the Phylocom 4.2 software (Webb et al. 2008) was used to assign ages to the nodes and to uniformly space the latter among them; the age of the 104 nodes used was provided by TIMETREE (<http://timetree.org/>). This phylogeny calibrated in time (My), shown in Fig. S1, was later used for the calculation of indices of phylogenetic diversity.

We calculated two measures of phylogenetic structure for each community studied (16 plots of 20 × 40 m) using the *Picante* package in R (Kembel et al. 2010). We calculated Net relatedness index (NRI) and Nearest taxon index (NTI) based on incidence (Webb 2000; Kraft et al. 2007). The NRI of each quadrat are

generated from the sum of branch lengths of branches that connect all co-occurring taxa (MPD: mean pairwise distances) while NTI is derived from the average branch length to the nearest co-occurring taxon (MNTD: mean nearest neighbor distance) (Webb 2000; Webb et al. 2002). Observed values of MPD and MNTD were compared with the expected phylogenetic distances under 9999 null communities corresponding to a given site (*-SES.mpd* and *-SES.mntd*, respectively). Both indices NRI and NTI are described by the formula: $SES_{Metric} = [- (Metric_{obs} - Metric_{null}) / SD (Metric_{null})]$, where $Metric_{obs}$ is the mean of MPD/MNTD observed in a given site, $Metric_{null}$ is the mean of MPD/MNTD for that site in 9999 null communities, and $SD (Metric_{null})$ is the standard deviation of MPD/MNTD for that site in 9999 null communities. These indices can be used to identify patterns of phylogenetic clustering or overdispersion in each subplot; positive values of NRI or NTI indicate phylogenetic clustering of the species at each site sampled, while negative values reveal overdispersion (Cadotte and Davies 2009). While NRI explores the relationships of the species within the phylogeny, NTI does it towards the tips.

Null models and phylogenetic beta diversity (PBD)

To determine if the phylogenetic structure observed differs from that expected by chance, we used a type 4 null model in Phylocom 4.2 (Kembel 2009). This null model uses the *independent swap* algorithm (Gotelli 2000; Gotelli and Entsminger 2003) to generate null communities, considering all the species in regional phylogeny and producing scenarios where the ability of these species to colonize any subplot is proportional to their frequency in the regional community (Gotelli and Entsminger 2003). This null model maintains the frequency of occurrence and species richness while randomizing the co-occurrence patterns of species in the community (Kembel and Hubbell 2006; Webb et al. 2008).

We calculated two estimators of phylogenetic beta diversity (PBD; *comdist* and *comdistnt*) for juveniles and adult tree communities. These indices of dissimilarity were based on incidence among the 16 subplots and between each of the treatments. COMDIST is a measure that computes the mean phylogenetic distance between species that co-occur in two different sites, it is a basal node metric (Jost 2007; Webb et al. 2008). COMDISTNT, on other hand, is a measure of dissimilarity that computes the mean phylogenetic distance between every species in a plot and the nearest phylogenetic neighbor in another plot. Therefore, it is a terminal node metric (Swenson 2011; Duarte et al. 2014). This metric was computed using the *Picante* package of R (Kembel et al. 2010) and the results were reported in a classification diagram of the sites based on the dissimilarity of the species they harbor.

Statistical analysis

In this study, we examined the role of two physiographic factors to explain tree-habitat association patterns over different life stages by splitting the tree communities into juvenile and adult sub-communities based on their DBH, specifically using species-specific DBH cutoffs. Some studies such as Baldeck et al. (2013) have suggested that differences in the community structure may be associated with the number of individuals and/or composition of the community. A first categorization of individuals based on a strict cut off of DBH (juveniles < 9.9 cm and adults ≥ 10 cm) generated a spurious pattern and suppress several species from the adult category. Therefore, we categorized the population of each species using the range of DBH and we considered the smallest half as juveniles, while the largest half

was considered as adults. We considered this categorization as the best available proxy to approach the structuring of tropical dry forest tree species. Thus, the sub-communities of juveniles and adults showed an almost identical taxonomic composition and abundance (Fig. S2b). For our species-specific analysis, only 41 out of 53 species were included in the study, as we used a minimum of five individuals and 12 species did not reach this number.

We used a multivariate approach to explore the relationships between community structure and the environmental habitat variables related to drought, (Legendre and Legendre 1998). Using the set of 41 species, we conducted principal component analyses (PCA) to assess the importance of the physiographic factors and environmental variables underlying tree-habitat associations and the taxonomic, functional and phylogenetic structure of the tree community in the two different life-stages. Two separate PCA analyses were performed for i) structural and ii) functional traits, using the mean of each trait for each subplot. This procedure enabled us to explore whether a particular stand structural attribute (e.g. basal area, species richness) or a particular functional trait (e.g. WD, Xwc) of the woody species community are associated with a particular physiographic factor. A PERMANOVA test was used to assess these differences. This is a non-parametric test that uses distance matrices to analyze multivariate variance (Anderson 2001).

All the statistical analyzes were carried out using the package *vegan* ver. 2.4.5 (Oksanen et al. 2017) in the statistical program R version 3.4.2. (R Development Core Team, 2014).

Habitat association of species

We evaluated habitat associations of the species using two methods. In the first, we compared the multivariate abundance of the species observed among the different habitat types and evaluated significance using a PERMANOVA test. We \log_{10} transform ($N + 1$) the abundance matrix of the species to reduce the biasing effect of very abundant species. The second method, a Monte Carlo randomization test, was used to assess the habitat preference of species to both habitat types. We performed this test to avoid the problem of non-independence that invalidates the tables of contingency, which is produced by the non-independence of the spatial distribution of juveniles and adults in adult-preferred habitats due to dispersal limitation (Hubbell 1979, Clark et al. 1998; Webb and Peart 2000). With this method, we randomize the type of habitat in which each of the species occurs and calculate a deviation statistic based on the abundance of species in each habitat: $\sum[(\text{Randomized} - \text{Expected})^2 / \text{Expected}]$. We repeated this randomization 1000 times for each species, and compared the values of the observed deviation with the distribution of random values. We consider significant habitat association as observed values greater than 95% of the randomized values. We also used this second method to evaluate the conservation of habitat association patterns at higher taxonomic levels (genera and family).

