



**UNIVERSIDAD MICHOACANA DE SAN
NICOLÁS DE HIDALGO**



Instituto de Investigaciones sobre los Recursos Naturales

**Patrones de asociación y coexistencia de
especies leñosas en distintos estadios de
vida en una selva seca del noroeste de
México**

TESIS

Como requisito parcial para obtener el grado de

**MAESTRO EN CIENCIAS EN ECOLOGÍA
INTEGRATIVA**

P R E S E N T A

Abdieel Quisehuatl Medina

**Director de tesis: Dr. Leonel A. López Toledo
Co-Directora: Dra. Clementina González Zaragoza**

Morelia, Michoacán, Marzo 2019

AGRADECIMIENTOS

Al Instituto de Investigaciones sobre los Recursos Naturales (INIRENA) de la UMSNH, por la formación y flexibilidad académica, clave para la realización de este trabajo.

Al CONACyT, por el apoyo económico brindado a través de estos dos años de formación, y por brindarme el apoyo complementario para realizar una estancia de investigación en un país extranjero.

A la universidad de Alaska-Fairbanks. A Steffi Ickert-Bond por el cálido recibimiento al Herbario del Museo del Norte en Alaska.

A Cam Webb, por hacer que mi estancia fuera provechosa en todos los sentidos. Por los valiosos consejos, por despertar aún más mi interés por la generación de conocimiento científico y hacer investigación desde una perspectiva más amplia. Por tu valiosa amistad, gracias.

A Holly y Azal, por abrirme las puertas de su hogar y apoyarme en lo necesario para que mi estancia sea cómoda y placentera, siempre los llevaré en mi memoria.

Al comité evaluador, mi co-asesora la Dra. Clementina González, el Dr. Moisés Méndez, la Dra. Denisse Spaan y el Dr. Jorge Alejandro Ávila, por sus importantes observaciones.

A mi asesor y amigo, el Dr. Leonel López-Toledo. Gracias Leo por la oportunidad y la confianza brindada durante todo el tiempo que nos conocemos, por el tiempo que has dedicado para mi formación. Por tus consejos, por la libertad que me has brindado y el apoyo en las decisiones que he tomado durante este proyecto y en mi vida personal. Por alentarme a brincar nuevas fronteras, por todo eso, ¡¡¡muchas gracias amigo!!!

Gracias al equipo de campo en Alamos Sonora, al Cholo, Gaby, Carlitos, Crucita, Luis, Susana y Johnny por su apoyo en el censo de la vegetación.

A mi familia, por su incondicional apoyo en las decisiones importantes de mi vida y motivarme a ser mejor cada día.

A mis amigos, a Sofía por tan bonita amistad; a Malia por apoyarme con el idioma durante mi estancia en Alaska; a Ariana, por abrirme un espacio en tu hogar y compartir bonitos momentos siendo my roommate.

A mi amigo Arturo por las experiencias académicas y de vida, después de tantos años sigues estando ahí amigo mío, gracias.

A mi Angy, porque a pesar de todas las altas y las bajas de nuestras vidas, te has sabido mantener conmigo y para mí, tú tienes mi cariño y mi respeto. A donde quiera que fueses siempre tendrás un lugar en mi corazón, por todo lo que has dado para verme feliz, gracias amor.

A todas las personas que durante este corto trayecto formaron parte de mi vida.

A CADA UNO DE USTEDES, ¡MUCHAS GRACIAS!

ÍNDICE

RESUMEN	1
ABSTRACT	2
CAPITULO I	
INTRODUCCIÓN GENERAL	3
Ensamble por nicho ecológico.....	4
Ensamble por dispersión (Teoría Neutral).....	6
Ensamble de las comunidades de bosques tropicales.....	7
JUSTIFICACIÓN	11
OBJETIVOS	12
 CAPITULO II <i>Topographic factors drive taxonomic, functional and phylogenetic patterns of trees in a tropical dry forest of Northwestern Mexico.</i>	
ABSTRACT	14
INTRODUCTION	15
METHODS	17
Study site.....	17
Data collection.....	18
Phylogenetic construction.....	19
Null models and Phylobetadiversity.....	21
Statistical analysis.....	21
Habitat association of species.....	23
Phylogenetic structure.....	23
RESULTS	24
Community structure.....	24
Functional traits of the community (CWM).....	26
Patterns of habitat association.....	26
Phylogenetic diversity.....	27
DISCUSSION	28
CONCLUSION	33
LITERATURE CITED	34
SUPPORTING INFORMATION	46

LISTA DE TABLAS Y FIGURAS

CAPITULO I

Figura 1. Modelo de ensamble por nicho	5
Figura 2. Mecanismos de ensamble por dispersión.....	7

CAPITULO II

Table 1. Habitat association of species trees juvenile and adult	40
Figure 1. Mean values of structural attributes.....	41
Figure 2. PCA based on structural and functional attributes.....	42
Figure 3. PCA of species abundance between life stages	43
Figure 4. Phylogenetic diversity between life stages	44
Figure 5. Phylobetadiversity	45

RESUMEN

El origen y mantenimiento de la diversidad de especies es uno de los tópicos más importantes en ecología. Actualmente, existen dos principales posturas las cuales explican el mantenimiento y/o la distribución de la diversidad de especies. La teoría de *nicho ecológico*, destaca el papel del ambiente (condiciones abióticas y bióticas) para dirigir el ensamblaje de una comunidad local. A través de esta tesis se hace referencia a este concepto como *filtrado ambiental*, el cual es definido como un proceso en el cual las características físicas o químicas, así como las interacciones interespecíficas limitan el establecimiento y la prevalencia de especies en un hábitat dado. Por otro lado, el ensamble por dispersión, destaca los procesos de dispersión, extinción local y eventos históricos como la especiación como los responsables del mantenimiento de la diversidad de especies y los patrones de coexistencia de especies en un hábitat dado.

En el **capítulo II** se intenta conocer el efecto de dos factores fisiográficos sobre la estructura taxonómica, funcional y filogenética de la comunidad de especies leñosas en distintos estados de vida, en una selva seca al sur de Sonora. En esta tesis, además de caracterizar los patrones de estructuración taxonómica de la vegetación y los patrones de asociación de preferencial de hábitat de las especies leñosas, se utiliza un enfoque funcional, caracterizando estrategias funcionales de las plantas a través de una media ponderada de la comunidad de rasgos funcionales de la madera. De igual manera, se hace uso de filogenias e índices de diversidad filogenética, para inferir los mecanismos que dirigen el ensamblaje de comunidades de vegetación leñosa en una selva seca al sur de Sonora.

Las características fisiográficas de Orientación de pendiente (OP) y Posición topográfica (PT), asociadas a condiciones micro-ambientales, son factores inherentes al filtrado ambiental, determinantes en la organización comunidades y co-ocurrencia de especies leñosas. El efecto de estos factores fisiográficos sobre la estructuración taxonómica, funcional y filogenética no ha sido abordado desde un enfoque multifacético en México. El estudio fue conducido al interior de un Plot 50 ha en Alamos, Sonora. Se caracterizó la estructura taxonómica, funcional y filogenética y los patrones de asociación de hábitat de especies leñosas en distintos estados de vida (Juveniles y Adultos) en un bosque tropical seco al noroeste de Mexico. Dicha caracterización se llevó acabo en 16 sub-parcelas de 20 x 40 m c/u. localizados en dos aspectos de SO (norte y sur) y PT (alto y bajo). Se describieron siete atributos estructurales, cuatro funcionales y dos representativos índices de diversidad filogenética. Los principales resultados son destacados por el efecto primordial de la OP en cada estado de vida. Dicho factor fisiográfico mostro tener un efecto relativamente distinto entre estados de vida, teniendo un efecto superior respecto a la PT en la estructura taxonómica, funcional y filogenética de la comunidad de estudio.

Palabras clave: *Asociación de hábitat; diferenciación de nicho; estados de vida; factores fisiográficos; filtrado ambiental, diversidad filogenética.*

ABSTRACT

The origin and maintenance of species diversity is one of the most important topics in ecology. Currently, there are two main positions that explain the maintenance and distribution of species diversity. The ecological niche theory highlights the role of the environment (abiotic conditions and biotics) to direct the assembly of a local community. Through this thesis, this concept is referred to as *environmental filtering*, which is defined as a process in which physical or chemical characteristics, as well as interspecific interactions, limit the establishment and prevalence of species in a given habitat. On the other hand, the assembly by dispersion highlights the processes of dispersion, local extinction and historical events such as speciation as responsible for the maintenance of the diversity of species and the patterns of coexistence of species in a given habitat.

In **chapter II** we try to know the effect of two physiographic factors on the taxonomic, functional and phylogenetic structure of the community of woody species in different life stages, in a tropical dry forest (TDF) from south of Sonora. In this thesis, besides characterizing the taxonomic structuring patterns of the vegetation and the preferential habitat association patterns of the woody species, a functional approach is used, characterizing the functional strategies of the plants through a community weighted mean of functional traits of wood. Similarly, phylogenies and indexes of phylogenetic diversity are used to infer the mechanisms that direct the assembly of woody species communities in a TDF of Sonora.

The physiographic characteristics of slope orientation (SO) and topographic position (TP), associated with micro-environmental conditions, are inherent factors in environmental filtering, determining factors in the organization of communities and co-occurrence of woody species. The effect of these physiographic factors on the taxonomic, functional and phylogenetic structuring has not been approached from a multifaceted approach in Mexico.

The study was conducted inside a Plot 50 ha in Alamos, Sonora. The taxonomic, functional and phylogenetic structure and habitat association patterns of woody species in different life stages (Juveniles and Adults) in a TDF of northwest Mexico were characterized. This characterization was carried out in 16 subplots of 20 x 40 m each, located in two aspects of SO (north and south) and TP (high and low). Seven structural attributes were described, four functional traits and two representative indices of phylogenetic diversity. The main results are highlighted by the mainly effect of the SO in each life stage. This physiographic factor showed to have a relatively different effect between life stages, having an effect superior to the TP in the taxonomic, functional and phylogenetic structure of the communities of study.

Key words: *Habitat association; niche differentiation; life stages; physiographic factors; environmental filtering; phylogenetic diversity.*

CAPÍTULO I

INTRODUCCIÓN GENERAL

La diversidad biológica es un concepto representativo de la variabilidad de la vida en todos sus niveles de organización, con escalas que trascienden desde el nivel genético, hacia la complejidad de las especies (sus formas de vida y roles funcionales), hasta la constitución de paisajes estructuralmente diferenciados (Colwell 2012). Durante décadas, dentro de la ecología de comunidades no ha habido quizás mayor desafío como el de explicar los patrones de origen, mantenimiento y pérdida de la diversidad (Hubbell 2001), principalmente en los bosques tropicales (Losos and Leigh 2004), convirtiéndolo en uno de los tópicos más importantes de investigación. Al día de hoy, estas preguntas siguen siendo un tema central en ecología (Chesson 2000; Yuan 2014).

El constante interés predictivo de la distribución de la diversidad de especies a través de escalas, actualmente ha dado lugar al surgimiento de múltiples modelos, teorías e hipótesis que intentan explicar los patrones de dicha diversidad, en su mayoría siendo variantes u análogas una de otra. Algunos modelos describen el ensamble de las comunidades como resultado de procesos relacionados a las características ambientales y las interacciones intra e interespecíficas y/o multitróficas (Teorías de Nicho, MacArthur and Levins 1967; Fig. 1); mientras que otros destacan eventos estocásticos de dispersión, colonización y extinción local y procesos históricos de especiación regional para explicar la coexistencia espacio-temporal de las especies (Teoría Neutral, Hubbell 2001; Fig. 2). En ambos enfoques, aunque son contrastantes, podrían operar simultáneamente los mecanismos de ensamble que rigen la estructuración de las comunidades ecológicas (Chave 2004; Gravel et al. 2006; Hérault 2007). A continuación se describen ambas posturas.

ENSAMBLE POR NICHOS ECOLÓGICOS

La teoría de nicho ha resultado ser un enfoque fundamental para explicar los patrones de diversidad en muchas de las comunidades naturales (Chesson 2000; Wright 2002; Tan et al. 2013). La evolución conceptual del nicho desde su idealización hace poco más de un siglo hasta la actualidad ha sido muy evidente (Chase & Leibold 2003), sin embargo en la literatura ecológica se destaca un aspecto fundamental, que es la diferenciación ecológica entre las especies (Chesson 2000). Para fines prácticos, los ecólogos históricos y contemporáneos resaltan la necesidad de que, para que ocurra una coexistencia estable por nicho ecológico, es necesario que exista una respuesta diferencial de las especies a las condiciones bióticas y abióticas del ambiente (MacArthur & Levins 1967). En esta tesis se hace referencia a un ensamble por nicho ecológico cuando la composición de especies que constituyen una comunidad es el resultado de la acción de filtros ambientales tanto bióticos como abióticos. Bajo este marco conceptual, son las interacciones competitivas intra e interespecíficas, así como las restricciones ambientales las que juegan el papel central en el ensamblaje de las comunidades (Morin 2011).

Un substancial número de investigaciones se han sido llevados a cabo con el objetivo de explicar los mecanismos que mantienen la diversidad de especies de vegetación tropical, sin embargo, la mayoría suelen ser variantes u análogas una de otra (para una revisión véase Chesson 2000; Wright 2002). Chesson (2000) mostró una robusta revisión teórica de los mecanismos de coexistencia de especies, resaltando aquellos que respaldan la coexistencia por nicho ecológico. En dicha revisión, Chesson contrasta y analiza modelos básicos como el de Lotka-Volterra, que destacan la dinámica de competencia interespecífica, hasta el modelo Lotería del cual se derivan dos mecanismos de coexistencia: i) el efecto de captura y ii) la no-linealidad relativa (Chesson 1981; Yuan 2014). Un supuesto de estos modelos es la dinámica

en la disposición de recursos en una comunidad, la cual de acuerdo al principio de exclusión competitiva, puede ser un factor que limite la similitud entre las especies que coexisten en ella (Hardin 1960; MacArthur & Levins 1967; Abrams 1983; Tilman 1985).

Por un lado, mientras la variabilidad ambiental, al ser regular y/o determinística (ej. estacionalidad en un bosque decido), genera patrones de agregación de especies ecológicamente similares (MacArthur & Levins 1967; Webb 2002; Comita et al. 2009; Kraft & Ackerly 2014). Por otro lado, los mecanismos de exclusión competitiva propuestos originalmente desde 1859 por Darwin, tienden a generar patrones no aleatorios de segregación entre individuos conespecíficos, influyendo en el ensamblaje local de las comunidades y estructurando su diversidad a nivel regional (Hardin 1960; Wright 2002; Cavender-Bares et al. 2009). Es importante destacar que, a pesar de existir otros mecanismos (ej. facilitación), que pueden generar patrones de uniformidad o sobredispersión de conespecíficos (*sensu* Webb 2002), estos siguen siendo diferentes de lo esperado por azar, lo cual podría esperarse cuando una comunidad está organizada bajo la acción de mecanismos estocásticos (p.e. eventos de especiación). Bajo esta premisa, dichos patrones de uniformidad o sobredispersión siguen siendo el resultado de procesos determinísticos inherentes al ensamblaje por nicho ecológico (Webb 2002).

