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**Influencia de la topografía sobre la dinámica
y las estrategias ecológicas de una
comunidad arbórea en un bosque tropical
seco de Michoacán, México**

TESIS

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P R E S E N T A

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1. RESUMEN GENERAL

La topografía juega un papel determinante no solo en la distribución de las especies de plantas en el bosque tropical estacionalmente seco BTES, sino también en la dominancia de ciertas especies, en la diversidad filogenética, la riqueza funcional, la presencia de determinados grupos de rasgos, en la presencia de ciertas estrategias ecológicas y funcionales, y en la dinámica comunitaria que experimentan los árboles que se desarrollan en este tipo de ambientes. Se analizó la importancia de los filtros ambientales impuestos por dos factores topográficos: la orientación de la pendiente (norte y sur) y la posición topográfica (alta, media y baja) en la dinámica, los cambios porcentuales temporales de la estructura y la diversidad, la dominancia o subordinación, la diversidad filogenética, la riqueza funcional y la importancia de ciertos conjuntos de rasgos y estrategias CSR de las especies presentes en una comunidad de árboles en un BTES ubicado en la parte baja de la Cuenca del Balsas, Michoacán, México. La pregunta central de este estudio fue: ¿Cómo afectan los filtros ambientales impuestos por la topografía (orientación de la ladera y posición topográfica), a la dinámica y los cambios porcentuales en la estructura y diversidad, la dominancia, la diversidad filogenética, la riqueza funcional, los conjuntos de rasgos y la presencia de estrategias CSR de una comunidad de plantas de BTES ubicada en la parte Baja de la Cuenca del Balsas, Michoacán, México? A lo largo de los capítulos que componen la tesis, se abordaron los siguientes cuestionamientos: 1) ¿Cómo cambia la dinámica, y la ganancia/pérdida de atributos estructurales y de diversidad de la vegetación en función de los factores topográficos analizados?; 2) ¿Existen especies dominantes o subordinadas y cómo cambia esta dominancia a través de los factores topográficos?; 3) ¿Existe un efecto de los filtros ambientales impuestos por topografía sobre la diversidad filogenética y la riqueza funcional a nivel comunitario?; 4) ¿Ofrecen los conjuntos de rasgos individuales o las estrategias CSR un mejor resumen del funcionamiento de la comunidad de plantas?; 5) ¿Existe correlación entre los rasgos que involucran cantidades de materia y energía con respecto a los valores de las estrategias ecológicas CSR, en función de los factores topográficos estudiados? Con respecto a la dinámica comunitaria, se encontró que la mortalidad y el reclutamiento de árboles fue mayor en las posiciones altas de las montañas en comparación con los sitios más bajos. De manera general, la estructura y la diversidad de la comunidad parecen permanecer estables durante el tiempo. Sin embargo, se presentaron ganancias (%) temporales en el número de tallos e individuos hacia las posiciones bajas, lo cual se encuentra en función de los resultados para la dinámica, y en conjunto con la exposición a un mayor riesgo de sequía para las

plantas que viven en sitios altos; podrían explicar la presencia de este tipo de patrones en donde se interrelacionan la topografía con dichos atributos comunitarios de la vegetación. Por otra parte, se detectaron ocho especies dominantes en la comunidad y cuarenta y siete subordinadas, destacando *Cordia elaeagnoides* como una especie dominante en todos los tratamientos. La diversidad filogenética es mayor en las laderas norte que en la sur, y la riqueza funcional aumenta de forma creciente hacia las posiciones más altas. La vegetación está caracterizada por una selección C a S en el triángulo CSR de Grime, y es predominantemente tolerante al estrés. Los conjuntos de rasgos que mejor explican el funcionamiento de las plantas están relacionados con un eje de variación principal relacionado con el uso y aprovechamiento del agua (contenido de agua en la corteza y el xilema) y la evitación al riesgo de sequía (densidad de la madera y tiempo de retención de la hoja). Las estrategias CSR parecen representar un eje secundario de variación para la comunidad de plantas. Y las relaciones que se establecieron entre los rasgos restringidos, no restringidos y las estrategias CSR se presentaron principalmente entre el contenido de agua en la corteza y el xilema, la densidad la madera y el tiempo de retención de la hoja, con relaciones consistentes hacia sitios con altos niveles de estrés hídrico (posiciones altas y laderas orientadas al sur). Finalmente, los resultados presentados durante los dos capítulos que componen el contenido principal de esta tesis, resaltan la importancia de los filtros ambientales impuestos por la topografía, pero especialmente por la posición topográfica, la cual puede representar ventanas de disponibilidad del recursos hídrico a través del gradiente de elevación, influyendo de manera significativa en los patrones relacionados con la dinámica, la dominancia de las especies, la diversidad filogenética, la riqueza funcional y el espectro de forma y función de las plantas que habitan en el BTES estudiado.