Phylogenetic structure

We evaluated differences in phylogenetic structure by comparing phylodiversity patterns between both physiographic factors (SO and TP) and between each life stage. In each case we used the NTI/NRI values for each of the 16 plots and tested with a *t-student* two-tailed test. We evaluated the phylogenetic beta

diversity patterns in the different life stages using the COMDIST and COMDISTNT functions of Phylocom (Webb et al. 2008) and used a PERMANOVA test to determine significance between habitat types and between treatments.

Solar radiation incidence

For each vegetation sampling location, we computed solar radiation incidence (SRI, i.e. direct + diffuse) as a proxy of plot potential energy income (PEI). Thus SRI values per plot were derived by using ArcGis 10 v ESRI (2009), based on a 20 m digital elevation model obtained for the studied landscape. We used the “area solar radiation” module from Spatial Analyst Tools in ArcGis to derive PEI values, defined as the quantity of solar energy on each pixel (20 × 20 m) of the image (MJ/m²). Some studies have documented that high SRI values can affect water content in the soil through evapotranspiration (Galicia et al. 1999). We contrasted the mean values of SRI among the physiographic factors, for the dry season (November-June) and the rainy season (July-October), and evaluated their differences using the Wilcoxon rank-sum test.

Results

Community structure

We registered a total of 6034 individuals of trees and shrubs corresponding to 53 species, 41 genera and 23 families in the 1.28 ha area sampled (Table S1). Fabaceae was the family that comprised the highest number of species (30%), followed by the families of Burseraceae (9%), Cactaceae (9%) and Euphorbiaceae (7%). The latter was dominant in terms of number of individuals, mainly due to *Croton fantzianus* (~ 52%). Based on previous botanical work of Van Devender et al. (2000) and Felger et al. (2001) we recognized that 77.1% were trees, 20.3% were shrubs and 2.5% were arborescent cacti.

For the species-specific DBH cutoffs, we used 6016 individuals (99% of total) corresponding to 41 species, which belong to 30 genera and 18 families. We left 18 individuals out of the analysis, representing 12 species, due to the very low number of individuals. Five species were represented by only one individual (e.g. *Cochlospermum vitifolium*, *Conzattia multiflora* and *Pseudobombax palmeri*; Table S1).

We did not find any significant effect of topographic position (TP), as the high and low plots in general showed similar values either in habitat association patterns of species, or in structural, functional and phylogenetic aspects. Also the interaction of TP with slope orientation, did not show any significance. Therefore, henceforth we only discuss the effects of slope orientation.

On one hand, the univariate analysis did not detect any effect of SO on structural attributes, except on the number of stems and basal area for adults (Table S2). Similarly, the multivariate analysis of the structural attributes also was not significantly different between slopes in either life stages (Table 1; Fig. 2a, b).

Table 1

Results of the multivariate analysis using a PERMANOVA, evaluating the effect of slope orientation and topographic position on the structural and functional attributes in two life stages (adults and juveniles) of a TDF in northwestern Mexico. Significant terms are indicated with an asterisk.

Attributes	Slope orientation		Topographic position		SO:TP	
	R ²	P	R ²	P	R ²	P
Juveniles						
Structural	0.04	0.56	0.02	0.79	0.03	0.64
Functional	0.35	0.009*	0.09	0.15	0.005	0.88
Adults						
Structural	0.09	0.27	0.001	0.98	0.02	0.77
Functional	0.27	0.02*	0.07	0.22	0.001	0.97

In subsequent sections, we focus on functional structure, patterns of tree-habitat association, and phylogenetic diversity, each of which showed significant patterns depending on habitat type.

Functional traits of the community

Using CWM values, we found that functional trait differences of trees are strongly associated to SO and this pattern is consistent in both life stages (Fig. 2c; d). As mentioned, none of the functional trait variation was explained by TP or by the interaction between SO and TP (Table 1; S3). For the juvenile stages, the north-facing subplots had significantly higher CWM values for traits such as *Xwc*, *Bwc*, *Bt*, and *Hmax*, in comparison to the south-facing CWM values for traits (Fig. 2c; d; Table S3). The first PCA axis of the juveniles was strongly associated with the SO and showed a clear differentiation of habitat types, where species distributed in north-facing sites have significantly different functional trait values than those of south-facing (Table 1, Fig. 2c). In the adult stage, the pattern is the same, differences in functional traits and underlying adaptive strategies appear to be equally mediated by the environment of each slope. The two habitat types are clearly defined on PCA ordination axis, based on slope orientation, differing in CWM values of functional traits (Table 1; Fig. 2d).

Patterns of habitat association

The results of the PCA based on abundance and composition of woody species indicate a clear differentiation between the habitat types of slope orientation, suggesting that this is a physiographic factor that gives rise to the differential association of TDF's woody species in the both life stages (Fig. 3) and the PERMANOVA analysis confirms the same results.

Based on the randomization methods, out of 41 species with sufficient numbers of individuals for contingency analysis, 29 species (71%) showed non-random association patterns with some habitat type

at some life history stage, while 12 species (29%) showed no habitat association at all. Twenty-two out of 41 species were significantly associated with a habitat type (Table 2), although only fifteen of these were similarly associated with the same habitat both as juveniles and as adults (Table 2). That is, seven species were habitat-associated as juvenile but not as adults and the other seven were habitat-associated as adults, but not as juveniles (Table 2). The fact that juveniles and adults are similarly associated may suggest that deterministic mechanisms (e.g. localized dispersal) are operating at even earlier stages of development (seeds-seedlings, see discussion). With respect to habitat type, juveniles of ten tree species were associated with south-facing and twelve with north-facing orientation; whereas, in adult stages, eleven were associated with north-facing and the rest with south-facing orientation. Finally, only 12 species were not associated with any habitat type and most of these species (66%) were widely abundant (Table S1).

Table 2

Species association of juvenile and adult trees to a particular slope orientation (N = north-facing and S = south-facing). The taxa correspond to the 41 species, present in juvenile and adult stages. The significance of the associations was evaluated with Monte Carlo randomization tests (see methods). Asterisk show those species that as juvenile and adult trees are associated with the same habitat (see Fig. S6).