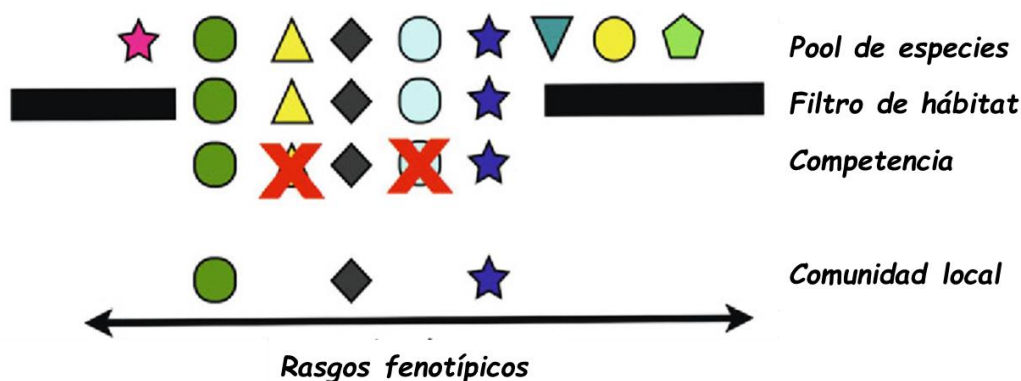


Figura 1. Modelo conceptual básico del ensamblaje por nicho ecológico. Las diferentes formas geométricas representan los rasgos fenotípicos de las especies. Del pool de especies de una metacomunidad, el filtro de hábitat restringe el rango de la variación fenotípica, permeando solo

aquellos suficientemente capaces para sobrevivir y establecerse en un sitio. En este punto la proporción de rasgos fenotípicos del pool de especies ha cambiado. Posteriormente, la competencia favorece la coexistencia de especies que difieren en el uso y requerimiento de recursos, lo cual es un reflejo de los rasgos fenotípicos, resultando en la estructuración de una comunidad local. Modificado de Kraft & Ackerly (2014).

ENSAMBLE POR DISPERSIÓN (TEORÍA NEUTRAL)

La Teoría Neutral Unificada de la Biogeografía y la Biodiversidad (Hubbell 2001), también llamada teoría de ensamble por dispersión fue desarrollada por Hubbell (1979, 1997, 2001) en conexión con sus estudios a gran escala en la Isla de Barro Colorado (BCI), Panamá. Tras su publicación, esta teoría causó una gran controversia al presentar una drástica simplificación de procesos ecológicos y una relativamente compleja abstracción matemática de los mismos (Rosindell et al. 2011). Aquí, el papel de la competitividad tiene una participación casi nula, y son los mecanismos biogeográficos y evolutivos los que tienen el papel central en la estructuración de las comunidades a través de escalas espacio-temporales (MacArthur and Wilson 1967; Hubbell 2001). El supuesto fundamental de Hubbell es que los individuos de todas las especies en una comunidad son competitivamente equivalentes (*neutralidad*) desde una perspectiva de reproducción, muerte, dispersión y especiación. Esta invariabilidad infraespecífica ocurre a una escala local y de metacomunidad. Procesos como la extinción a nivel local y de especiación a nivel de la metacomunidad tienden a presentar un equilibrio (dinámica suma-cero) para el ensamblaje de las comunidades (Fig. 1). El cumplimiento de este supuesto depende de la capacidad de los organismos para colonizar nuevos hábitats, por lo que aquí, el ensamble de las comunidades es el resultado de eventos estocásticos de muerte y reclutamiento de individuos (Hubbell 1997, 2001).

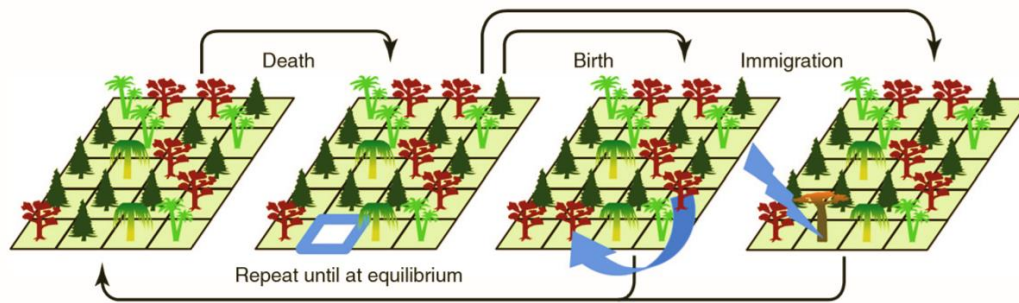


Figura 2. Mecanismos del ensamble por dispersión, Teoría Neutral (*sensu* Hubbell 2001). La teoría exhibe dos principales supuestos: i) La comunidad local es finita y ii) la equivalencia de los individuos de todas las especies en la comunidad local. El cumplimiento de estos supuestos da como resultado una dinámica suma cero. La muerte de un individuo es una oportunidad de colonización para los individuos del pool local de especies, la identidad de dicho individuo representa una función probabilística del número de especies y sus abundancias relativas en la comunidad local. La pérdida de la diversidad local es compensada por la tasa de inmigración desde la metacomunidad. Mientras que la diversidad de especies en la metacomunidad se mantiene a través de eventos esporádicos de especiación. Modificado de Rosindell et al. (2011).

Ambos enfoques (neutral y de nicho), a pesar de ser comúnmente evaluados como hipótesis alternativas (Gaston and Chown 2005), pueden tener un carácter integrativo, pudiendo explicar los patrones de coexistencia de especies; cada una siendo relativamente más importantes en un tiempo y espacio determinado (Chave 2004; Gravel et al. 2006; Letcher et al. 2012; Chai et al. 2016).

ENSAMBLE DE LAS COMUNIDADES DE BOSQUES TROPICALES

La disponibilidad de nuevos métodos para el estudio de la dinámica de la vegetación tropical (p.e parcelas permanentes de 50 ha), permitieron grandes avances en la comprensión y robustez de los hipótesis que han permitido el esclarecimiento de patrones y procesos que determinan la coexistencia de especies en estos ecosistemas (Hubbell 2001; Webb 2000; Losos & Leigh 2004)

Wright (2002) expuso una revisión de las principales hipótesis y los mecanismos que pueden explicar los patrones de diversidad de especies en bosques tropicales. La mayoría de

estas hipótesis son el resultado de estudios de la vegetación a largo plazo. Por otro lado, Losos & Leigh (2004), resumen en *Tropical Forest Diversity and Dynamism* los más recientes avances de estudios de la vegetación tropical a nivel global en estas parcelas de 50 ha. tras dos décadas de monitoreo continuo. Sin embargo, actualmente aún existe una gran discrepancia respecto al número de estudios realizados en los sistemas tropicales secos, siendo escasos en estos últimos, lo que refleja un gran sesgo en la comprensión de la estructuración de las comunidades de bosques tropicales. En México, esta no es la excepción; un hecho importante a considerar es que mucho del conocimiento generado de las selvas secas en México se ha restringido a unas cuantas localidades o regiones relativamente bien conocidas, como es el caso de la Estación de Biología de Chamela, Jalisco (Sánchez-Azofeifa et al. 2014). Esto resulta en un conocimiento fragmentado de la vegetación que caracteriza a estos ecosistemas a lo largo de su distribución en México.

Basado en los análisis de las tasas de deforestación, cambio climático, grado de fragmentación, densidad de población humana y el precario estado de conservación, las selvas secas desde principios de los 90s y hasta la actualidad, han sido consideradas mundialmente como el ecosistema tropical más amenazado, incluso por encima de los bosques tropicales húmedos (Janzen 1988; Miles et al. 2006; Linares-Palomino et al. 2011). Esta premisa se extiende también a México, donde a pesar de ser el ecosistema tropical mejor representado, es también uno de los más amenazados (Ceballos et al. 2010), la mayor cobertura de estos ecosistemas se encuentra en la vertiente del pacífico desde la depresión central de Chiapas hasta el estado de Sonora. Es en la región de Alamos, Sonora, donde este ecosistema, alcanza la distribución más norteña en el continente Americano (Martínez-Yrizar et al. 2000). Esto le confiere una gran importancia biológica ya que cuenta con una mezcla de elementos florísticos de origen Neártico y Neotropical y escalas de transición altitudinal entre asociaciones vegetales como el matorral espinoso en las zonas bajas y el bosque de *Pinus-*

Quercus en las zonas altas (Van Devender et al. 2000). La accidentada topografía (cañones y barrancas) de la Sierra de Álamos provee cambios graduales de las condiciones abióticas y por consiguiente, una multitud de hábitats para las especies de la selva seca (Martin and Yetman 2000). La variabilidad topográfica, dada por distintos aspectos de orientación de pendiente puede jugar un papel determinante en la distribución de especies leñosas, cuyo éxito estaría asociado a las condiciones ambientales que imperan en cada ladera (Gallardo-Cruz *et al.* 2009; Méndez-Toribio et al. 2017). Este mismo principio se aplica a la posición topográfica, en donde, tanto las zonas bajas y altas de ladera, están asociadas a condiciones ambientales particularmente distintas y por consiguiente, estas pueden albergar comunidades estructuralmente diferentes. Estas características fisiográficas, aunado a los niveles de precipitación y características del suelo han sido reportadas como los principales factores que afectan la variabilidad y disponibilidad de agua estos ecosistemas estacionalmente secos (Engelbrecht *et al.* 2007; Comita et al. 2009). Dicho efecto podría ser mayor hacia latitudes medias o altas en el hemisferio norte, dado que las pendientes orientadas al Sur reciben mayor Incidencia de Radiación Solar (IRS) que las pendientes orientadas al Norte (Galicía *et al.* 1999); como resultado del efecto combinado de la topografía y el gradiente latitudinal, podría esperarse que la diferenciación ambiental sea fuertemente marcada en apenas escalas espaciales pequeñas. Las selvas secas de México brindan una importante oportunidad para estudiar el papel de los filtros ambientales y ayudar a entender los procesos evolutivos de adaptación y coexistencia de especies leñosas de selva seca en una escala relativamente pequeña (Balvanera et al. 2011; Méndez-Alonzo et al. 2012; Méndez-Toribio et al. 2017).

Aunado a esto, recientemente han surgido grandes esfuerzos por integrar técnicas de la biología evolutiva y la ecología de comunidades mediante el uso de filogenias en ecología, con el fin de esclarecer los patrones de coexistencia de especies a múltiples escalas espacio-temporales (Webb et al. 2002; Qian and Jiang 2014). La integración de información

ecológica y filogenética puede permitir identificar las relaciones de las especies presentes en una comunidad local, y permitiendo la inferencia de mecanismos subyacentes de coexistencia de especies (ej. competencia) cercanamente relacionadas. En el año 2000, Webb desarrolló elegantemente dos índices de diversidad filogenética relativamente simples que permiten cuantificar las relaciones conespecíficas en escalas inter e intracomunidad, ofreciendo una mejor comprensión de los aspectos ecológicos, evolutivos y biogeográficos de ensamble en las comunidades (Webb 2000; Kraft et al. 2007; Cavender-Bares et al. 2009). Posteriormente, fue desarrollado un amplio marco lógico que utiliza la estructura filogenética de una comunidad para descubrir los procesos deterministas o reglas de ensamblaje que dirigen el ensamble mismo de las comunidades (Webb et al. 2002; Cavender-Bares et al. 2009). Según Webb et al. (2002) bajo este marco, son dos las fuerzas selectivas que pueden generar patrones no-aleatorios, sean estos de agrupamiento o sobredispersión filogenética en una comunidad (Fig. 2). Estas son: i) el filtro ambiental, también llamado filtros de hábitat o filtro abiótico, y ii) la competencia interespecífica (exclusión competitiva). Estos filtros son selectivos en la medida que una especie persista en la comunidad, con base en su tolerancia a las condiciones ambientales y como ésta responde ante las interacciones que limitan su coexistencia (competencia). Por lo tanto, una agrupación filogenética (especies cercanamente emparentadas evolutivamente) en una comunidad, puede ser el resultado de fuerzas como el filtrado ambiental (Kembel & Hubbell 2006). Aunque, desde una visión más compleja de la coexistencia de especies, la competencia también puede derivar en un patrón de ensamblaje similar si se considera: la diferenciación en la habilidad competitiva y de nicho de las especies en una comunidad (Mayfield and Levine 2010). Mientras que por el contrario, cuando las especies son menos relacionadas de lo esperado por el azar (sobredispersión filogenética), Webb et al. (2002) sugiere que es la acción de la competitividad de especies fenotípicamente similares, lo que determinan el ensamble de la comunidad, o bien cuando el filtro ambiental

actúa en taxones distantemente relacionados y cuyos caracteres fenotípicos convergen en un nicho similar. Por otro lado, las interacciones mutualistas y/o de facilitación son igualmente tendientes a generar este patrón de sobre dispersión filogenética (Valiente-Banuet & Verdú 2007; Sargent & Ackerly 2008). Finalmente, es evidente que un patrón filogenético aleatorio, es decir, diferente a los descritos anteriormente, apuntaría a que la estructuración de una comunidad es resultado de la acción de procesos neutrales (Webb 2000).

De este modo, el uso de filogenias y técnicas relacionadas, empleadas en esta tesis, podría proporcionar información relevante sobre papel relativo que juegan los procesos determinísticos (basados en nicho) y estocásticos (neutrales) en el ensamble de las comunidades en los ecosistemas de selva seca en México.

JUSTIFICACIÓN

En este artículo nosotros intentamos conocer el efecto de los factores fisiográficos de orientación de pendiente y posición topográfica sobre la estructuración taxonómica, funcional y filogenética de la comunidad de leñosas y los patrones de asociación de hábitat especies arbóreas en distintos estados de vida (adultos y juveniles), en una selva seca al sur de Sonora. Esto con el fin de inferir los mecanismos que dirigen el la coexistencia especies leñosas de selva seca en los distintos estados de vida (adultos y juveniles). Este trabajo forma parte de un proyecto que conlleva en el establecimiento de una parcela permanente de 50 ha para el estudio de la dinámica de la selva seca del sur de Sonora. La información generada en esta tesis servirá de referente para posteriores estudios de ecología funcional, aplicados a la conservación y/o restauración de estos ecosistemas estacionalmente secos, además de servir como una línea base para futuros estudios relacionados con los cambios en la estructura de la vegetación como resultados de los efectos del cambio climático.

OBJETIVOS

- Evaluar el efecto de la orientación de la pendiente y la posición topográfica sobre la estructuración taxonómica, funcional y filogenética de la comunidad de leñosas en una selva seca al sur de Sonora.

OBJETIVOS PARTICULARES

- Identificar los mecanismos que median estructuración de la comunidad y los patrones de asociación de especies leñosas.
- Evaluar la preferencia de hábitat de las especies leñosas de selva seca en las distintas etapas del desarrollo.

CAPITULO II

LRH: Quisehuatl-Medina *et al.* 2019

RRH: Slope aspect driver the structure of trees of a TDF in northwest Mexico

Topographic factors drive taxonomic, functional and phylogenetic patterns of trees in a tropical dry forest of Northwestern Mexico.