Palabras clave: filogenética, orientación de la ladera, ecología funcional, CSR y ensamblaje comunitario

2. ABSTRACT

Topography plays a determining role not only in the distribution of plant species in the seasonally dry tropical forest (SDTF), but also in the dominance of certain species, in the phylogenetic diversity, the functional richness, the presence of certain groups of traits, in the presence of certain ecological and functional strategies, and in the community dynamics experienced by trees that develop in this type of environment. The importance of the environmental filters imposed by two topographic factors was analyzed: the orientation of the slope (north and south) and the topographic position (lower, middle and upper) in the dynamics, the temporal percentage changes of the structure and diversity, the dominance or subordination, the phylogenetic diversity, the functional richness and the importance of certain sets of traits and CSR strategies of the species present in a tree community in a SDTF located in the lower part of the Balsas Basin, Michoacán, Mexico. The central question of this study was: How do environmental filters imposed by topography (slope orientation and topographic position) affect the dynamics and percentage changes in structure and diversity, dominance, phylogenetic diversity, functional richness, trait sets, and the presence of CSR strategies of a SDTF plant community located in the lower part of the Balsas Basin, Michoacán, Mexico? Throughout the chapters that make up the thesis, the following questions were addressed: 1) How do the dynamics, and the gain/loss of structural attributes and vegetation diversity change based on the topographic factors analyzed?; 2) Are there dominant or subordinate species and how does this dominance change through topographic factors?; 3) Is there an effect of environmental filters imposed by topography on phylogenetic diversity and functional richness at the community level?; 4) Do individual trait sets or CSR strategies offer a better summary of plant community functioning?; 5) Is there a correlation between traits involving quantities of matter and energy with respect to the values of the CSR ecological strategies, based on the topographic factors studied? Regarding community dynamics, it was found that mortality and tree recruitment were higher in the upper positions of the mountains compared to the lower positions. In general, the structure and diversity of the community seem to remain stable over time. However, temporary gains (%) were presented in the number of stems and individuals towards the lower positions, which is based on the results for the dynamics, and together with the exposure to a greater risk of drought for plants that live in upper positions; they could explain the presence of this type of patterns where topography is interrelated with these community attributes of vegetation. On the other hand, eight dominant species in the community and forty-seven subordinate species were

detected, with *Cordia elaeagnoides* standing out as a dominant species in all treatments. Phylogenetic diversity is greater on the northern slopes than on the southern one, and functional richness increases increasingly towards the upper positions. The vegetation is characterized by ‘C’ to ‘S’ selection in Grime's CSR triangle, and is predominantly stress tolerant. The trait sets that best explain plant functioning are related to a main axis of variation related to water use and exploitation (bark and xylem water content) and drought risk avoidance (wood density and leaf retention time). CSR strategies seem to represent a secondary axis of variation for the plant community. And the relationships established between ‘constrained’, ‘unconstrained’ traits and CSR strategies were mainly between bark and xylem water content, wood density and leaf retention time, with consistent relationships towards sites with high levels of water stress (upper positions and south-facing slopes). Finally, the results presented during the two chapters that make up the main content of this thesis, highlight the importance of the environmental filters imposed by topography, but especially by the topographic position, which can represent windows of water resource availability through the elevation gradient, significantly influencing the patterns related to the dynamics, species dominance, phylogenetic diversity, functional richness and the spectrum of form and function of the plants that inhabit the studied SDTF.