Adults		
Juveniles	Non-associated	Associated
Non-associated	<i>Bursera fagaroides</i>	<i>Diphysa occidentalis</i> (S)
	<i>Bursera laxiflora</i>	<i>Erythrina flabelliformis</i> (N)
	<i>Fouquieria macdougalii</i>	<i>Haematoxylum brasiletto</i> (N)
	<i>Guazuma ulmifolia</i>	<i>Karwinskia humboldtiana</i> (N)
	<i>Ipomoea arborescens</i>	<i>Lonchocarpus hermannii</i> (N)
	<i>Jacquinia macrocarpa</i>	<i>Maclura tinctoria</i> (S)
	<i>Jatropha cordata</i>	<i>Randia echinocarpa</i> (S)
	<i>Jatropha malacophylla</i>	
	<i>Senna atomaria</i>	
	<i>Sp1.</i>	
	<i>Stenocereus thurberi</i>	
	<i>Wimmeria mexicana</i>	

Adults		
Associated	<i>Bursera penicillata</i> (S)	<i>Acacia cochliacantha</i> * (S)
	<i>Ceiba acuminata</i> (N)	<i>Brongniartia alamosana</i> * (S)
	<i>Croton fantzianus</i> (S)	<i>Bursera grandifolia</i> * (N)
	<i>Hintonia latiflora</i> (N)	<i>Bursera sp.</i> *(N)
	<i>Lysiloma divaricatum</i> (N)	<i>Cordia sonorae</i> * (S)
	<i>Senna palida</i> (N)	<i>Coursetia glandulosa</i> * (S)
	<i>Zanthoxylum fagara</i> (N)	<i>Croton flavescens</i> * (S)
		<i>Erythroxylum mexicanum</i> * (N)
		<i>Handroanthus impetiginosa</i> * (N)
		<i>Lysiloma tergimum</i> * (N)
		<i>Pachycereus pecten-aboriginum</i> * (S)
		<i>Randia thurberi</i> * (S)
		<i>Sebastiania pavoniana</i> * (N)
		<i>Sp3.</i> * (N)
		<i>Stenocereus montanus</i> * (S)

In the juvenile stage, the differentiation between habitat type was represented by the occurrence of some species adapted to sites where the availability of water is scarce and the levels of solar radiation were high (Fig. S3; south-facing [e.g. *Acacia cochliacantha*, *Brongniartia alamosana* and *Croton fantzianus*]), whereas other species less tolerant to drought (inferred from their functional traits) were associated with north-facing sites (e.g. *Bursera grandifolia*, *Karwinskia humboldtiana*, *Handroanthus impetiginosus*). For the case of adult trees the pattern was similar, with drought-tolerant species in south-facing orientation and drought-avoidance strategies in the north sites. Some of the species associated as adults with south-facing sites were: *Acacia cochliacantha*, *Brongniartia alamosana*, *Randia thurberi* and *Stenocereus montanus*, while adults associated with north-facing sites are represented by *Bursera grandifolia*, *Karwinskia humboldtiana*, *Handroanthus impetiginosus*, *Haematoxylum brasiletto* and *Sebastiania pavoniana* (Table 2).

We also used the randomization method to evaluate habitat associations for higher taxonomic levels. In this case 22 out of 30 genera (73%) and 13 out of 18 families (72%) were significantly associated with habitat type. Of these associated genera, eleven (50%) were similarly associated to the same habitat in both juveniles and adults stages. At the family level, six (33%) were similarly associated to the same habitat both as juvenile and adult.

Comparing the habitat association at the family (Fig. S4) and species level (Table 2) for juveniles, we found the following patterns: five families are associated with the same habitat as all their species, another five families and all their species were non-associated, four families are associated but have some non-associated species, and four families are not associated, but contained some associated species. For the case of adults, six families are associated with the same habitat as all their species, six other families and all their species were non-associated, three families are associated but have some non-associated species, and another three families are non-associated, but contained some associated species. The results of this analysis are summarized in Table 2 and Venn diagrams of supplementary material (Fig. S4).

Phylogenetic diversity, α and β

Our analysis of mean phylogenetic diversity showed similar habitat association patterns in juvenile and adult trees using NRI, but with an opposite trend when using NTI (Fig. 4). The phylogenetic structure was not significantly influenced by SO in juvenile stages, measured with NRI ($t = 0.92$, $df = 13.7$, $P = 0.36$) and NTI ($t = -1.62$, $df = 12.7$, $P = 0.12$); whereas at adult stages, the influence of the SO on phylogenetic diversity was significant using NRI ($t = 2.44$, $df = 9.08$, $P = 0.03$), but with not NTI ($t = -1.60$, $df = 13.3$, $P = 0.13$). In both life stages, the average phylogenetic diversity (NRI) on north-facing sites did have positive values, showing phylogenetic clustering, while south-facing sites harbor communities with phylogenetic overdispersion (Fig. 4a). By contrast, the NTI pattern was opposite, the north-facing sites with negative values (phylogenetic overdispersion) and south-facing with clustering (Fig. 4b). When we compare only the phylogenetic structure between the different life stages without considering habitat type, phylogenetic diversity was similar between juvenile and adult stages (NTI: $t = -0.06$, $df = 29.9$, $P = 0.95$; NRI: $t = -0.06$, $df = 29.8$, $P = 0.94$).

Phylogenetic beta diversity (PBD) on the other hand, using both COMDIST/COMDISTNT algorithms, showed non-random grouping patterns between sites (communities). Our study indicates that phylogenetically clustered communities tend to be more associated with slope orientation and this pattern is consistent between life stages (Fig. 5; Table S4). The dendrogram suggests that communities with values close to zero are evolutionarily similar and the species they harbor are more closely related (Fig. 5). The PERMANOVA applied to the distance matrix (*comdist* or *comdistnt*) indicated a strong discrepancy in the PBD values between SO in juvenile ($P < 0.001$) and adult ($P < 0.005$) stages (Table S4); while that no pattern was found for grouping with the TP. The formation of two large groups in both life stages (Fig. 5) indicates a marked habitat-association pattern of species between slope orientations but each habitat type harbors communities with similar evolutionary history. This last may be explained by a large portion of the communities belonging to abundant species (50%) associated with north-facing sites such as those from the Fabaceae family; while those significantly associated with south-facing sites belong to different lineages (Table 2; Fig. S4).