Abdieel Quisehuatl-Medina¹, Campbell O. Webb², Moisés Méndez-Toribio³,
Clementina González-Zaragoza¹, Stephen Hubbell & Leonel Lopez-Toledo^{1,4}

¹ Instituto de Investigaciones sobre los Recursos Naturales, Universidad Michoacana
de San Nicolás de Hidalgo, Morelia, Michoacán 58087, México

² University of Alaska Museum of the North, AK, USA

³ Instituto de Ecología, A.C., Red de Diversidad Biológica del Occidente Mexicano, Avenida
Lázaro Cárdenas 253, 61600 Pátzcuaro, Michoacán, México

⁴ Division of Applied Plant Ecology, Institute for Conservation Research, San Diego
Zoo Global, Escondido, California 92027, U.S.A.

Corresponding author; e-mail: **Lopez-Toledo, L.** (llopezt@umich.mx,
leonellopeztoledo@gmail.com)^{1,3}

ABSTRACT

The physiographic characteristics of slope orientation (SO) and topographic position (TP) and the micro-environmental conditions that have, are factors inherent to environmental filtering. Recent studies have documented the effect of these factors on patterns of community structuring and co-occurrence of species in tropical systems; however, few studies have evaluated the relative role of these physiographic characteristics from a taxonomic, functional and evolutionary approach in trees through different life stages. In this study we evaluated the relative effect of two physiographic factors on the patterns of taxonomic, functional and phylogenetic structuring of the woody community and habitat association patterns of species in different life stages (juveniles and adults) in a tropical dry forest (TDF) in the Northwest of Mexico. The principal components analysis (PCA) based on abundance of tree species showed a segregation of two large groups between aspects of (SO) in each one of the states of life, showing that the habitat association of TDF species begins in early stages of plant life stages (≥ 1 cm) and is maintained towards adult stages. Regarding the association of species, using the Monte Carlo randomization test, we found significant association in $\sim 41\%$ of species in juvenile and $\sim 33\%$ adult stages, with some physiographic habitat of SO. The SO also influenced the taxonomic, functional and phylogenetic structure of different ways in each states of life. Differences in functional traits and association of species, but not between the phylogenetic structure between the different life stages, suggest evidence of a mismatch in adaptive strategies across of life stages (niche differentiation), which could be seen as a mechanism that neutralizes the effect of competition and/or density-dependence among individuals of the same species in a given habitat.

Key words: *Habitat association; niche differentiation; life stages; physiographic factors; phylodiversity.*

INTRODUCTION

ENVIRONMENTAL FILTERING IS A HIGHLIGHTED TOPIC IN COMMUNITY ECOLOGY, and it is seen as a process driving the assembly of tree communities and patterns of species co-occurrence (Kraft *et al.* 2015; Cadotte *et al.* 2018). In tropical ecosystems, studies have demonstrated this process by investigating how species' distributions change across environmental gradients (Harms *et al.* 2001; Balvanera *et al.* 2011; Krishnadas *et al.* 2016; Muscarella *et al.* 2016). The mechanisms underlying environmental filtering have been widely studied in tropical humid ecosystems (Spasojevic & Suding 2012), however in tropical dry forests (TDF) this process have been less addressed. Highly seasonal ecosystems, such as TDFs, harbor a contrasting availability of resources, even at small spatial gradients (Engelbrecht *et al.* 2007; Méndez-Toribio *et al.* 2017). In these ecosystems, water availability is largely mediated by precipitation, topography and soil characteristics, and therefore water availability is considered one of the main factors influencing niche partitioning and spatial organization of TDF communities (Borchert 1994; Segura *et al.* 2003; Hall *et al.* 2004; Balvanera *et al.* 2011). Particularly in Mexico, TDF's are characterized by their marked seasonality and geological history (Martínez-Yrizar *et al.* 2000; Dirzo *et al.* 2011). The rugged topography in which these ecosystems occur (e.g. canyons and steep ravines) host different species compositions and adaptive strategies between slope orientation (SO) and topographic position (TP) (Gallardo-Cruz *et al.* 2009; Méndez-Toribio *et al.* 2017). Additionally, the relative effect of these physiographic factors (SO and TP) on tree species composition and adaptive strategies differ across TDF's in Mexico and other TDF sites of America (Borchert 1994; Gallardo-Cruz *et al.* 2009; Balvanera *et al.* 2011; Méndez-Toribio *et al.* 2017). At the Northern Hemisphere southern slopes are usually characterized as drier, with greater insolation and lower water availability than northern slopes (Galicía *et al.* 1999). The

physiographic differences, have allowed studying the relative importance of a factor, such as SO on a species' development and/or dominance of water use strategies as a function of water availability (Markestijn *et al.* 2011; Méndez-Alonzo *et al.* 2012; Pineda-García *et al.* 2015; Méndez-Toribio *et al.* 2017). For example, strategies of evasion and tolerance described in seasonally dry forests possess the prevalence of unique functional features of leaves and branches (e.g. pubescence, leaf retention time, wood density, xylem water content) that allow them to take advantage of the available water resource in short periods of time (Pineda-García *et al.* 2015).

Environmental filtering can lead to the establishment and prevalence of species in a community (Krishnadas *et al.* 2016) and the physiographic characteristics has been described as inherent factors to this process. Strictly several authors have suggested that this concept should be refer only to the action of abiotic factors (Kraft *et al.* 2015). However, given the complexity of distinguishing the action of an abiotic factor from the biotic interactions, in this study, environmental filtering refers to the action of both abiotic and biotic factors influencing the establishment and prevalence of species in community (Mayfield & Levine 2010).

Currently, the use of phylogenies calibrated in time can facilitate the identification of the relative dominance of processes on community organization (Webb *et al.* 2002; Cavender-Bares *et al.* 2009). Over the last decade, phylogenies have been used to study community assembly and species coexistence through the analysis of evolutionary relationships between species (Webb *et al.* 2002; Kraft *et al.* 2007). In tropical ecosystems phylogenies have provided information on the relative importance of ecological and evolutionary processes and mechanisms that maintain species diversity in these ecosystems (Webb *et al.* 2006; Kembel & Hubbell 2006; Vamosi *et al.* 2009). Although, the tools and indices of phylogenetic diversity have provided an elegant deductive simplicity for the recognition of mechanisms that guide the organization of a community, it is also clear that there are several mechanisms, such as

competition, facilitation and mutualism, which can provide similar phylogenetic patterns (Cavender-Bares *et al.* 2009). Therefore, distinguishing the relative role of these mechanisms is not an easy task, nevertheless the study of the structural and functional features, together with a correct phylogenetic inference, can increase the robustness in the detection of opposite assembly mechanisms (Spasojevic & Suding 2012; Kraft *et al.* 2017). Thus, the study of the structuring of communities based on an ecological and evolutionary approach becomes essential.

In this paper, we explored the effect of the physiographic factors of slope orientation and topographic position on the taxonomic, functional and phylogenetic structure of the woody plant community and habitat association patterns of the species in different life stages (juveniles and adults) in the northernmost TDF in the Americas. This will enable us to infer the mechanisms driving the distribution and co-occurrence of woody species in these ecosystems. We addressed the following questions: i) Is the distribution of juvenile and adult trees associated with some physiographic factor? If so, what is the most important factor structuring the TDF of Alamos, Sonora? ii) Do the adaptive strategies of different life stages differ among physiographic factors? and finally iii) what are the underlying mechanisms that drive the spatial distribution and species coexistence of TDF among different life stages? We expected that the slope orientation and to a lesser degree, topographic position affect taxonomic structure, functional traits and the phylogenetic structure of the TDF of Alamos, Sonora.

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.

A 50 ha plot was established within the Protected Area to study the dynamics of TDF vegetation. The total area (500 × 1000 m) was delimited by iron stakes every 20 m. With the help of a digital elevation model, 16 subplots (20 × 40 m each) were selected under different aspects of slope orientation (SO: North and South) and topographic position (TP: High and Low) within the 50 ha plot. These subplots reflected the different environmental conditions present in the 50 ha plot and represented four treatments: i) North-Low, sites with SO-North in low elevation areas near intermittent rivers or streams; ii) North-High, sites with SO-North in high elevation areas; iii) South-Low, sites with SO-South in low areas, and finally iv) South-High, sites with SO-South in high areas. Each of these treatments was 4-fold replicated.

DATA COLLECTION.-We used the standardized methodology proposed by the Center for Tropical Forest Studies (now ForestGeo) for long-term and large-scale census of plots in tropical systems (Condit 1998) to census individuals of woody species (trees and shrubs). In each of the 16 subplots, we characterized the structure and composition of woody species in a total area of 1.2 ha. All woody species ≥ 1.30 m in height and ≥ 1 cm diameter at breast height (dbh) were mapped and identified and their height and dbh measured. We obtained seven structural attributes: density of individuals, density and diversity of species (Fisher's alpha index), number of stems, basal area, biomass and maximum height of individuals. For each species recorded, we measured four main functional traits of branches: i) Wood density (WD), ii) Bark water content (Bwc, iii) Bark thickness (Bt) y iv) Xylem water content

(Xwc). These traits provide information that can be used to characterize and differentiate the distribution of the species according to the water use strategies that allow them to face the marked seasonality of TDFs (Chave *et al.* 2014; Muscarella & Uriarte 2016; Mendez-Toribio *et al.* 2017). During the dry season, five individuals of each species were randomly selected within the permanent plot in the Alamos region. From each of these individuals, we collected second order branches with a diameter of ~ 2.5 to 3 cm and 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. 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 & Wiemann 2010). The Xwc and Bwc were estimated as $Xwc/Bwc = ([\text{fresh weight} - \text{dry weight}] / \text{dry weight}) \times 100$. The fresh weight of the branches was obtained after a hydration period of 24 h in distilled water (Mendez-Toribio *et al.* 2017).

PHYLOGENETIC CONSTRUCTION.- We built a considerably appropriate 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.*, *in press*). The final list consisted of 105 tree and shrub species: 104 angiosperms and 1 outgroup (*Cycas revoluta*). For each species, we obtained a Nuclear Gene from GenBank (ITS, containing ITS1, 5.8s and ITS2). We used 8 sequences from congeneric taxa, because data of 8 out of the 58 species on the local list (Table S1) that occur in tropical forest habitats of the Americas were not available. 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 20 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 nodes was provided by TIMETREE (<http://timetree.org/>). This phylogeny calibrated in time (My) and showed in Fig S4, 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). These indices are generated from mean phylogenetic distances (MPD) and mean nearest neighbor distance (MNTD), when the standardized effect of the size of the phylogenetic distances observed between species is 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 place, $Metric_{null}$ 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-NTI indicate phylogenetic clustering of the species at each site sampled, while negative values reveal

overdispersion (Cadotte & Davies 2009). While NRI explores the relationships of the species within the phylogeny, NTI does it towards the tips.

NULL MODELS AND PHYLOBETADIVERSITY.-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 y 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 & 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 & Hubbell 2006; Webb *et al.* 2008).

We calculated estimators of phylobetadiversity (PBD) for adult and juvenile trees. These indices were based on incidence among the 16 sub-plots and between each of the treatments. COMDIST is a measure of dissimilarity that computes the mean phylogenetic distance between species that co-occur in two different sites (Jost 2007; Webb *et al.* 2008; 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 that harbor.

STATISTICAL ANALYSIS.-We performed a diametric categorization to differentiate life stages and we considered individuals with a dbh ≤ 9.9 cm as juveniles and a dbh ≥ 10 cm as adults. The analyzes were carried out on a total of 39 woody species (67.2% of the total recorded species) which had individuals in both juvenile and adult stages. Using this set of species, we conducted univariate analyses and evaluated the effect of slope orientation (SO)

and topographic position (TP), as well as the interaction (SO-TP) on the seven structural attributes, the four functional traits (based on CWM) and the phylogenetic structure index of the community. We also explored differences in these attributes between life stages (juveniles vs. adults) to demonstrate general patterns of life history. We tested differences through Generalized Linear Models (GLM) for count variables and analysis of variance (ANOVA) for continuous variables. For each response variable, saturated models were first produced considering main factors (SO, TP) and their interaction. Subsequently these models were reduced to an adequate minimum model eliminating interactions and/or non-significant factors (Crawley 2013). Therefore, the final model consists only of significant terms (Faraway 2004).

In addition, we used a PCA to explore the effect of both physiographic factors on the predominance of the structural attributes (e.g. abundance, species richness) and functional traits (e.g. WD and Xwc) of the woody species community. A PERMANOVA was used to test these differences. This is a non-parametric test which uses distances matrices to analyze multivariate variance (Anderson 2001). To evaluate patterns of change in abundance, composition and dominance of woody species between aspects of SO and TP as well as life stage, we elaborated rank-abundance curves between treatments and between life stages. These curves were constructed by plotting the logarithm of the abundance of each species according to their range of abundances in each community on the vertical axis (Mueller-Dombois & Ellenberg 1974). We considered the slopes of the line as an indicator of the evenness and dominance within subplots (Magurran 2004). An analysis of covariance (ANCOVA) allowed us to evaluate differences between slopes. Finally, we contrasted the transition juvenile-adult in the 16 most abundant species recorded among different SOs to explore if the response of a species to the conditions of a site differ between life stages.

HABITAT ASSOCIATION OF SPECIES.-We evaluated habitat association of the species using two methods: i) we first compared the abundance of the species observed among the different habitat types and evaluated significance using a PERMANOVA, ii) we used a Monte Carlo randomization test to evaluate the preference of each species to both habitat types. We performed this test to avoid the problem of non-independence generated by the tables of contingency (Clark *et al.* 1998; Webb & 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: $\sum[(\text{Randomized} - \text{Expected})^2 / \text{Expected}]$. This was repeated 1000 times for each species, and the values of the observed deviation were compared with the distribution of random values. We consider significant habitat association as observed values greater than 95% of the randomized values. We \log_{10} transformed $(N + 1)$ the abundance matrix of the species to homogenize the effect of the presence of very abundant species.

PHYLOGENETIC STRUCTURE.- We evaluated differences in phylogenetic structure by comparing phylodiversity patterns between both physiographic factors (SO and TP). We used the NTI/NRI values for each of the 16 plots and tested with a *t-student* two-tailed test. We evaluated the phylobetadiversity patterns in the different life stages using the COMDIST function of Phylocom (Webb *et al.* 2008) and used a PERMANOVA to determine significance between habitat types. Given that we found low or no effect of the TP factor and its interaction with SO on the structural, functional and phylogenetic attributes, we only report habitat preference in terms of SO.

We recorded Solar Radiation Incidence for both physiographic factors, for the dry season (November-June) and the rainy season (July-October), and evaluated differences using Wilcoxon rank-sum test. All the statistical analyzes were carried out using the package *vegan*

version 2.4.5 (Oksanen *et al.* 2017) in the statistical program R version 3.4.2. (R Development Core Team, 2014).

For each sampling vegetation plot potential energy income (PEI) was computed. Incident solar radiation (i.e. direct + diffuse) 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. The “area solar radiation” module from Spatial Analyst Tools in ArcGis was used to derive PEI values, defined as the quantity of solar energy on each pixel (20×20 m) of the image (MJ/m^2).