3. INTRODUCCIÓN GENERAL

Hasta hace un par de décadas, los estudios sobre comunidades de plantas habían centrado su atención en explicar los cambios en la diversidad y la abundancia de las especies a través de distintas escalas espacio-temporales. Este constante interés predictivo en la distribución de las especies dio como resultado el surgimiento de múltiples modelos, teorías e hipótesis que intentaban explicar los patrones de distribución de la biodiversidad (Lakićević and Srđević 2018). Dentro de las cuales, destacan por su relevancia la "Teoría de Nichos", en la cual el ensamblaje de las especies se concibe como resultado de procesos relacionados con las características ambientales y las interacciones intra/interespecíficas y/o multitróficas (MacArthur and Levins 1967). Y también la "Teoría Neutral" (Hubbell 2001), la cual intenta explicar la coexistencia espacio-temporal de las especies a través de eventos estocásticos donde destacan aspectos como la dispersión, la colonización y las extinciones locales. Estas dos teorías, a pesar de que utilizan argumentos que se contraponen para explicar la coexistencia de las especies, pueden operar a distintas escalas y de manera simultánea, determinando de esa manera la estructuración de las comunidades ecológicas (Chave 2004).

Desde el marco de la biogeografía, se ha propuesto que algunos atributos de la comunidad de árboles, tales como la diversidad, la dominancia, la composición de especies, la biomasa y la cobertura del dosel, se encuentran íntimamente correlacionados con ciertas características ambientales de los ecosistemas, como son las variables climáticas, edáficas y topográficas (Segura et al. 2003). La topografía ha sido planteada como un factor clave en la generación de paisajes forestales heterogéneos. Las características topográficas como la orientación de la pendiente y la posición topográfica, influyen fuertemente en la variación a mesoescala en la química y disponibilidad de agua en el suelo, así como en los niveles de estrés por sequía que experimentan las plantas que se desarrollan en este tipo de ambientes (Chadwick and Asner 2016; Gallardo-Cruz et al. 2009; Segura et al. 2003; Tiessen et al. 1994).

El Bosque Tropical Estacionalmente Seco

De acuerdo con Murphy & Lugo (1986) los BTES se ubican en áreas libres de heladas con una temperatura media anual superior a los 17 °C, precipitación media anual 250-2,000 mm, y la relación anual de evapotranspiración potencial/precipitación normalmente excede la unidad. Generalmente, este tipo de biomas se encuentran bajo climas estacionales similares a los de las sabanas, en donde la sequía suele durar de 4-7 meses, siendo absoluta en algunos años, mientras

que la estación lluviosa puede ser equiparable a la de algunos bosques húmedos del mundo (Janzen 1988; Pennington et al. 2018).

Los bosques tropicales secos varían mucho en estructura, presentan fisonomías que van desde bosques altos y cerrados hasta matorrales cortos con dosel abierto (Toby Pennington et al. 2000). En América Latina, este bioma se encuentra en suelos más ricos y menos ácidos que las sabanas, fertilidad que se ha asociado con desarrollo de una estructura vertical más alta y cerrada, la cual permite evitar con mayor frecuencia a los incendios (Pennington et al. 2018). Por lo regular, los bosques tropicales secos suelen tener una altura y estructura vegetal menos compleja que los bosques húmedos (Murphy and Lugo 1986). Esto debido principalmente a que el desarrollo de la estructura vegetal de los bosques secos se encuentra condicionada, en gran medida, por la disponibilidad de agua que hay en el suelo (Martínez-Yrizar et al. 2000; Segura et al. 2003; Pineda-García et al. 2007; Balvanera et al. 2011; Méndez-Toribio et al. 2016).

Los bosques tropicales secos abarcan el 42 % de las regiones de bosques tropicales y tienen “hotspots” de diversidad en América Central y del Sur, África, Asia Central, India y Australia (Miles et al. 2006). Sin embargo, estimaciones recientes resaltan el hecho de que, en algunos países, queda menos del 10 % de la superficie de su cobertura original, y solo el 8 % están protegidos de manera legal (Wright 2005; Dryflor et al. 2016; Stan and Sanchez-Azofeifa 2019). Se sabe que los bosques tropicales estacionalmente secos del continente americano tienen altos niveles de biodiversidad, contando con hasta 12 grupos florísticos distintos en América Central y del Sur, y el número de especies en rodales varía desde 100 en latitudes altas, hasta más de 1000 cerca del Ecuador (Dryflor et al. 2016; Golicher et al. 2012). La mayoría de los bosques estacionalmente secos neotropicales comparten una gran cantidad de familias y géneros, siendo Fabaceae y Bignoniaceae las familias que usualmente dominan en las comunidades de plantas leñosas y lianas, respectivamente. El género *Handroantus* suele ser el más dominante en estos ecosistemas, otros géneros leñosos predominantes son *Casearia*, *Trichilia*, *Erythroxylum*, *Randia*, *Capparis*, *Bursera*, *Acacia* y *Coccoloba* (Gentry 1995). En el continente americano se distinguen dos grupos de bosques secos, el primero ubicado predominantemente en el norte y que comprende regiones como: México, las Antillas, Centroamérica - norte de Sudamérica y los valles interandinos del norte; y, por otra parte, los bosques secos ubicados predominantemente el sur, que comprenden sitios como: la Caatinga, la región central de Brasil, Misiones, Tarapoto-Quillabamba, Piedmont y Apurímac-Mantaro (Linares-Palomino et al. 2011; Dryflor et al. 2016). Estos dos tipos de bosques secos en