Topographic environment

Environmental variation using SRI was significantly different between SO but not between TP; this pattern was similar both in the dry season ($W = 56$, $P = 0.001$), and in the wet season ($W = 0$, $P < 0.001$; Fig. S3).

The highest SRI values during the dry season were reported on the south-facing slopes (mean \pm SE: 452.8 \pm 3.9 Mj/m²) and were 20% higher than the north-facing slopes. Similarly, during the wet season the SRI values were higher on the south-facing slopes (mean \pm SE: 554.1 \pm 2.2 Mj/m²), being 10% higher than on the north-facing slopes.

Discussion

In this study, we found that slope orientation (SO) was a more important physiographic aspect than topographic position in determining species-habitat association patterns within the AFDP, at the northernmost tropical dry forest of the Americas. In general, SO influences on the habitat preference of species, the CWM values of functional traits, and the phylogenetic structure of the woody vegetation, were similar in both life stages analyzed. Only the taxonomic structure was not influenced by physiographic factors in both life stages.

Comparison of juveniles and adults patterns of habitat association

Our study indicates that habitat preference of many of the species of the TDF is significantly associated with variation in topography, specifically with slope orientation, and that these associations are detectable during relatively early stages of plant ontogeny (\geq 1 cm) and these preferences are maintained into adult life. This result supports the hypothesis idea that a habitat filtering process is operating during the early life stages of trees, perhaps among seedling or small sapling stages (Webb and Peart 2000; Comita et al. 2007; Baldeck et al. 2013). This idea only makes sense if we consider the seed dispersal patterns of TDF trees (see below).

In tropical forests, topographic variation on a local scale is linked to a broad set of abiotic conditions (e.g. temperature, nutrient content and soil water availability), which in turn influence species distribution and the structuring of communities in their different facets (Valencia et al. 2004; John et al. 2007; Comita et al. 2009; Metz et al. 2012; Condit et al. 2013; Pineda-Garcia et al. 2015). Specifically in seasonally dry tropical forests, it is expected that this topographic variation shows a certain degree of habitat association. Therefore, we expected a high proportion of species significantly associated to a given habitat and this was the case. Of the 42 species evaluated in this study, 69% showed non-random association patterns with some habitat type. That is, the abundances of these species in one habitat (north-facing or south-facing) were significantly higher or lower respect to other habitat than might be expected by chance. This proportion of associated species was higher than those reported in studies of humid tropical forests in plots of 50 ha, which using similar statistical methods found that less than 50% of the species analyzed were associated to a habitat type (Hubbell and Foster 1986; Webb and Peart 2000; Comita et al. 2007). It should be mentioned that currently there are few studies of seasonally dry forests that directly evaluate the physiographic habitats association patterns and that allow contrasting the results obtained between different life stages.

Our study shows that most of the 22 species associated with a habitat (fifteen species) showed a pattern where both juvenile and adult trees are similarly associated (Webb and Peart 2000); that is, trees of a species in juvenile stage are significantly associated with the same habitat in adult stage. This pattern could be the result of possible events of a localized dispersal, where seeds of a species are dispersed in the preferred habitat of adults (Harms et al. 2001; Comita et al. 2007). This may imply a high rate of establishment and prevalence of individuals recruited in early stages of development. However, considering the spectrum of seed dispersal reported by several studies of the seasonally dry forest of the Mexican Pacific, this hypothesis can be discarded. In general, Neotropical dry forest trees have the dispersal syndrome of anemochory (wind-dispersed) slightly more often than the zoochory (mainly endozoochory) (Frankie et al. 1974; Gentry 1982; Bullock 1995; Greene et al. 2008; Lopezaraiza-Mikel et al. 2014). Both dispersal syndromes disseminate a fraction of their seeds out of the immediate local habitat. This would imply the action of a random component in the arrival of new species to a given habitat and a subsequent habitat filtering driving its establishment.

In our study site, very few species showed an indication of limited dispersal based on occurrence and/or frequency in one or several sites distributed in both types of habitat; such is the case of species such as *Erythrina flabeliformis* and *Sebastiania pavoniana*, whose distribution in both life stages is restricted only to north-facing sites, while *Stenocereous thurberi* and *Stenocereous montanus* are restricted to south-facing sites. The rest of the species were distributed in both habitats types (see Table S1).

Since the functional and phylogenetic structure showed the same habitat differentiation pattern of species in both life stages, we suspect that the observed patterns may be supported rather by a historical-evolutionary component, i.e., consistent functional differences exist between different evolutionary clades. Many studies that contrast the tree habitat-association in different development stages argue that this pattern of the species by itself does not provide solid information for the hypothesis that habitat specialization can determine distribution and coexistence species (Webb & Peart 2000; Harms et al. 2001; Comita et al. 2007). However, the consistent functional and evolutionary segregation of species in juvenile and adult stages between two markedly heterogeneous habitats supports the idea that the observed patterns are derivative from processes, such as topographic habitat specialization. In this sense, the phylogenetic approach contributes to understanding the historical evolutionary processes that history of the assembly of tropical tree communities (Webb et al. 2002; Cavender-Bares et al. 2009), and the functional approach additionally supports these findings (Baraloto et al. 2012; Spasojevic and Suding 2012; Muscarella et al. 2016). Based on our PBD analysis, we found evidence that in both life stages, north-facing sites have evolutionarily similar communities, but are more distantly related to communities on south-facing slopes. The functional structure showed a similar pattern in both life stages. North- and south-facing slope communities had distinct CWM functional traits combinations, but were functionally similar in communities within each slope orientation. Because we can detect these differences from a relatively early stage of tree development (juveniles), this suggests that environmental filtering of functional traits occurs early, in seedling- and small-sapling stages and that they are, in term of species lineages, phylogenetically conserved within each slope category (niche differentiation).