RESULTS

COMMUNITY STRUCTURE.-We registered a total of 6033 individuals of trees and shrubs corresponding to 53 species, 41 genera and 23 families in the 1.2 ha area sampled (Table S1). Fabaceae was the family that recorded the highest number of species (30%), followed by the families of Burseraceae, Cactaceae and Euphorbiaceae. The latter also dominant in terms of the number of individuals (52%). Of the total number of registered species, 77.1% were trees, 20.3% were shrubs and 2.5% were arborescent cacti. Based on our diametric categorization criteria, we used the data of 5871 individuals of 39 species belonging to 30 genera and 16 families, which had individuals present in both juvenile and adult stages. The univariate analysis of juveniles detected differences in maximum height (SO: $F_{1, 13} = 10.3$, $P < 0.01$) and species diversity (SO: $F_{1, 13} = 4.75$, $P < 0.05$) between SO, but not by TP. The maximum height of trees was higher in North sites (mean \pm SE: 10.3 ± 0.6 m), compared to those of the South (mean \pm SE: 7.8 ± 0.3 m; Fig. 1e). Similarly, Northern sites presented higher values of species diversity (Fisher α mean \pm SE: 5.21 ± 0.4 ; Fig. 1d) than Southern sites. Density of individuals, species density, basal area, biomass, and number of stems were not affected by any physiographic factors (Table S2). Contrastingly, in adult trees we found that SO affected

the vegetation attributes. Southern sites had a significantly higher density of individuals (mean \pm SE: 71 ± 5.1 ; SO: $\chi^2 = 5.65$, df = 1, $P < 0.05$; Fig 1g) and higher number of stems (mean \pm SE: 278.6 ± 29.8 ; SO: $\chi^2 = 9.99$, df = 1, $P < 0.01$) than Northern sites. Basal area was significantly affected both by the slope orientation (SO: $F_{1,13} = 6.23$, $P < 0.05$) and topographic position (TP: $F_{1,13} = 4.75$, $P < 0.05$) (Fig. 1g). Density of species, maximum height, biomass and species diversity of adults did not differ between SO and TP (Table S2). The slope of the rank-abundance curves used here as an approximation of the species diversity/evenness between SO (N and S) and TP (L and H), were not significantly different for juvenile nor adult stages. However, the comparison between life stages (Juv vs Ad), showed differences in species evenness ($F_{1,74} = 20.8$, $P < 0.001$). Thus, juveniles showed greater dominance of few species ($b = -0.14$), whereas adult trees showed greater species evenness ($b = -0.11$). *Lysiloma divaricatum*, *Croton fantzianus*, *Jatropha malacophylla* and *Brogniartia alamosana* were among the 10 most dominant species in both juvenile and adult stages (Fig. S1).

The multivariate analysis of structural and functional attributes provides additional information on the significance of SO and TP on these attributes in the different stages of tree development (Fig. 2). The PCA of the structural attributes (Fig. 2a, b) indicated a differentiation between the SO in the adult life stages ($R^2 = 0.32$, $P = 0.009$) but not among the juveniles ($R^2 = 0.05$, $P = 0.44$). For adult trees, first axis of the PCA was more strongly correlated to the SO; the density of individuals, species density and species diversity, and basal area were positively correlated with the Southern orientation, while the second axis of the PCA was correlated only with maximum tree height (Fig. 2b). The PCA of the structural attributes of juvenile and adult trees explain respectively 82.6% and 78.4% of the variation in the first two axes.

FUNCTIONAL TRAITS OF THE COMMUNITY (CWM).- Regarding the functional dominances of traits, evaluated through Community-Weighted Means (CWM) between physiographic aspects, only the xylem water content (Xwc) showed to be affected by the SO in the juveniles ($F_{1,13} = 7.24, P = 0.01$); this attribute was higher in the North sites (mean \pm SE: $70.1 \pm 9.8 \%$), compared to those in the South (mean \pm SE: $41.8 \pm 3.1 \%$), while none of the four functional attributes showed differences between the physiographic factors for adults (Table S3). Analyzing the functional differences only between life stages, interestingly CWM for the wood density showed to be significantly higher on juvenile tree communities (mean \pm SE= 0.67 ± 0.02 ; $F_{1,30} = 10.7, P = 0.002$, Fig. S3) compared with and adult trees (mean \pm SE= 0.58 ± 0.01). The bark thickness was also significantly different between the life stages ($F_{1,30} = 12.2, P = 0.001$), showing the same pattern, in which the juvenile trees have the highest values of this attribute (mean \pm SE= 0.96 ± 0.04).

The PCA of the functional traits showed general patterns of the adaptive strategies of the species in the community. We did not find any effect of the physiographic factors evaluated on the prevalence of these attributes in adults (Fig. 2d). However, in juveniles the PERMANOVA indicated that functional traits were affected by SO ($R^2 = 0.28, P = 0.03$, Fig. 2c). None of the functional attributes were affected by TP or by the interaction SO-TP (Table S4).

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 SO, suggesting that this is a physiographic factor that gives rise to the differential association of TDF's woody species in the different life stages (Fig. 3).

In the juvenile stages, 16 out of 39 species showed preference for a particular slope orientation, nine were associated with southern and seven with northern orientations (Table

1). In the case of adults, seven showed preference for southern and six for northern orientations for a total of 13 species (~33%). In general, the community of woody species were strongly associated a type of habitat from early developmental stages and this association was conserved into later stages. In the juvenile stages, this differentiation between habitats was represented by the presence of some species adapted to places where the availability of water was scarce and the levels of solar radiation were high (South: e.g. *Acacia cochliacantha*, *Brongniartia alamosana* and *Croton fantzianus*); while, on the other hand, some species less tolerant to drought were associated with Northern sites (e.g. *Bursera grandifolia*, *Karwinskia humboldtiana*, *Tabebuia* sp). The former species have been characterized as representative of early stages of secondary succession in the Alamos region; while the latter ones are representative of advanced stages of secondary succession (Quisehuatl-Medina *et al.*, *in press*). In the case of adult trees the pattern is different. The species associated with Southern habitats were represented by: *Coursetia glandulosa*, *Pachycereus pecten-aboriginum*, *Randia thurberi* and *Stenocereus montanus*, while the species associated with North sites are represented by *Erythrina flabelliformis*, *Lonchocarpus hermannii*, *Lysiloma divaricatum* and *Sebastiania pavoniana* (Table 1).

PHYLOGENETIC DIVERSITY.-The results of both indices (NRI/NTI) were different for juveniles and adults when evaluating the mean phylogenetic diversity patterns between slope orientation (Fig. 4). The phylogenetic structure was not influenced by SO in juvenile stages, measured with NRI ($t = -0.13$, $df = 13.5$, $P=0.89$) and NTI ($t = -0.94$, $df = 12.5$, $P=0.36$) whereas in adult stages, SO did have a significant effect on phylogenetic patterns using NTI ($t = -2.16$, $df = 10.1$, $P=0.04$, Fig.4d), but not with NRI ($t = -1.0$, $df = 13.2$, $P=0.33$). When only the phylogenetic structure between the different life stages was compared, phylogenetic

diversity was similar between juvenile and adult stages (NTI: $t = -0.29$, $df = 28.9$, $P=0.77$; NRI: $t = 0.68$, $df = 28.9$, $P=0.49$).

Phylobetadiversity (PBD) on the other hand, using the COMDIST algorithm, showed a pattern of non-random grouping between sites. This pattern seems to be more associated with slope orientation and is consistent between life stages (Fig.5). The dendrogram suggests that communities with values close to zero are evolutionarily similar and the species they harbor are more closely related. The PERMANOVA applied to the distance matrix (*comdist*) indicated a strong discrepancy in the PBD values between SO in juvenile ($P < 0.004$) and adult ($P < 0.001$) stages, however, no pattern was found for grouping with the TP. The formation of two large groups in both life stages (Fig. 5) indicates a marked differentiation between slope orientation with evolutionarily similar communities in each habitat.

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. S5). The highest SRI values during the dry season were reported on the southern slopes (mean \pm SE: 452.8 ± 3.9 Mj/m²) and were 1.2 times higher than the northern slopes. Similarly, during the wet season the SRI values were higher on the southern slopes (mean \pm SE: 554.1 ± 2.2 Mj/m²), being 1.1 times higher than on the northern slopes.

DISCUSSION

In this study we found that slope orientation (SO) was the most important physiographic factor defining patterns of species association. In general, SO influences the taxonomic composition, functional traits and the phylogenetic structure of the woody vegetation in different ways in both of the life stages analyzed (Table S4, Fig. 2 and 4). On one hand, juvenile trees were not influenced structurally nor phylogenetically by any physiographic

factor and only maximum height and species diversity differed between North and South slopes. Nevertheless, the composition and dominance of functional traits of this stage varied between SO (Table S4). In adult trees on the other hand, structure, composition, and the phylogenetic structure of the vegetation were affected by the SO, although no effect was found on the functional traits of woody species (Fig. 2c).

The results of this study indicate that habitat association of TDF's species begins during early stages of plant life (≥ 1 cm) and it is maintained towards adult stages, thereby suggesting that habitat filtering may be acting at even earlier stages of development (seedlings or saplings <1 cm). Our results are consistent with other studies that analyze the relative role of habitat heterogeneity and the environmental conditions associated with environmental filtering, on the structuring of tropical tree communities in different life stages (Valencia *et al.* 2004; Metz 2012; Baldeck *et al.* 2013). Although, we found the pattern of species habitat association to be similar in adults and juveniles, its dominant functional strategies differed (Table S4, Fig. 2c, d; Fig S3). These differences in functional traits at the plot level reflect a different response in the ability of individuals to assimilate the same resource through its different life stages of a plant (Metz 2012).

The Solar Radiation Interception (SRI), used here as an approximation of the deficit of water in a habitat, was higher for southern slopes suggesting a greater water deficit with respect to the northern slopes. In turn, this may be affecting the prevalence of the species found between habitats in the different life stages differently (Fig. S2). Some studies have documented that high SRI values can affect water content in the soil through evapotranspiration (Galicía *et al.* 1999). Others have demonstrated that changes in the requirements to assimilate the same resource through the ontogeny of a species (Donovan & Ehleringer 1992, Comita *et al.* 2007), which suggests the differential use of adaptive strategies among juveniles and adults. This

may explain the effect of SO on functional traits, but not on the structural attributes of juveniles (Table S4).

Interestingly, we found that juvenile trees show higher values in CWM of WD and Bt than adults. High values of both traits are characteristic of drought-tolerant species (e.g. *Haematoxylum brasiletto* and *Brongniartia alamosana*). These species are generally slow-growing species with resistance to hydraulic cavitation, but with only limited efficiency in water conduction (Hacke *et al.* 2001). In contrast, low values of these attributes are characteristic of species with strategies of drought avoidance (e.g. *Bursera grandifolia* and *Jathropha cordata*), which store water in their tissues in response to the short periods of water availability (Pineda-García *et al.* 2015; Méndez-Toribio *et al.* 2017). Initially, juveniles were expected to have low values of WD and Bt in response to the short availability of water resources in the presence of adult individuals (Méndez-Toribio *et al.* 2017), however, this pattern was opposite to the expected, although similar to previous studies (Francis *et al.* 2017). As mentioned above, the high values WD and Bt reflect a strategy of drought tolerance and protection against possible herbivory events (Hacke *et al.* 2001; Ferrenberg & Mitton, 2014). Mainly in juvenile trees, where the low development of root systems limited access to deeper and wet layers of soil (Frazer & Davis 1988), are making them mostly dependent on available water. We believe that in arid environments as our study site, drought tolerance and the herbivory across of high WD and Bt values, become a priority in this life stage.

Furthermore, the low availability of water in the soil as a result of the thin soils in the study area (Martínez-Yrizar *et al.* 2000), might be intensify the competition of this resource among juveniles and generate a reduction and/or exclusion of conspecifics. The prevalence patterns of species reported in this study could support this premise, since it is on the southern slopes that most of the species showed a marked reduction in abundance towards adult life stages (Fig S2). Thus, the functional traits of the plants, as well as characteristics of the habitat, may

have a strong effect on their competitive ability through the differentiation of strategies for the use of resources between the different life stages (niche differentiation, *sensu* Fowler 1986).

In a scenario where conspecific juvenile and adult trees share the same habitat, the effect and/or competitive response between both life stages may be due to: i) the suppression of neighbors (competitive exclusion) or its competitive effect (Chesson 2000); or because of the ability to tolerate the competitive effect of its neighbor (Goldberg 1996); these could lead to the structuring of the community in different ways. We then suspect this niche differentiation could be seen as a mechanism that neutralizes the effect of competition and/or density-dependence among individuals of the same species in a habitat.

The juvenile-adult transition patterns of species also seem to be influenced by the type of habitat (North and South) since the abundance of a species was considerably high in one habitat, but low in another. This pattern is more evident in south-facing sites, where solar radiation seems to play an important role in the prevalence of a species towards more advanced stages. These observed patterns provide relevant information on the capacity of species to tolerate changing conditions (Fig. S2). Additionally, these patterns allow us to explore the habitat preferences of the species according to their adaptive strategies and/or life history characteristics. These results suggest that for some species, the sites may initially be beneficial for their establishment but not for survival or prevalence from one stage to another. Currently, there are several studies that show a high correlation between the variability of physiographic characteristics (e.g. soil depth, drainage) and the distribution and establishment of woody species in tropical systems (Harms *et al.* 2001, Valencia *et al.* 2004; Engelbrecht *et al.* 2007). Furthermore, others studies have identified that the topography does not always affect the vegetation attributes in the same way, especially if we consider sites through latitudinal gradients (Gallardo-Cruz *et al.* 2009). For example, when contrasting the SRI values between sites where TDF is distributed in the northern hemisphere (low latitudes such

as Oaxaca, through Michoacán, Jalisco and up to the state of Sonora; northern limit distribution of TDFs in Mexico), the differences seem more pronounced towards more northern latitudes, suggesting changes in the relative importance of physiographic factors such as SO in determining the dominance of water use strategies and the spatial distribution of woody species in these ecosystems (Gallardo-Cruz et al., 2009; Balvanera et al., 2011; Méndez-Toribio et al., 2017, the present study). In this study the juvenile stages showed higher values of Xwc in North orientation sites, suggesting that in these sites the species tend to adopt a strategy of drought avoidance. The trees in these sites have soft tissue, with stems adapted to store large amounts of water and a short period of leaf retention (Méndez-Alonso et al. 2012). Interestingly, our results contrast those of Méndez-Toribio et al. 2017, which reports that drought avoidance strategies are characteristics of sites where the time of water availability and the period of growth is relatively short (upper parts of slopes), especially those facing south in a TDF in central Mexico. These differences may be associated with differences in sampling scale and/or the size categories evaluated between the studies. For example Méndez-Toribio et al. 2017 used plots of 10 x 10 m and trees ≥ 2.5 cm DBH; while in our study we consider plots of 20 x 40 m and size categories trees ≥ 1 cm.

We observed that the non-random pattern of habitat association in juvenile trees is conserved in adult stages. Given that the evenness of species in juvenile stages was significantly lower with respect to adult stages (Fig. S1b), we suspect that the habitat association in adults may be the result of adjustments in the species dominance (abundance of individuals) present in juvenile stages; the latter as a consequence of differences in mortality rates and species prevalence. This idea has been suggested to explain the conservation of patterns of species association between life stages in tropical communities, mainly from seedlings to juveniles (Queenborough et al. 2007, Metz 2012).