el continente se distinguen principalmente por presentar diferencias florísticas y estructurales. Los grupos florísticos del centro de Brasil, Caatinga y México contienen la mayor cantidad de especies (1344, 1112 y 1072 especies, respectivamente), y los valles interandinos centrales y los valles interandinos de Apurimac-Mantaro contienen la menor cantidad (165 y 78 especies, respectivamente) (Dryflor et al. 2016).

No obstante, la preservación de estos ecosistemas que son importantes en cuanto a su biodiversidad y a los servicios ecosistémicos que prestan (incluidos el almacenamiento de carbono, la conservación de los ciclos de nutrientes y el almacenamiento y suministro de agua), es un tema que aún se encuentra pendiente para el ser humano, el cual representa la principal amenaza debido a una gran variedad de presiones antropogénicas a la que se encuentran expuestos este tipo de ambientes (Miles et al. 2006).

Por otro lado, la productividad primaria neta de los bosques secos del neotrópico parece estar relacionada directamente con la precipitación, con rangos que van desde los 98 Mg ha⁻¹ en los sitios más secos hasta 320 Mg ha⁻¹ en sitios con mayor precipitación (Murphy and Lugo 1995). Sin embargo, evidencias recientes han mostrado que en los bosques secos también se puede presentar mayor productividad primaria en suelos ricos en nutrientes y con baja disponibilidad de agua (Caleño-Ruiz et al. 2023). Asimismo, no existe un patrón claro entre la precipitación y la diversidad en estos ecosistemas, es de decir, los bosques secos más diversos del neotrópico usualmente se encuentran en sitios con menor precipitación (Gentry 1995).

En el caso de los bosques tropicales estacionalmente secos de México, Trejo and Dirzo (2002) ofrecen una descripción general muy completa acerca de los atributos ambientales, estructurales y de diversidad que presenta este ecosistema, el cual tiene su distribución más sureña en Copalita (15°50') en el estado de Oaxaca y alcanza su límite más norteño en Álamos (27°15') en el estado de Sonora (Figura 1). Asimismo, Trejo and Dirzo (2002) señalan que estos ecosistemas regularmente se establecen en sitios con pendientes moderadas a empinadas en los que predominan suelos poco profundos y con abundante afloramiento rocoso. No obstante, los estudios sobre distribución de los bosques secos en México antes de la perturbación antropogénica extensa señalan que vegetaciones espinosas similares ocuparon tierras más bajas con suelos más profundos (Rzedowski 2006). La precipitación anual total tiene un rango que va desde los 450 mm en Cosalá-Sinaloa a los 1,370 mm en las Flores-Tamaulipas, la temperatura media anual oscila entre 19-27.4°C y en Infiernillo-Michoacán se localiza el bosque seco más caliente del país (27.4°C). La

evapotranspiración potencial tiene un rango que fluctúa a partir de los 935.9 hasta los 1,691.8 mm (Thornthwaite index) siendo Caleta-Michoacán el sitio donde hay mayor evapotranspiración.

La riqueza de especies de plantas en los bosques secos mexicanos (árboles con DAP ≥ 1 cm en 0.1 ha) se ha estimado entre 29 y 123 especies, siendo los sitios que se encuentran en la costa del Pacífico aquellos con mayor diversidad y Caleta-Michoacán el sitio más rico en especies. El número promedio de familias es 32, de géneros 61 y de especies es 74, respectivamente. Asimismo, no existe una relación directa entre la precipitación y la diversidad, pero si con la evapotranspiración, en donde existe una mayor diversidad de especies en sitios con mayor disponibilidad de agua para las plantas (Trejo and Dirzo 2002).