An environmental factor that proved to be strongly correlated with topography and that can help us understand the nature of these patterns is the Solar Radiation Interception (SRI), used here as an approximation of water deficit (Galicia et al. 1999). SRI was significantly higher for south-facing slopes, suggesting that south-facing sites have higher water deficit with respect to northern slopes. In seasonally dry systems, the marked dry season and strong contrasts in soil water availability lead to the selection of a variety of functional traits to cope with environmental conditions that are often influenced by topography, thus promoting niche differentiation between species since their establishment. In these ecosystems, multiple functional traits of stem, leaves and/or roots have been studied (Lebrija-Trejos et al. 2010; Mendez-Alonzo et al. 2012; Méndez-Toribio et al. 2017; Bruelheide et al. 2018). This variety of functional traits has made it possible to identify two main trait syndromes to cope with drought in TDFs. At one extreme is the syndrome for drought-avoidance, characteristic of species with functional traits adapted for rapid acquisition of resources and growth when water is available. Its efficiency is limited for very short periods of time (Mendez-Toribio et al. 2017). At the other extreme, the drought-tolerance syndrome is made up of species with resource-conserving traits, to cope with the low availability of resources in unfavorable periods (Méndez-Alonzo et al. 2012; Pineda-Garcia et al. 2013, 2015). Under this premise, the high values of traits such as X_{wc} and B_{wc} , are associated with syndrome for drought-avoidance, whereas high values of B_t confers desiccation tolerance. H_{max} on the other hand, is associated with competitive ability in water-limited environments (Muscarella et al. 2016) and it can be constrained by water or nutrient availability (Westoby et al. 2002). In this study, both juvenile and adult stages showed high CWM values of X_{wc} , B_{wc} , H_{max} and B_t attributes in north-facing sites; although not all showed a significant difference (Table S3, Fig. 1), which suggests that in these sites the species tend to traits for drought avoidance (e.g. *Bursera grandifolia*, *Sebastiania pavoniana* and *Handroanthus impetiginosa*); while those from south-facing sites have traits for drought tolerance (e.g. *Croton fantzianus*, *Brongniartia alamosana* and *Acacia cochliacantha*). We also found that species from the south-facing slope have also been reported as representative of early stages of secondary succession in the Alamos region. Similarly, these representative species in north-facing slope sites are also representative in advanced stages of succession (Quisehuatl-Medina et al. 2020). This premise is important considering that early successional stages are the most challenging for the establishment of less drought tolerant species, while advanced successional stages host species adapted to conditions of higher humidity and less insolation (Buzzard et al. 2016). We believe that south-facing conditions are similar to early successional stages, while those from north-facing slope sites are more similar to advanced successional stages.

Interestingly, our results differ from those of Méndez-Toribio et al. (2017) in a TDF from lower latitudes (Central Mexico), which reports that drought avoidance trait syndromes are characteristic of tree species in sites where the time period of high water availability and the period of growth is relatively short (upper parts of slopes), especially those south-facing. On the contrary, we believe that the marked seasonality of our study site (8 months drought), coupled with the disproportionate topographic effect on the levels of insolation and humidity on each slope has led to the specialization of species for topographic habitats, reflected in their traits to cope with drought.

Topographic habitat differentiation

Ashton (1988) has conducted studies aimed at showing that selection can act on different character traits at different taxonomic levels; suggesting that the habitat association may occur on higher taxonomic levels (family, genus). If this is true, we would expect to find taxa at low levels tending to share the same topographic habitat association. However, we found that the proportion of taxa exhibiting significant habitat association decreased considerably from the species to family level. Only a third of families and genera have taxa at lower levels with the same habitat association (e.g. Boraginaceae, Erythroxylaceae; Fig. S4); while most taxa showed tendencies to specialization at low taxonomic levels, e.g. Cactaceae, whose genera were similarly associated with the family habitat, but with at least one species not associated. Other families (juveniles, e.g. Euphorbiaceae) showed similar habitat association as their genera, but with non-associated species. Therefore, our data does not support the idea that habitat specialization occurs primarily at genus and family level.

Specifically for this analysis, it is important to take into account two aspects that can influence the observed habitat specialization trends: (i) families that include more than one species (most of the families evaluated have a single genus and species), generated a bias when concluding that TDF taxa are specialized at a higher hierarchical level than at the species level; and (ii) unregistered species, since we only included those species with an abundance > 5 individuals, excluding rare species whose distribution may be restricted to a given habitat. In both cases, analysis of patterns in all species may reveal different trends at different taxonomic levels.

Mechanisms behind differentiation of communities

A limiting factor for TDF's species to be widely distributed and abundant at a site is dispersal limitation. As mentioned above, the possibility that habitat preference patterns are driven by the dispersal limitation may be low considering that most of species are largely dispersed by the wind (Gentry 1982; Bullock 1995; Greene et al. 2008). However, it is important to consider some aspects that can restrict dispersal (even due to wind) and that could help us explain the patterns observed in this study. One of them is the rugged topography of the TDF, which exhibits continuous geographic barriers for any dispersal agent (Williams et al. 2010). Another important aspect to consider the close relationship between the marked seasonality of our study site (8 months of drought) and the coordinated evolution of the species phenology, their flowering and dispersal (Usinowicz et al. 2012; Lopezaraiza-Mikel et al. 2014; Cortés-Flores et al. 2016; Lasky et al. 2016). In TDF a large proportion of species are dispersed during the dry season (Frankie et al. 1974; Bullock 1995), whereby we can intuit that other animal dispersers are usually absent or latent during this period. Linked to the latter, an aspect that has been widely studied in tropical forests and that can determine the directionality of the assembly of communities in our study is the trophic interaction plant-herbivore or plant-pathogen, which is often considered a higher impact mechanism than competition (Carson & Root 2000; Gilbert 2002; Cavender-Bares et al. 2009). The presence of a natural enemy and the degree of specialization of the interaction (attack on a plant species and its congeners) can further promote functional and phylogenetic divergence between habitats and

maintain species specialization on each slope. This might be occurring mainly in the early development stages (seeds-seedlings), where species are more vulnerable to contrasts in water availability and physical damage and attack by herbivores and pathogens (Janzen 1970; Connell 1971; Fine et al. 2004; Paine et al. 2011). In a phylogenetic context, an analysis of the relationship of natural enemies with abiotic gradients and/or their demographic dynamics through seasonal gradients could help to better understand the patterns of topographic habitat specialization observed in our study. In theory, the selective pressure of natural enemies on plants will drive the divergence of functional traits and their strategies in each topographic habitat (Cavender-Bares et al. 2009), promoting the patterns of habitat specialization observed in TDF's communities.