Another explanation, although not evaluated in this study, may be that the events of a localized dispersion of adults distributed in a similar preferential habitat may contribute to explain similar association patterns of juveniles and adults (Hubbell 1979; Comita *et al.* 2007). This may imply a high rate of establishment and prevalence of individuals recruited in preferred habitat by adults or that the initial composition established in juvenile stages is conserved only through the adjustment in the dominance patterns or co-dominance of their species towards adult stages (Fig. S1). The latter could also explain the phylogenetic patterns among the different life stages, where both α and β phylogenetic structure tend to be similar between life stages. Contrasting the phylogenetic structure of juveniles and adults, it seems to be led by a random component, being similar in both cases, suggesting the rotation of species with lineages randomly distributed between both life stages.

The results of the phylogenetic structure observed within each life stage demonstrate that the communities are evolutionarily distinct between North and South slopes, but phylogenetically similar within each slope. This is important, as it suggest that SO is usually the most important physiographic factor when describing community assembly patterns of seasonally dry ecosystems in the northwest of Mexico. Additionally, our results highlight the importance of large scale studies across latitudinal gradients contrasting the relative role of physiographic factors from a structural, functional and phylogenetic context, but this will remain open for further studies.

CONCLUSION

As predicted, our results indicate that slope orientation is a physiographic factor that contributes to the association patterns of woody species between different life stages. We believe these patterns are the result of environmental differentiation of each slope and provide

strong evidence for the role of water availability in driving the patterns of species distribution and taxonomic and functional structure in seasonally dry ecosystems. The differences in functional traits and species association, but not between the phylogenetic structure between the different life stages, suggest evidence of the differential use of adaptive strategies between both life stages; strategies that allow them to face the low availability of water and high radiation rates, characteristics of TDFs.

LITERATURE CITED

- BALDECK, C. A., K. E. HARMS, J. B. YAVITT, R. JOHN, B. L. TURNER, R. VALENCIA, H. NAVARRETE, S. BUNYAVEJCHEWIN, S. KIRATIPRAYOON, A. YAACOB, M. N. N. SUPARDI, S. J. DAVIES, S. P. HUBBELL, G. B. CHUYONG, D. KENFACK, D. W. THOMAS, and J. W. DALLING. 2013. Habitat filtering across tree life stages in tropical forest communities. *Proceedings of the Royal Society B: Biological Sciences* 280: 20130548–20130548.
- BALVANERA, P., S. QUIJAS, and A. PÉREZ-JIMÉNEZ. 2011a. Distribution Patterns of Tropical Dry Forest Trees Along a Mesoscale Water Availability Gradient: Tree Distribution Along Water Availability Gradient. *Biotropica* 43: 414–422.
- BARALOTO, C., O. J. HARDY, C. E. T. PAINE, K. G. DEXTER, C. CRUAUD, L. T. DUNNING, M.-A. GONZALEZ, J.-F. MOLINO, D. SABATIER, V. SAVOLAINEN, and J. CHAVE. 2012a. Using functional traits and phylogenetic trees to examine the assembly of tropical tree communities: *Assembly of tropical tree communities*. *Journal of Ecology* 100: 690–701.
- BARALOTO, C., F. MORNEAU, D. BONAL, L. BLANC, and B. FERRY. 2007b. SEASONAL WATER STRESS TOLERANCE AND HABITAT ASSOCIATIONS WITHIN FOUR NEOTROPICAL TREE GENERA. *Ecology* 88: 478–489.
- BORCHERT, R. 1994a. Soil and Stem Water Storage Determine Phenology and Distribution of Tropical Dry Forest Trees. *Ecology* 75: 1437–1449.
- BORCHERT, R. 1994b. Soil and Stem Water Storage Determine Phenology and Distribution of Tropical Dry Forest Trees. *Ecology* 75: 1437–1449.
- BRUNO, J. F., J. J. STACHOWICZ, and M. D. BERTNESS. 2003a. Inclusion of facilitation into ecological theory. *Trends in Ecology & Evolution* 18: 119–125.
- CADOTTE, M. W. 2014a. Including distantly related taxa can bias phylogenetic tests. *Proceedings of the National Academy of Sciences* 111: E536–E536.
- CADOTTE, M. W., R. DINNAGE, and D. TILMAN. 2012a. Phylogenetic diversity promotes ecosystem stability. *Ecology* 93: S223–S233
- CADOTTE, M. W., T. JONATHAN DAVIES, J. REGETZ, S. W. KEMBEL, E. CLELAND, and T. H. OAKLEY. 2010a. Phylogenetic diversity metrics for ecological communities: integrating species richness, abundance and evolutionary history. *Ecology Letters* 13: 96–105.
- CADOTTE, M. W., AND T. JONATHAN DAVIES. 2009. *Phylogenies in Ecology: a guide of concepts and methods*. Princeton.

- CADOTTE, M. W., and C. M. TUCKER. 2018a. Difficult decisions: Strategies for conservation prioritization when taxonomic, phylogenetic and functional diversity are not spatially congruent. *Biological Conservation* 225: 128–133.
- CAVENDER-BARES, J., K. H. KOZAK, P. V. A. FINE, and S. W. KEMBEL. 2009a. The merging of community ecology and phylogenetic biology. *Ecology Letters* 12: 693–715.
- CHASE, J. M. 2010a. Stochastic Community Assembly Causes Higher Biodiversity in More Productive Environments. *Science* 328: 1388–1391.
- CHASE, J. M., N. J. B. KRAFT, K. G. SMITH, M. VELLEND, and B. D. INOUE. 2011a. Using null models to disentangle variation in community dissimilarity from variation in α -diversity. *Ecosphere* 2: art24.
- CHAVE, J. ET AL. 2014a. Improved allometric models to estimate the aboveground biomass of tropical trees. *Global Change Biology* 20: 3177–3190.
- CHAVE, J., H. C. MULLER-LANDAU, T. R. BAKER, T. A. EASDALE, H. TER STEEGE, and C. O. WEBB. 2006a. Regional and Phylogenetic Variation of Wood Density across 2456 Neotropical Tree Species. *Ecological Applications* 16: 2356–2367.
- CHEESMAN, A. W., N. D. PREECE, P. VAN OOSTERZEE, P. D. ERSKINE, and L. A. CERNUSAK. 2018. The role of topography and plant functional traits in determining tropical reforestation success N. Butt (Ed.). *Journal of Applied Ecology* 55: 1029–1039.
- CHESSON, P. 2000a. Mechanisms of maintenance of species diversity. *Annual review of Ecology and Systematics* 343–366.
- COMITA, L. S., R. CONDIT, and S. P. HUBBELL. 2007. Developmental Changes in Habitat Associations of Tropical Trees. *Journal of Ecology* 95: 482–492.
- COMITA, L. S., and B. M. J. ENGELBRECHT. 2009. Seasonal and Spatial Variation in Water Availability Drive Habitat Associations in a Tropical Forest. *Ecology* 90: 2755–2765.
- CONDIT, R., B. M. J. ENGELBRECHT, D. PINO, R. PEREZ, and B. L. TURNER. 2013. Species distributions in response to individual soil nutrients and seasonal drought across a community of tropical trees. *Proceedings of the National Academy of Sciences* 110: 5064–5068.
- CONDIT, R. 1998. *Tropical Forest Census Plots: Methods and Results from Barro Colorado Island, Panama and a Comparison with Other Plots*. Springer-Verlag.
- CRAWLEY, M. J. 2013. *The R book* Second edition. Wiley, Chichester, West Sussex, United Kingdom.
- DAWS, M. I., C. E. MULLINS, and W. DALLING. Topographic position affects the water regime in a semideciduous tropical forest in Panama. 12.
- DIRZO, R. ed. 2011. *Seasonally dry tropical forests: ecology and conservation*. Island Press, Washington.
- DONOGHUE, M. J. 2008. A phylogenetic perspective on the distribution of plant diversity. *Proceedings of the National Academy of Sciences* 105: 11549–11555.
- DONOVAN, L. A., and J. R. EHLERINGER. 1992. Contrasting Water-Use Patterns Among Size and Life-History Classes of a Semi-Arid Shrub. *Functional Ecology* 6: 482.
- EDGAR, R.C. 2004. MUSCLE: MULTIPLE SEQUENCE ALIGNMENT WITH HIGH ACCURACY AND HIGH THROUGHPUT. *NUCLEIC ACIDS RES.* 32:1792–1797.
- EMERSON, B. C., and R. G. GILLESPIE. 2008. Phylogenetic analysis of community assembly and structure over space and time. *Trends in Ecology & Evolution* 23: 619–630.
- ENGELBRECHT, B. M. J., L. S. COMITA, R. CONDIT, T. A. KURSAR, M. T. TYREE, B. L. TURNER, and S. P. HUBBELL. 2007a. Drought sensitivity shapes species distribution patterns in tropical forests. *Nature* 447: 80–82.
- FARAWAY, J. J. 2004. *Extending Linear Model With R*. Chapman & Hall/CRC, London
- FOWLER, N. *The Role of Competition in Plant Communities in Arid and Semiarid Regions*.

- FRANCIS, E. J., H. C. MULLER-LANDAU, S. J. WRIGHT, M. D. VISSER, Y. IIDA, C. FLETCHER, S. P. HUBBELL, and A. R. KASSIM. 2017. Quantifying the role of wood density in explaining interspecific variation in growth of tropical trees. *Global Ecology and Biogeography* 26: 1078–1087.
- FRAZER, J. M., and S. D. DAVIS. 1988. Differential survival of chaparral seedlings during the first summer drought after wildfire. *Oecologia* 76: 215–221.
- GALICIA, L., J. LÓPEZ-BLANCO, A. . ZARCO-ARISTA, V. FILIPS, and F. GARCÍA-OLIVA. 1999. The relationship between solar radiation interception and soil water content in a tropical deciduous forest in Mexico. *CATENA* 36: 153–164.
- GALLARDO-CRUZ, J. A., E. A. PÉREZ-GARCÍA, E. A. and J. A. MEAVE. 2009. Beta-Diversity and vegetation structure as influenced by slope aspect and altitude in a seasonally dry tropical landscape
- GARZON-LOPEZ, C. X., P. A. JANSEN, S. A. BOHLMAN, A. ORDONEZ, and H. OLFF. 2014. Effects of sampling scale on patterns of habitat association in tropical trees S. Scheiner (Ed.). *Journal of Vegetation Science* 25: 349–362.
- GOLDBERG, D. E. 1996. Competitive Ability: Definitions, Contingency and Correlated Traits. *Philosophical Transactions: Biological Sciences* 351: 1377–1385.
- GOTELLI, N. J. 2000. NULL MODEL ANALYSIS OF SPECIES CO-OCCURRENCE PATTERNS. 81: 16.
- GRAHAM, C. H., and P. V. A. FINE. 2008. Phylogenetic beta diversity: linking ecological and evolutionary processes across space in time. *Ecology Letters* 11: 1265–1277.
- GRAVEL, D., C. D. CANHAM, M. BEAUDET, and C. MESSIER. 2006. Reconciling niche and neutrality: the continuum hypothesis: Reconciling niche and neutrality. *Ecology Letters* 9: 399–409.
- GUNATILLEKE, C. V. S., I. A. U. N. GUNATILLEKE, S. ESUFALI, K. E. HARMS, P. M. S. ASHTON, D. . F. R. P. BURSLEM, and P. S. ASHTON. 2006. Species-Habitat Associations in a Sri Lankan Dipterocarp Forest. *Journal of Tropical Ecology* 22: 371–384.
- HARDIN, G. 1960. The Competitive Exclusion Principle. *Science, New Series* 131: 1292–1297.
- HARIHAR, A., P. CHANCHANI, R. K. SHARMA, J. VATTAKAVEN, S. GUBBI, B. PANDAV, and B. NOON. 2013. Conflating “co-occurrence” with “coexistence.” *Proceedings of the National Academy of Sciences* 110: E109–E109.
- HARMS, K. E., R. CONDIT, S. P. HUBBELL, and R. B. FOSTER. 2001a. Habitat associations of trees and shrubs in a 50-ha Neotropical forest plot. *Journal of Ecology* 89: 947–959.
- HERAULT, B. 2007. Reconciling niche and neutrality through the Emergent Group approach. *Perspectives in Plant Ecology, Evolution and Systematics* 9: 71–78.
- HIETZ, P., S. ROSNER, U. HIETZ-SEIFERT, and S. J. WRIGHT. 2017. Wood traits related to size and life history of trees in a Panamanian rainforest. *New Phytologist* 213: 170–180.
- HILL, M. O. 1973. Diversity and Evenness: A Unifying Notation and Its Consequences. *Ecology* 54: 427–432.
- HUBBELL, S. P. 1979. Tree Dispersion, Abundance, and Diversity in a Tropical Dry Forest. *Science* 203: 1299–1309.
- HUBBELL, S. P. 2001a. The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton.
- HURTT, G. C., and S. W. PACALA. 1995a. The consequences of recruitment limitation: reconciling chance, history and competitive differences between plants. *Journal of Theoretical Biology* 176: 1–12.
- JABOT, F., R. S. ETIENNE, and J. CHAVE. 2008. Reconciling Neutral Community Models and

- Environmental Filtering: Theory and an Empirical Test. *Oikos* 117: 1308–1320.
- JIANG, J., J. A. M. MOORE, A. PRIYADARSHI, and A. T. CLASSEN. 2017. Plant-mycorrhizal interactions mediate plant community coexistence by altering resource demand. *Ecology* 98: 187–197.
- JIN, Y., S. E. RUSSO, and M. YU. 2018. Effects of light and topography on regeneration and coexistence of evergreen and deciduous tree species in a Chinese subtropical forest F. Gilliam (Ed.). *Journal of Ecology* 106: 1634–1645.
- KANAGARAJ, R., T. WIEGAND, L. S. COMITA, and A. HUTH. 2011. Tropical tree species assemblages in topographical habitats change in time and with life stage: Habitat-driven tree species assemblages. *Journal of Ecology* 99: 1441–1452.
- KEMBEL, S. W. 2009. Disentangling niche and neutral influences on community assembly: assessing the performance of community phylogenetic structure tests. *Ecology Letters* 12: 949–960.
- KEMBEL, S. W., and S. P. HUBBELL. 2006a. The phylogenetic structure of a neotropical forest tree community. *Ecology* 87.
- KEMBEL, S. W., COWAN, P. D., HELMUS, M. R., CORNWELL, W. K., MORLON, H., ACKERLY, D. D. *et al.* 2010. Picante: R tools for integrating phylogenies and ecology. *Bioinformatics* 26: 1463–1464.
- KRAFT, N. J. B., P. B. ADLER, O. GODOY, E. C. JAMES, S. FULLER, and J. M. LEVINE. 2015. Community assembly, coexistence and the environmental filtering metaphor J. Fox (Ed.). *Functional Ecology* 29: 592–599.
- KRAFT, N. J., W. K. CORNWELL, C. O. WEBB, and D. D. ACKERLY. 2007. Trait evolution, community assembly, and the phylogenetic structure of ecological communities. *The American Naturalist* 170: 271–283.
- LAI, J., X. MI, H. REN, and K. MA. 2009. Species-habitat associations change in a subtropical forest of China. *Journal of Vegetation Science* 20: 415–423.
- LOPEZ-TOLEDO, L., C. HORN, and B. A. ENDRESS. 2011. Distribution and population patterns of the threatened palm *Brahea aculeata* in a tropical dry forest in Sonora, Mexico. *Forest Ecology and Management* 261: 1901–1910.
- MACARTHUR, R., and R. LEVINS. 1964. Competition, Habitat Selection, and Character Displacement in a Patchy Environment. *Proceedings of the National Academy of Sciences of the United States of America* 51: 1207–1210.
- MACARTHUR, R., and R. LEVINS. 1967a. The Limiting Similarity, Convergence, and Divergence of Coexisting Species. *The American Naturalist* 101: 377–385.
- MAGURRAN, A. E. 2004. *Measuring biological diversity*. Blackwell Pub, Malden, Ma.
- MARKESTEIJN, L., L. POORTER, F. BONGERS, H. PAZ, and L. SACK. 2011. Hydraulics and life history of tropical dry forest tree species: coordination of species' drought and shade tolerance. *New Phytologist* 191: 480–495.
- MARTIN, P. S., D. YETMAN, M. FISHBEIN, P. JENKINS, T. VAN DEVENDER, AND R. K. WILSON. 1998. *Gentry's Río Mayo plants: The tropical deciduous forest and environs of northwest México*. The University of Arizona Press. Tucson, USA.
- MARTÍNEZ-YRÍZAR, A., A. BÚRQUEZ, J. M. MAASS. 2000. Structure and functioning of tropical deciduous forest in western Mexico. *In* R. H. Robichaux and D. A. Yetman (Eds.). *The tropical deciduous forest of Alamos: biodiversity of a threatened ecosystem in Mexico*, pp. 19-35. University of Arizona, Tucson, USA.
- MAYFIELD, M. M., and J. M. LEVINE. 2010a. Opposing effects of competitive exclusion on the phylogenetic structure of communities: Phylogeny and coexistence. *Ecology Letters* 13: 1085–1093.
- MÉNDEZ-ALONZO, R., H. PAZ, R. C. ZULUAGA, J. A. ROSELL, and M. E. OLSON. 2012.