We are far from reaching robust conclusions given the limited spatial scale of our study (Garzon-Lopez et al. 2014), and possibly we do not take into account other assembly mechanisms that are operating simultaneously on a regional scale (e.g. limited dispersal or density-dependence). Therefore, we highlight the importance of conducting similar studies in other forests spanning the large geographical range of Mexican TDF.

Our results reveal strong habitat associations of species with the physiographic characteristics of the Alamos seasonally dry forest. Specifically, we found that slope compass orientation is a physiographic factor more important than topographic position in driving the habitat-association patterns of TDF's species on two life stages evaluated. We believe these patterns are the result of habitat filtering of different trait syndromes on south- and north-facing slopes, with a drought-tolerance syndrome of traits on south-facing slopes, and a drought-avoidance syndrome of traits on north-facing slopes. The contrasting periods of water availability in the soil and the high levels of solar radiation on each slope have revealed emerging patterns of topographic habitat specialization.

Our study contributes to the growing body of evidence that suggests that many tropical tree species are non-randomly distributed with respect to habitat variables at a local scale (Clark et al. 1998; Webb and Peart 2000; Harms et al. 2001; John et al. 2007; Comita and Engelbrecht 2009; Balvanera et al. 2011; Condit et al. 2013). Furthermore, due to the few studies on the habitat association of species carried out in tropical dry forests in Mexico, our findings mark a milestone in the understanding of the mechanisms that determine the distribution of species and the assembly of communities of these ecosystems. On the other hand, our study also demonstrates the importance of considering different facets of diversity from a local scale, mainly in TDFs, whose environmental heterogeneity is reflected in small spatial gradients. Finally, we emphasize the need to incorporate multiple life stages when evaluating the habitat association patterns of woody species, especially in environments with high seasonal variability.

Declarations

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Compliance with ethical standards

Conflict of interest

The authors declare no conflict of interest

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Figures

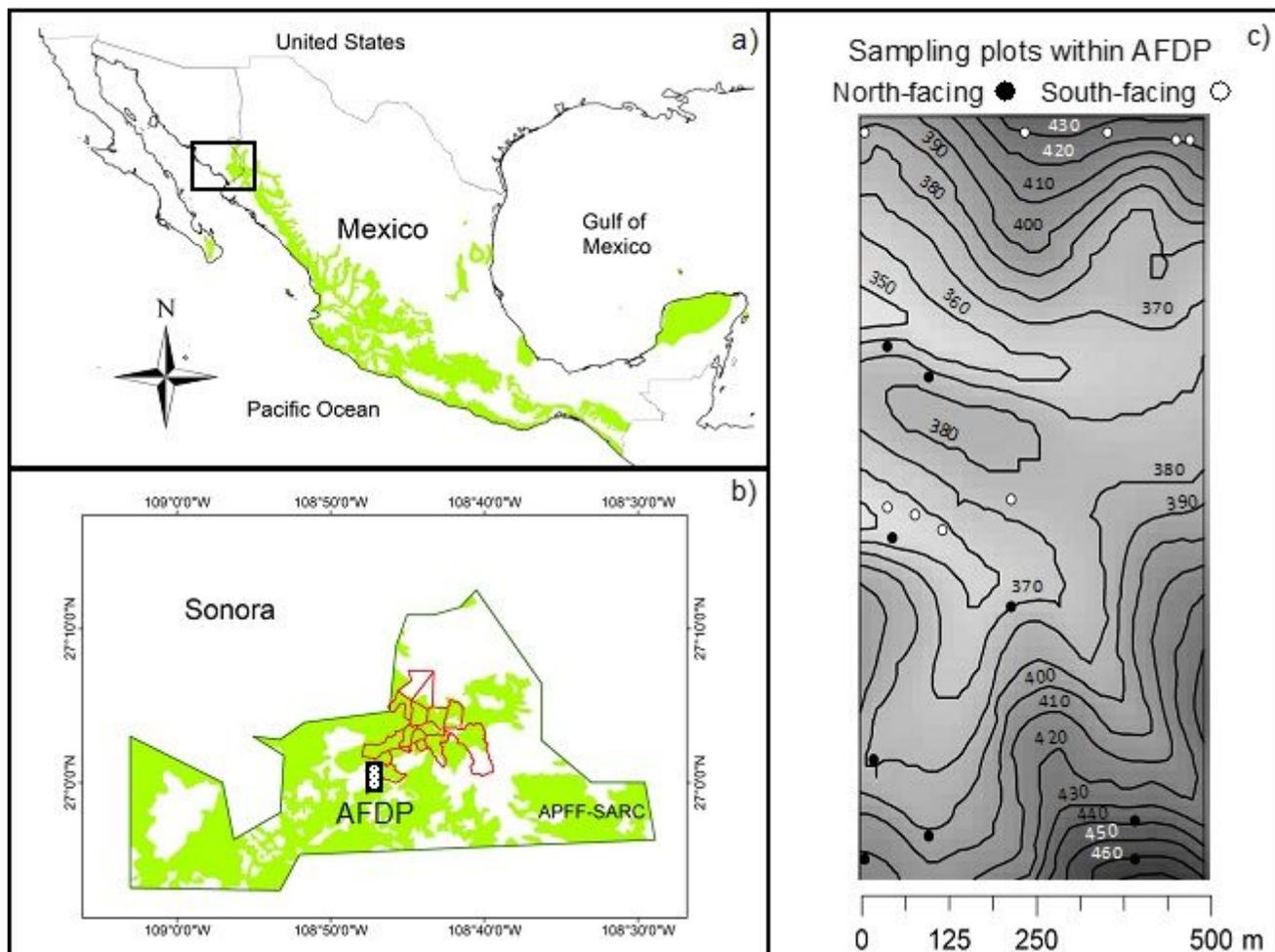


Figure 1

The AFDP is located at the northernmost distribution of the seasonally tropical dry forest in the Americas (a). The AFDP is found within the Reserva Ecológica Monte Mojino (red polygon) deep in the heart of the Area for Protection of Flora and Fauna Sierra de Álamos in Sonora, Mexico (b). The AFDP is a 500 x 1000 m and subplots were scattered through the 50 ha plot (c).

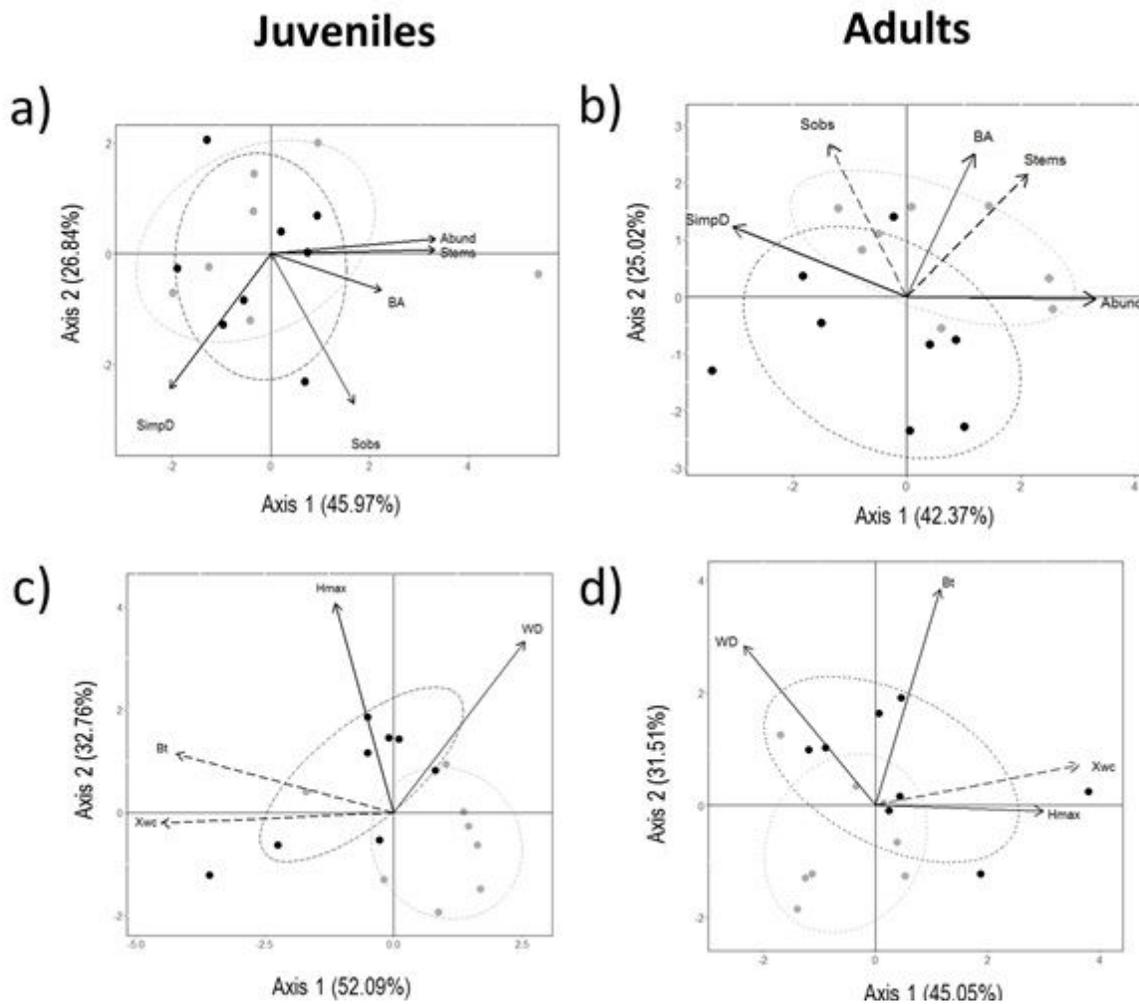


Figure 2

PCA of the structural and functional attributes evaluated between two slope orientations (SO). Plots of ordination with SO based on structural attributes of a) juveniles and b) adults. The ordination based on functional attributes for c) juveniles and d) adults. The structural attributes: BA (basal area); Abund (density of individuals); Sobs (density of species); Dfish (Fisher's α). The functional attributes: WD (wood density); Bwc (bark water content); Xwc (xylem water content); Bt (Bark thickness); Hmax (maximum height). Ellipses represent 75% confidence level and in each graph the black circles correspond to north-facing sites, while gray circles correspond to south-facing sites.