- Coordinated evolution of leaf and stem economics in tropical dry forest trees. *Ecology* 93: 2397–2406.
- MÉNDEZ-TORIBIO, M., G. IBARRA-MANRÍQUEZ, A. NAVARRETE-SEGUEDA, and H. PAZ. 2017a. Topographic position, but not slope aspect, drives the dominance of functional strategies of tropical dry forest trees. *Environmental Research Letters* 12: 085002.
- METZ, M. R. 2012. Does habitat specialization by seedlings contribute to the high diversity of a lowland rain forest?: *Seedling habitat associations and tropical diversity*. *Journal of Ecology* 100: 969–979.
- MILLER, E. T., D. R. FARINE, and C. H. TRISOS. 2017. Phylogenetic community structure metrics and null models: a review with new methods and software. *Ecography* 40: 461–477.
- MUSCARELLA, R., and M. URIARTE. 2016. Do community-weighted mean functional traits reflect optimal strategies? *Proceedings of the Royal Society B: Biological Sciences* 283: 20152434.
- NORDEN, N., S. G. LETCHER, V. BOUKILI, N. G. SWENSON, and R. CHAZDON. 2012. Demographic drivers of successional changes in phylogenetic structure across life-history stages in plant communities. *Ecology* 93: S70–S82.
- PAINE, C. E. T., C. BARALOTO, J. CHAVE, and B. HÉRAULT. 2011. Functional traits of individual trees reveal ecological constraints on community assembly in tropical rain forests. *Oikos* 120: 720–727.
- PAVOINE, S., A. GASC, M. B. BONSALE, and N. W. H. MASON. 2013. Correlations between phylogenetic and functional diversity: mathematical artefacts or true ecological and evolutionary processes? A. Prinzing (Ed.). *Journal of Vegetation Science* 24: 781–793.
- PAZ, H., F. PINEDA-GARCÍA, and L. F. PINZÓN-PÉREZ. 2015. Root depth and morphology in response to soil drought: comparing ecological groups along the secondary succession in a tropical dry forest. *Oecologia* 179: 551–561.
- PINEDA-GARCÍA, F., H. PAZ, F. C. MEINZER, and G. ANGELES. 2015. Exploiting water versus tolerating drought: water-use strategies of trees in a secondary successional tropical dry forest G. Goldstein (Ed.). *Tree Physiology* tpv124.
- POSADA, D. 2008. jModelTest: phylogenetic model averaging. *Mol. Biol. Evol.* 25: 1253–1256.
- QIAN, H., and L. JIANG. 2014b. Phylogenetic community ecology: integrating community ecology and evolutionary biology. *Journal of Plant Ecology* 7: 97–100.
- QUEENBOROUGH, S. A., D. F. R. P. BURSLEM, N. C. GARWOOD, and R. VALENCIA. 2007. Habitat niche partitioning by 16 species of Myristicaceae in Amazonian Ecuador. *Plant Ecology* 192: 193–207.
- QUISEHUATL-MEDINA, A. 2016. ESTRUCTURA Y COMPOSICION DE LA COMUNIDAD DE LEÑOSAS EN LA SUCESION SECUNDARIA DE LA SELVA SECA DEL SUR DE SONORA. TESIS DE LICENCIATURA. UMSNH
- R Core Team. 2013. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>.
- ROLLAND, J., M. W. CADOTTE, J. DAVIES, V. DEVICTOR, S. LAVERGNE, N. MOUQUET, S. PAVOINE, A. RODRIGUES, W. THULLER, L. TURCATI, M. WINTER, L. ZUPAN, F. JABOT, and H. MORLON. 2012b. Using phylogenies in conservation: new perspectives. *Biology Letters* 8: 692–694.
- SAMANI, Z. Estimating Solar Radiation and Evapotranspiration Using Minimum Climatological Data (Hargreaves-Samani equation). 13.
- SEGURA, G., P. BALVANERA, E. DURÁN, and A. PÉREZ. 2003. Tree Community Structure and Stem Mortality along a Water Availability Gradient in a Mexican Tropical Dry Forest.

- Plant Ecology 169: 259–271.
- SPASOJEVIC, M. J., and K. N. SUDING. 2012a. Inferring community assembly mechanisms from functional diversity patterns: the importance of multiple assembly processes: *Functional diversity along gradients*. *Journal of Ecology* 100: 652–661.
- SWENSON, N. G., and B. J. ENQUIST. 2007. Ecological and Evolutionary Determinants of a Key Plant Functional Trait: Wood Density and Its Community-Wide Variation across Latitude and Elevation. *American Journal of Botany* 94: 451–459.
- SWENSON, N. G., and B. J. ENQUIST. 2009. Opposing Assembly Mechanisms in a Neotropical Dry Forest: Implications for Phylogenetic and Functional Community Ecology. *Ecology* 90: 2161–2170.
- TRAUTZ, A. C., T. H. ILLANGASEKARE, and I. RODRIGUEZ-ITURBE. 2017. Role of co-occurring competition and facilitation in plant spacing hydrodynamics in water-limited environments. *Proceedings of the National Academy of Sciences* 114: 9379–9384.
- VALENCIA, R., R. B. FOSTER, G. VILLA, R. CONDIT, J.-C. SVENNING, C. HERNANDEZ, K. ROMOLEROUX, E. LOSOS, E. MAGARD, and H. BALSLEV. 2004. Tree species distributions and local habitat variation in the Amazon: large forest plot in eastern Ecuador. *Journal of Ecology* 92: 214–229.
- VALIENTE-BANUET, A., and M. VERDÚ. 2007. Facilitation can increase the phylogenetic diversity of plant communities. *Ecology Letters* 10: 1029–1036.
- VAN DEVENDER, T. R., A. C. SANDERS, R. K. WILSON, AND S. A. MEYER. 2000. Vegetation, flora and seasons of the Río Cuchujaqui, a tropical deciduous forest near Alamos. *In* R. H. Robichaux and D. A. Yetman (Eds.). *The tropical deciduous forest of Alamos: biodiversity of a threatened ecosystem in Mexico*, pp. 36-101. University of Arizona, Tucson, USA.
- WEBB, C. O. 2000a. Exploring the Phylogenetic Structure of Ecological Communities: An Example for Rain Forest Trees. *The American Naturalist* 156: 145–155.
- WEBB, C. O., D. D. ACKERLY, M. A. MCPEEK, and M. J. DONOGHUE. 2002a. Phylogenies and Community Ecology. *Annual Review of Ecology and Systematics* 33: 475–505.
- WEBB, C. O., and D. R. PEART. 2000. Habitat Associations of Trees and Seedlings in a Bornean Rain Forest. *Journal of Ecology* 88: 464–478.
- WEBB, C.O., ACKERLY, D.D. & KEMBEL, S.W. 2008. Phylocom: software for the analysis of phylogenetic community structure and trait evolution. *Bioinformatics* 24: 2098–2100.
- WILLIAMSON, G. B., and M. C. WIEMANN. 2010. Measuring wood specific gravity...Correctly. *American Journal of Botany* 97: 519–524.
- ZILLIO, T., and R. CONDIT. 2007. The impact of neutrality, niche differentiation and species input on diversity and abundance distributions. *Oikos* 116: 931–940.
- ZUPPINGER-DINGLEY, D., B. SCHMID, J. S. PETERMANN, V. YADAV, G. B. DE DEYN, and D. F. B. FLYNN. 2014a. Selection for niche differentiation in plant communities increases biodiversity effects. *Nature* 515: 108–111.

Table 1. Species association of juvenile and adult trees to a particular slope orientation (N= North and S= South). The species correspond to the 39 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.

ADULTS

JUVENILES	Non-associated	Associated
Non-associated	<i>Bursera fagaroides</i> <i>Bursera laxiflora</i> <i>Chloroleucon mangense</i> <i>Diphysa occidentalis</i> <i>Fouquieria macdougalii</i> <i>Guazuma ulmifolia</i> <i>Ipomoea arborescens</i> <i>Jacquinia macrocarpa</i> <i>Jatropha cordata</i> <i>Jatropha malacophylla</i> <i>Ceiba acuminata</i> <i>Randia echinocarpa</i> <i>Senna atomaria</i> <i>Sp1.</i> <i>Stenocereus sp.</i> <i>Zanthoxylum fagara</i>	<i>Erythrina flabelliformis</i> (N) <i>Haematoxylum brasiletto</i> (N) <i>Lonchocarpus hermannii</i> (N) <i>Lysiloma divaricatum</i> (N) <i>Maclura tinctoria</i> (S) <i>Pachycereus pecten-aboriginum</i> (S) <i>Stenocereus montanus</i> (S)
Associated	<i>Brongniartia alamosana</i> (S) <i>Bursera grandifolia</i> (N) <i>Bursera penicillata</i> (S) <i>Cordia sonorae</i> (S) <i>Croton fantzianus</i> (S) <i>Croton flavescens</i> (S) <i>Hintonia latiflora</i> (N) <i>Karwinskia humboldtiana</i> (N) <i>Sp3.</i> (N) <i>Tabebuia sp.</i> (N)	<i>Acacia cochliacantha</i> (S)* <i>Bursera sp</i> (N)* <i>Coursetia glandulosa</i> (S)* <i>Erythroxylum mexicanum</i> (S)* <i>Randia thurberi</i> (S)* <i>Sebastiania pavoniana</i> (N)*

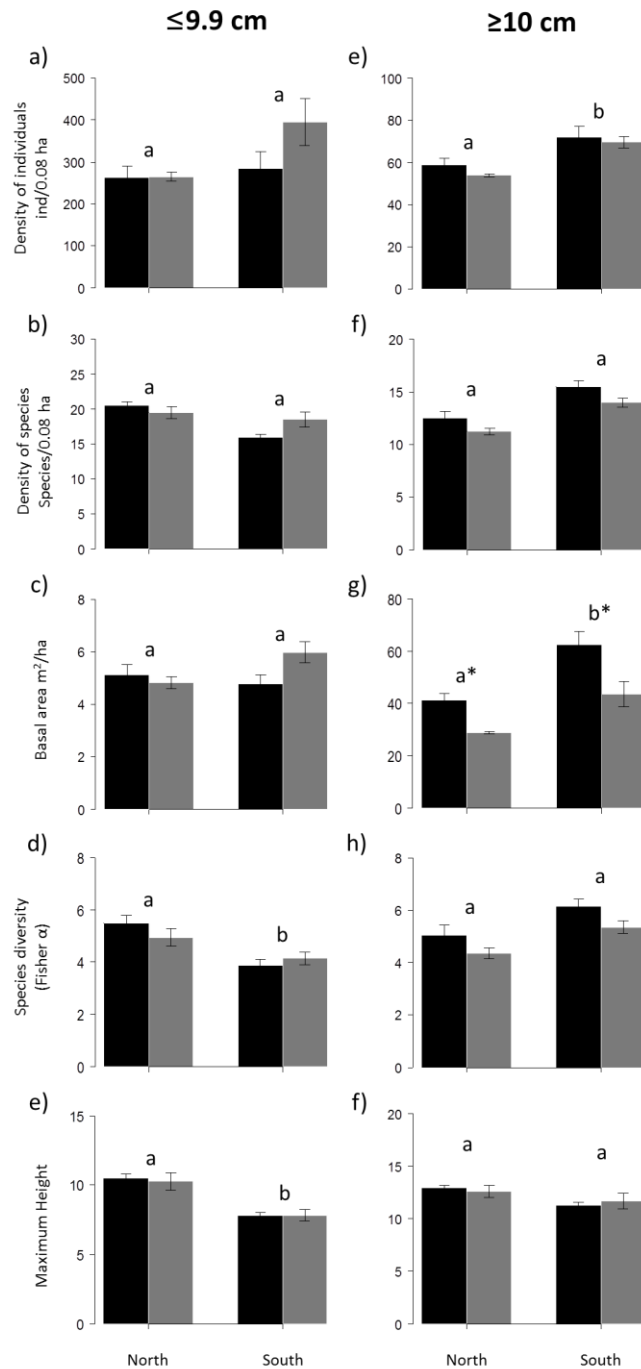


Figure 1. Mean values (\pm SE) of five structural attributes of a TDF tree community in the northwest of Mexico, evaluated between slope orientation: SO (North and South) and topographic position: TP (High and Low, black and gray bars respectively). Significant differences between SO are denoted by different letters, while * indicate differences between TP. The significance was evaluated with a value of $P < 0.05$.