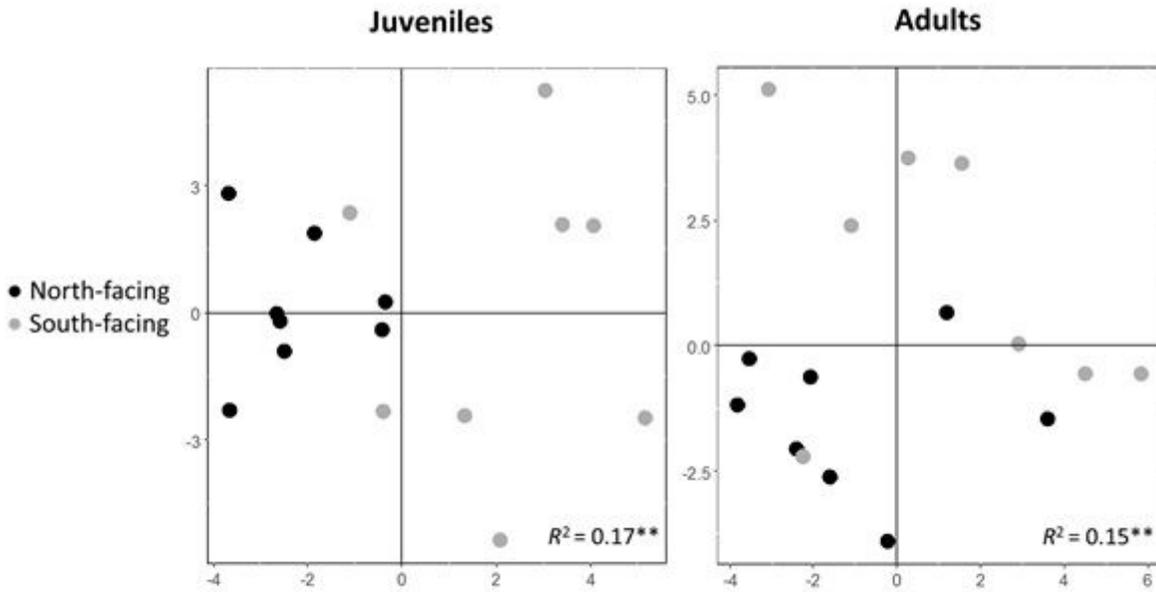


Figure 3

PCA of species abundance of juvenile and adult stages present in 16 sites of 20 x 40m in a TDF to northwest of Mexico with different slope orientation (north-facing and south-facing). Log10 (N + 1) was used for species abundance (see methods).

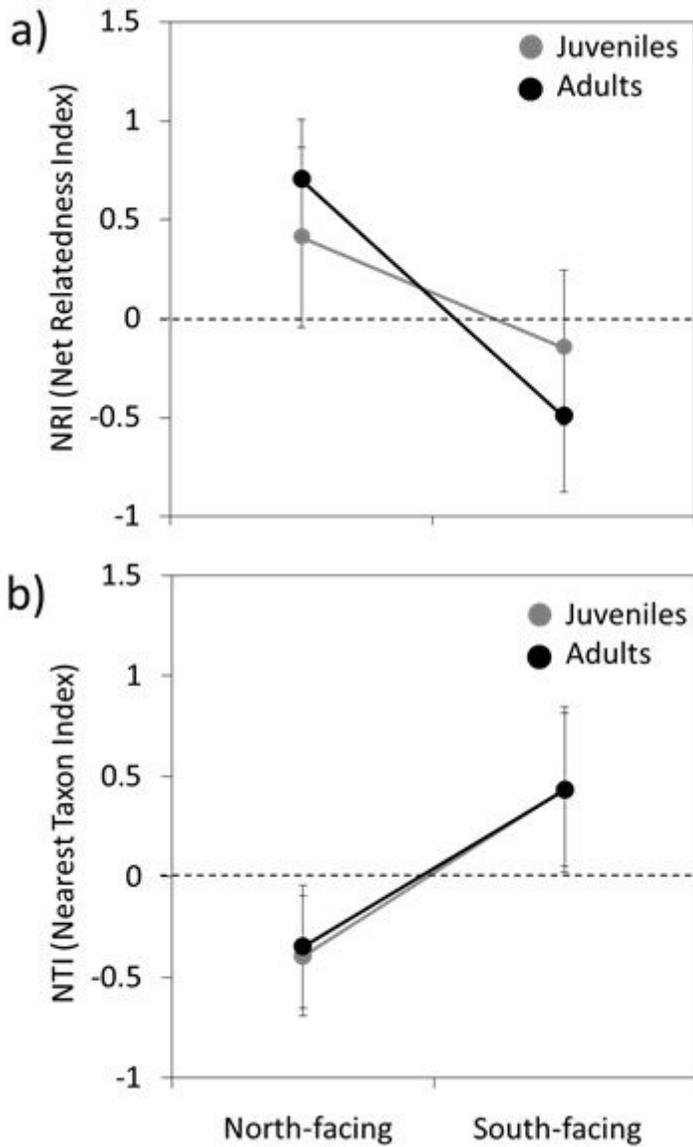


Figure 4

Patterns of NRI (Net Relatedness Index) and NTI (Nearest Taxon Index) patterns of juvenile and adult stages between north-facing (North) and south facing (South) sites. NRI or NTI values < 0 represents phylogenetic overdispersion, while > 0 indicates phylogenetic clustering.

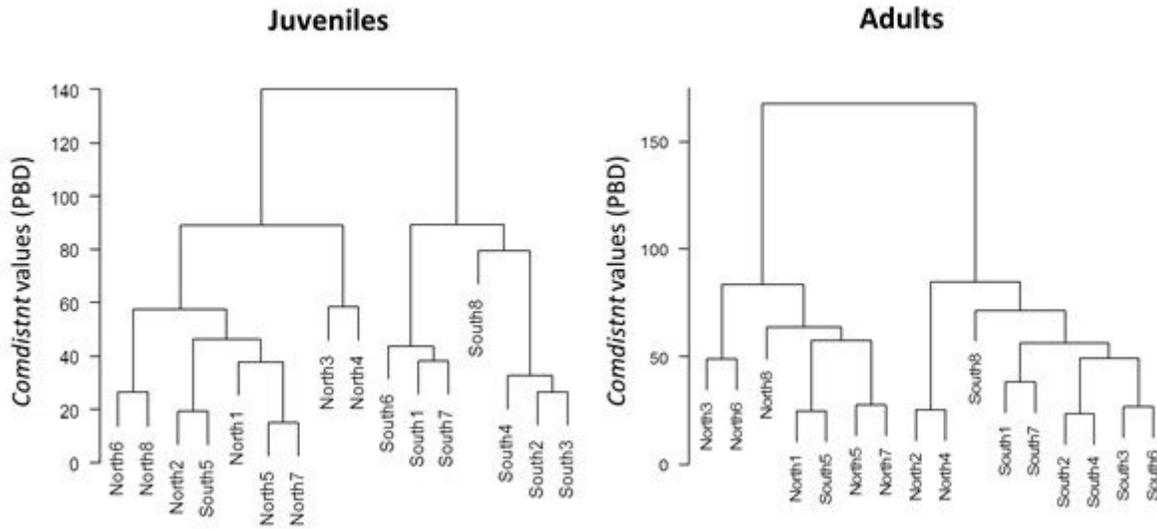


Figure 5

Phylogenetic beta diversity (PBD). Dendrogram of dissimilarity of juvenile and adults tree stages using Comdistnt algorithm. Values close to zero indicates sub-communities more closely related.

Supplementary Files

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