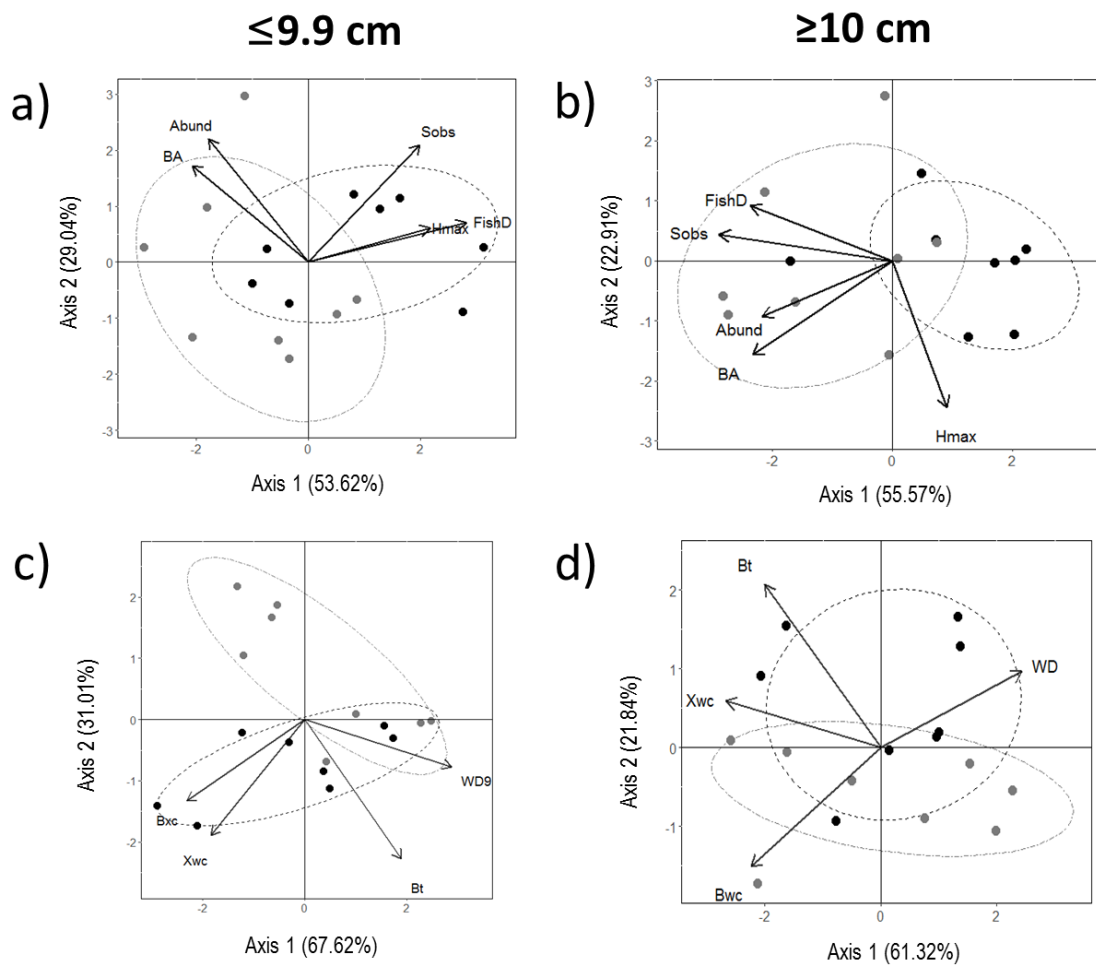


Figure 2. PCA based on structural and functional attributes. Plots of ordination with SO North and South based on structural attributes of a) juveniles and b) adults. The ordination based on functional attributes for c) juveniles and d) adults. The structural attributes: BA (basal area); Abund (density of individuals); Sobs (density of species); Hmax (maximum height); Dfish (Fisher's α). The functional attributes: WD (wood density); Bwc (bark water content); Xwc (xylem water content); Bt (Bark thickness). Ellipses represent 75% confidence level and in each graph the black circles correspond to North sites and while gray circles correspond to South sites.

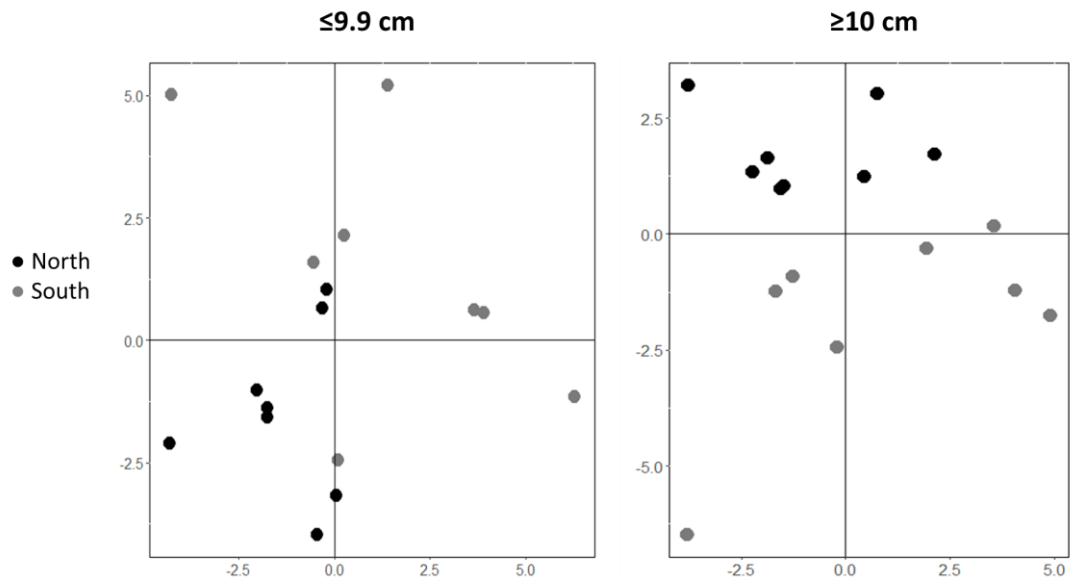


Figure 3. PCA of species abundance of juvenile and adult stages present in 16 sites of 20 x 40m in a TDF to northwest of Mexico with different slope orientation (North and South). $\text{Log}(N + 1)$ was used for species abundance (see methods).

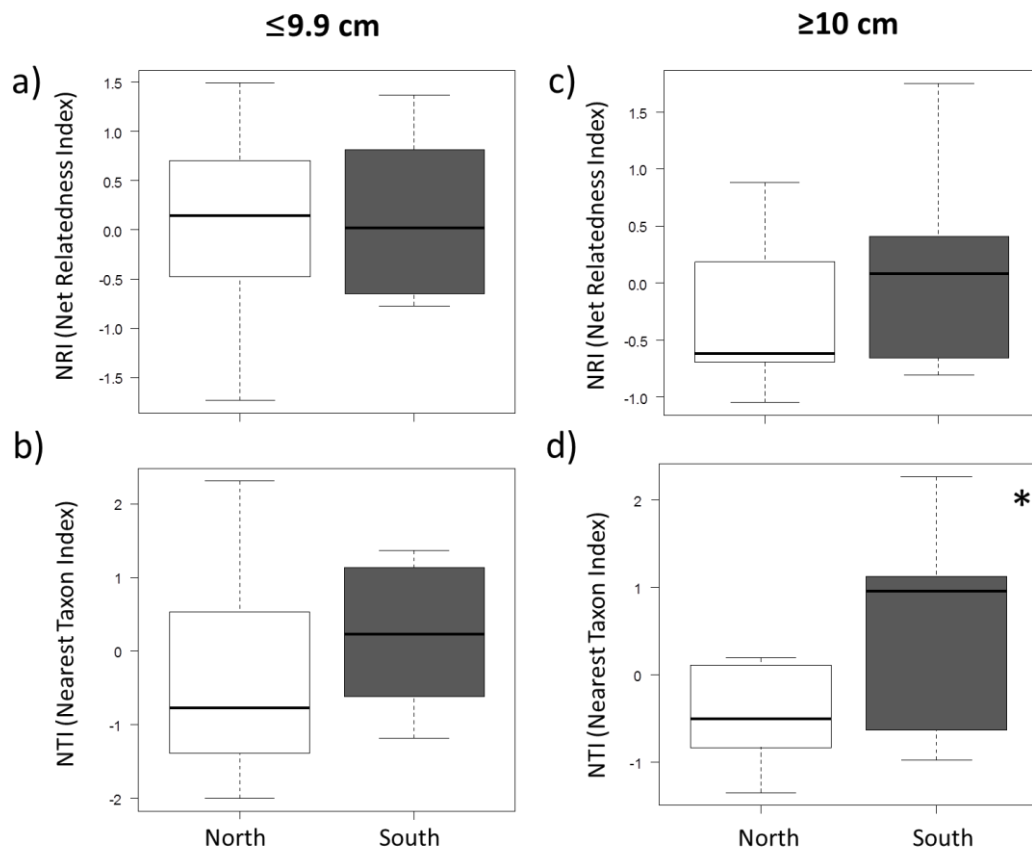


Figure 4. Phylogenetic diversity (mean \pm SD) between juvenile (a, b) and adult (c, d) stages. Significant differences between habitats are denoted with an *.

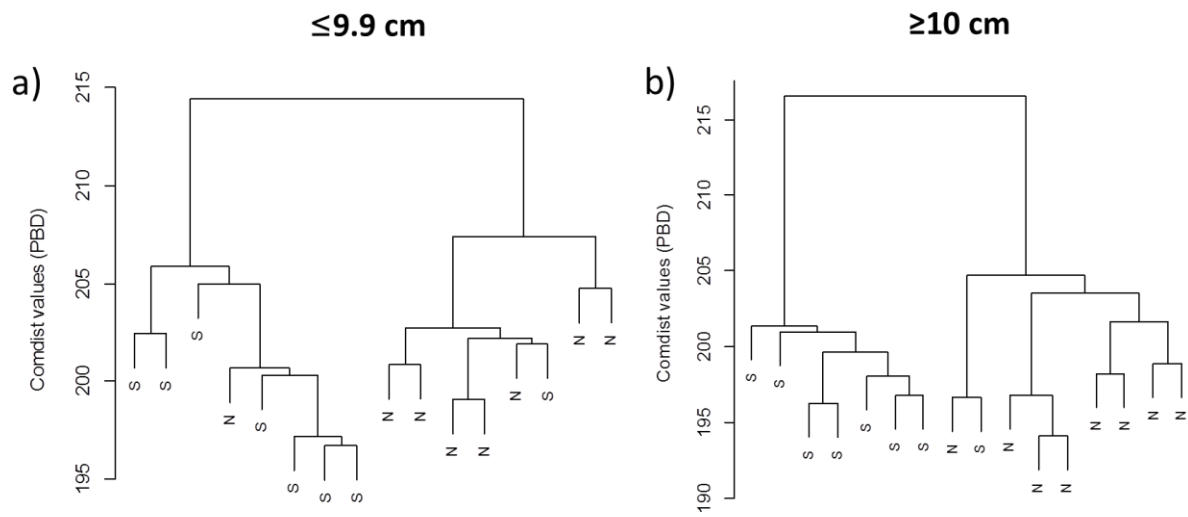


Figure 5. Phylobetadiversity (PBD). a) Dendrogram of dissimilarity between 16 TDF sites of juvenile tree stages (≤ 9.9 cm) and b) adult stages (≥ 10 cm).

**Topographic factors drive taxonomic, functional and
phylogenetic patterns of trees in a tropical dry forest of
Northwestern Mexico.**

Abdieel Quisheuatl-Medina¹, Campbell O. Webb², Moisés Méndez-Toribio³,
Clementina González-Zaragoza¹, Stephen Hubbell & Leonel Lopez-Toledo^{1,4}

¹ Instituto de Investigaciones sobre los Recursos Naturales, Universidad Michoacana
de San Nicolás de Hidalgo, Morelia, Michoacán 58087, México

² University of Alaska Museum of the North, AK, USA

³ Instituto de Ecología, A.C., Red de Diversidad Biológica del Occidente Mexicano, Avenida
Lázaro Cárdenas 253, 61600 Pátzcuaro, Michoacán, México

⁴ Division of Applied Plant Ecology, Institute for Conservation Research, San Diego
Zoo Global, Escondido, California 92027, U.S.A.

Table S1. Density of individuals (ind/0.32 ha⁻¹) of woody species recorded at different physiographic aspects of slope (North and South) in a tropical dry forest in Alamos, Sonora, Mexico. An asterisk reflects the species used in the analysis of this study. Tr=Tree, Sh=Shrub, Ar=Arborescent.

Family/Species	Form	Juveniles		Adults	
		North	South	North	South
Asteraceae					
<i>Montanoa rosei</i>	Tr	1	0	0	0
Bignoniaceae					
<i>Tabebuia impetiginosa</i> *	Tr	256	55	11	10
Bixaceae					
<i>Cochlospermum vitifolium</i>	Tr	1	0	0	0
Bombacaceae					
<i>Ceiba acuminata</i> *	Tr	5	1	8	10
Boraginaceae					
<i>Cordia sonorae</i> *	Tr	12	53	0	4
Burseraceae					
<i>Bursera fagaroides</i> *	Tr	9	8	4	7
<i>Bursera grandifolia</i> *	Tr	31	3	8	6
<i>Bursera laxiflora</i> *	Tr	1	1	0	4
<i>Bursera penicillata</i> *	Tr	17	45	11	25
<i>Bursera spp.</i> *	Tr	11	4	8	0
Cactaceae					
<i>Cylindropuntia thurberi</i>	Sh	0	0	0	1
<i>Pachycereus pecten-aboriginum</i> *	Ar	4	13	18	92
<i>Pilosocereus alensis</i> *	Ar	1	0	0	1
<i>Stenocereus montanus</i> *	Ar	0	1	0	14
<i>Stenocereus thurberi</i>	Ar	0	0	0	8
Celastraceae					
<i>Wimmeria mexicana</i>	Tr	4	1	0	0
Convolvulaceae					
<i>Ipomoea arborescens</i> *	Tr	0	4	2	2
Erythroxylaceae					
<i>Erythroxylum mexicanum</i>	Sh	39	4	17	8
Euphorbiaceae					
<i>Croton fantzianus</i> *	Tr	983	1507	53	52
<i>Croton flavescens</i> *	Sh	132	264	2	3
<i>Jatropha cordata</i> *	Tr	17	11	4	5
<i>Jatropha malacophylla</i> *	Sh	31	50	9	25
Fabaceae					
<i>Acacia cochliacantha</i> *	Tr	6	52	1	11

<i>Lysiloma tergeminum</i>	Sh	47	22	0	0
<i>Brongniartia alamosana</i> *	Tr	30	102	6	16
<i>Chloroleucon mangense</i> *	Tr	0	1	0	1
<i>Conzattia multiflora</i>	Tr	1	0	0	0
<i>Coursetia glandulosa</i> *	Tr	2	114	1	17
<i>Diphysa occidentalis</i> *	Sh	1	6	0	3
<i>Erythrina flabelliformis</i> *	Sh	2	0	4	0
<i>Haematoxylum brasiletto</i> *	Tr	35	45	22	56
<i>Heliocarpus attenuatus</i>	Tr	0	0	1	0
<i>Lonchocarpus hermannii</i> *	Tr	18	25	15	6
<i>Lysiloma divaricatum</i> *	Tr	43	41	194	131
<i>Lysiloma watsonii</i>	Tr	0	0	2	1
<i>Sebastiana pavoniana</i> *	Tr	91	0	20	0
<i>Senna atomaria</i> *	Tr	5	1	0	2
<i>Senna pallida</i>	Sh	39	28	0	0
Fouquieriaceae					
<i>Fouquieria macdougalii</i> *	Tr	8	12	7	5
Lamiaceae					
<i>Vitex mollis</i>	Sh	1	1	0	0
Malvaceae					
<i>Pseudobombax palmeri</i>	Tr	0	0	0	1
Moraceae					
<i>Maclura tinctoria</i> *	Tr	1	6	0	7
Nyctaginaceae					
<i>Pisonia capitata</i>	Sh	0	2	0	0
Opiliaceae					
<i>Agonandra racemosa</i>	Tr	0	1	0	0
Rhamnaceae					
<i>Karwinskia humboldtiana</i> *	Tr	16	5	2	1
Rubiaceae					
<i>Hintonia latiflora</i> *	Tr	40	11	10	11
<i>Randia echinocarpa</i> *	Sh	50	60	3	12
<i>Randia thurberi</i> *	Sh	5	31	0	9
Rutaceae					
<i>Zanthoxylum fagara</i> *	Sh	149	157	3	9
Sterculiaceae					
<i>Guazuma ulmifolia</i> *	Tr	13	9	1	0
Theophrastaceae					
<i>Jacquinia macrocarpa</i> *	Tr	0	4	2	2
ND					
Sp 1*	Sh	7	4	1	0
Sp 3*	Tr	44	14	4	1

Table S2. Results of analysis of variance and deviance evaluating the effect of the physiographic factors of slope orientation and topographic position on the structural attributes of the woody community in two states of life (juveniles and adults). The values of F are provided by the ANOVA and value of χ^2 for GLM's. Significant terms are indicated by an asterisk.

Attributes	Slope orientation		Topographic position	
	F/ χ^2	P	F/ χ^2	P
≤9.9 cm (4839 ind)				
Density of individuals	1.16	0.28	0.63	0.42
Density of species	3.32	0.20	0.25	0.72
Number of stems	3.66	0.05	1.19	0.27
Maximum height	9.53	<0.01*	0.01	0.89
Basal area	0.34	0.56	0.40	0.53
Biomass	0.05	0.81	0.03	0.85
Fisher α	4.47	0.04*	0.05	0.81
≥10cm (1019 ind)				
Density of individuals	5.82	0.01*	0.35	0.55
Density of species	2.48	0.11	0.56	0.45
Number of stems	10.53	0.001*	0.009	0.97
Maximum height	1.59	0.23	0.002	0.96
Basal area	6.23	<0.05*	4.75	<0.05*
Biomass	1.57	0.23	3.50	0.08
Fisher α	3.56	0.08	1.79	0.20

Table S3. Results of ANOVA evaluating the effect of the physiographic factors of slope orientation and topographic position on the functional traits of the woody community in two states of life (juveniles and adults). Significant terms are indicated by an asterisk.

Functional traits	Slope Orientation		Topographic position	
	F	P	F	P
≤9.9 cm				
Wood Density	0.004	0.94	0.68	0.42
Xwc	8.10	0.01*	0.19	0.66
Bwc	3.04	0.10	0.04	0.83
Bt	1.91	0.18	0.69	0.42
≥10cm				
Wood Density	3.88	0.07	0.16	0.68
Xwc	0.59	0.45	0.43	0.52
Bwc	0.40	0.53	0.89	0.36
Bt	2.55	0.13	0.04	0.94

Table S4. 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

PERMANOVA	Slope Orientation		Topographic position		SO:TP	
	R ²	P	R ²	P	R ²	P
≤9.9 cm						
Structural	0.05	0.44	0.04	0.51	0.03	0.58
Functional	0.28	0.03*	0.003	0.95	0.007	0.92
≥10cm						
Structural	0.32	0.009*	0.08	0.19	-0.01	0.99
Functional	0.01	0.89	0.06	0.38	0.03	0.57

Figure S1. Rank-abundance curves of woody species from two life stages of a seasonally dry forest in Alamos, Sonora, Mexico, used to compare regression lines between the different stages of development. The figure represents the total number of species present in each life stage. The six important sea species of each life stage are: Burpen=*Bursera penicillata*, Broala=*Brongniartia alamosana*, Crofan=*Croton fantzianus*, Crofla=*Croton flavescens*, Cougla=*Coursetia glandulosa*, Erymex=*Erythroxylum mexicanum*, Haebra=*Haematoxylum brasiletto*, Hanimp=*Handroanthus impetiginosa*, Hinlat=*Hintonia latiflora*, Jatmal=*Jatropha malacophylla*, Lysdiv=*Lysiloma divaricatum*, Lonher=*Lonchocarpus hermannii*, Pacpec=*Pachycereus pecten-aboriginum*, Ranech=*Randia echinocarpa*, Sebpav=*Sebastiania pavoniana*, Zanfag=*Zanthoxylum fagara*.

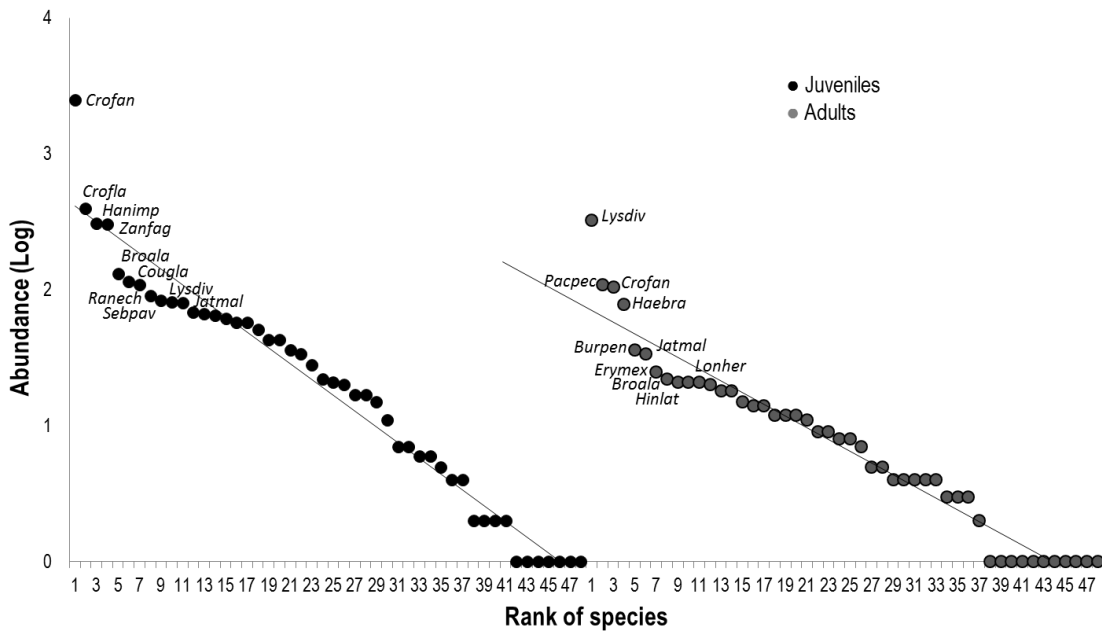


Figure S2. Juvenile-Adult transition patterns mediated through the changes in abundance between one life stage to another, those patterns are contrasted in 16 species distributed between North or South slope orientation in a seasonally dry forest of Alamos, Sonora. Gray squares represent the change in the abundance of a species on South slopes, while black squares represent such changes on North slopes.

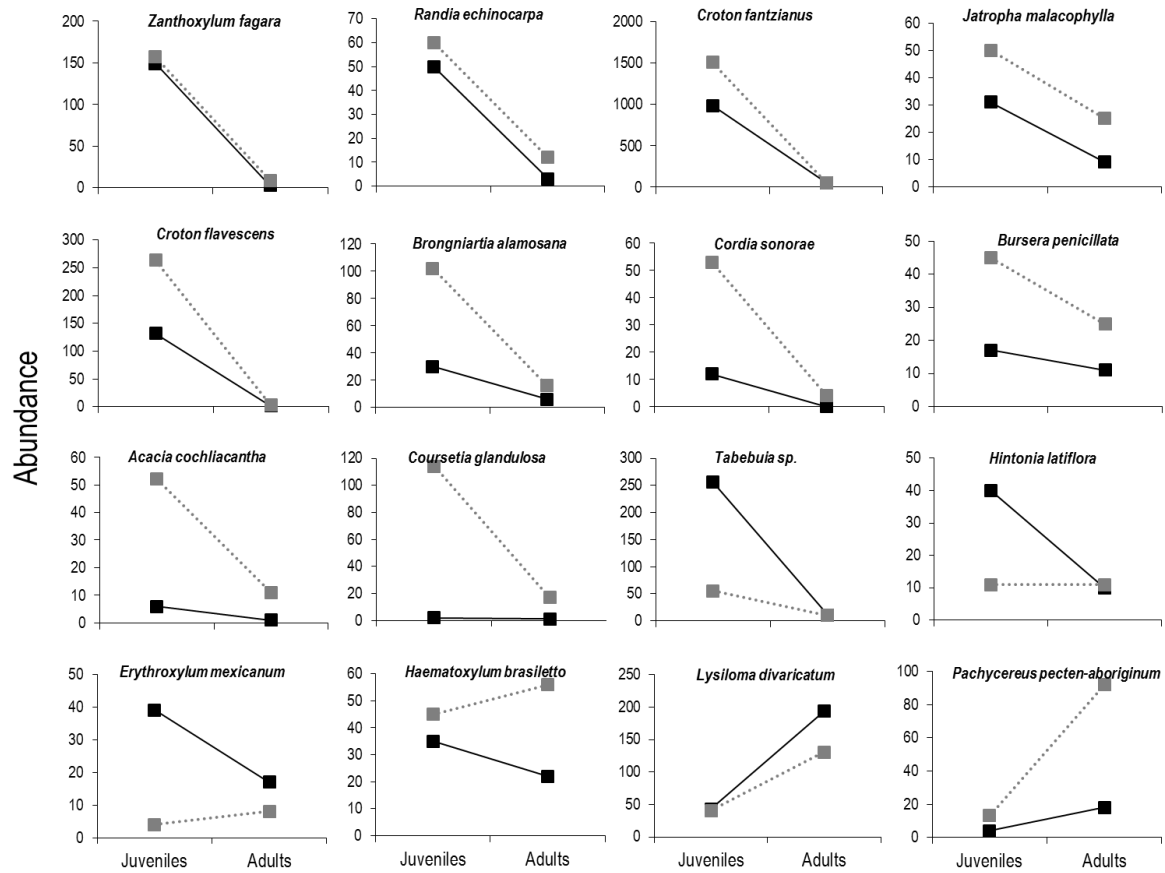


Figure S3. Differences of two functional traits at the plot level (CWM) (CWM), a) Wood density (g/cm^3) and b) Bark thickness (cm), between tree life stages in a seasonally dry forest of Northwest Mexico. Asterisk indicates significant differences ($P < 0.05$) between life stages, using a *t*.student test.

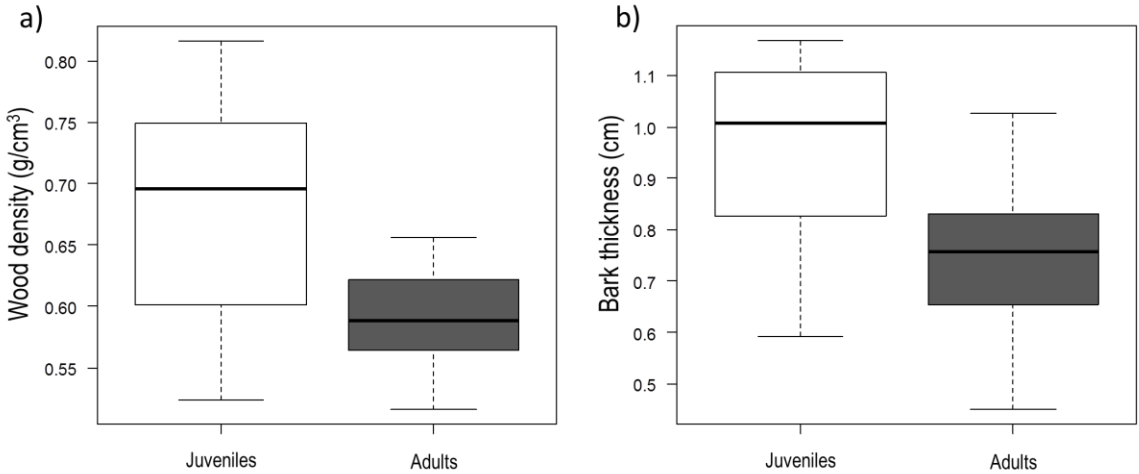


Figure S4. Summary of the composition of the phylogenetic tree assembled through Bayesian Molecular Inference, composed of 105 taxa of trees and shrubs of a TDF in Alamos Sonora, Mexico. The mean estimated dates of the nodes and the scale of the branches are in millions of years (Myr).

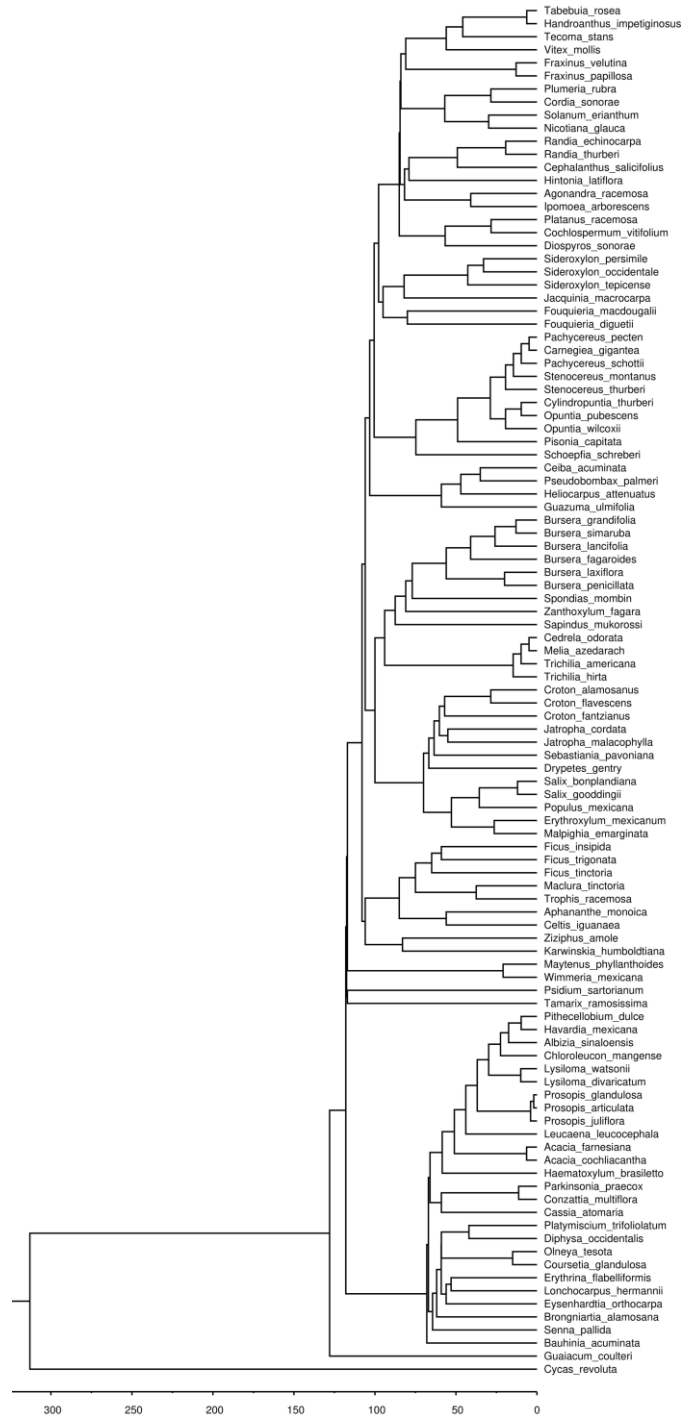


Figure S5. Differences in mean values of solar radiation interception (Mj/m^2) in dry and dry seasons between North and South slopes, letters indicate significant differences between slopes ($P < 0.05$) using a Wilcoxon rank-sum test.