Figura 1. Extensión y distribución de los bosques tropicales secos mexicanos (Fuente: CONABIO).

La topografía y el gradiente de sequía

Es bien sabido que las condiciones climáticas y geológicas a escala local, en teoría, presentan características homogéneas. No obstante, existen factores abióticos como la topografía (Orientación de la Pendiente: OP y la Posición Topográfica: PT), que condicionan la distribución de la radiación solar, los procesos hidrológicos y la exposición a los disturbios que experimentan las comunidades de plantas (Segura et al. 2003; Suzaki et al. 2005; Méndez-Toribio et al. 2017). Por un lado, se ha postulado que, en el hemisferio norte del planeta, las laderas orientadas hacia el sur reciben mayor radiación solar que las que miran hacia el norte (Holland and Steyn 1975). Esta

distribución no equitativa de la radiación con respecto a la orientación, influye sobre los patrones de diversidad de especies, la estructura vegetal y la dinámica de las comunidades de plantas, especialmente en los BTES, debido a principalmente a que generan gradientes de disponibilidad de agua y riesgo de sequía para las plantas que modifican los patrones de estos atributos de la vegetación (Galicia et al. 1999; Segura et al. 2003; Gallardo-Cruz et al. 2009; Balvanera et al. 2011; Méndez-Toribio et al. 2016). Sin embargo, se ha señalado que no solo las condiciones locales como la OP inciden en los niveles de radiación que recibe una montaña, sino también su posición latitudinal en la Tierra es un factor determinante de la radiación solar que reciben (Holland and Steyn 1975; Galicia et al. 1999). Es quizás por esta razón que no existen generalizaciones puntuales acerca cómo la OP influye sobre las comunidades vegetales (Gallardo-Cruz et al. 2009).

De igual manera, se ha planteado que la posición topográfica (es decir, la altura relativa que hay desde la base de una montaña hasta la parte más elevada) ejerce una fuerte influencia sobre el régimen de temperatura, la incidencia de la radiación solar, el almacenamiento de carbono, la disponibilidad de agua en el suelo y la perturbación antropogénica (Yimer et al. 2006; Zhu et al. 2014; Méndez-Toribio et al. 2016; Abebe et al. 2020). La disponibilidad de agua para las plantas parece ser uno de los principales impulsores de los cambios en la estructura, la diversidad, las estrategias funcionales de las plantas y la dinámica en las comunidades de plantas (Western 1975; Yang et al. 2011; Nielsen et al. 2019); especialmente para el bosque tropical estacionalmente seco, en donde, al agua se le considera un recurso sumamente importante dada su limitación espacial y temporal (Trejo and Dirzo 2002; Segura et al. 2003; Gallardo-Cruz et al. 2009; Suresh et al. 2010; Balvanera et al. 2011; Carvalho and Felfli 2011; Markesteijn et al. 2011; Méndez-Toribio et al. 2017, 2020). Y como tal, a ésta se le ha relacionado con la altitud como resultado de dos procesos principales (Gallardo-Cruz et al. 2009).

Por un lado, la evapotranspiración disminuye hacia las partes altas como resultado de la presencia de menores niveles de temperatura, reduciendo de esta manera la cantidad de agua disponible para las plantas en estas zonas (Gallardo-Cruz et al. 2009; Méndez-Toribio et al. 2016). Por otra parte, los sitios con mayor pendiente suelen tener menor disponibilidad de agua que los sitios planos, dado que tienen mayores salidas de ésta por escorrentía superficial y sub-superficial. Además, la escorrentía impulsada por el efecto de la gravedad de la Tierra provoca que se acumule mayor cantidad de agua en las partes bajas que en las altas (Gallardo-Cruz et al. 2009; Balvanera et al. 2011).

Por lo general, las posiciones altas y las laderas con orientación hacia el sur de las montañas se caracterizan por ser sitios con baja humedad y alta evapotranspiración del suelo debido a que se encuentran mayormente expuestos a la radiación solar, con respecto a las posiciones bajas y laderas con orientación norte (Galicía et al. 1999; Bellinghami and Tanner 2000; Segura et al. 2003; Gallardo-Cruz et al. 2009; Méndez-Toribio et al. 2016, 2017). En virtud de lo anterior, se ha propuesto que estas condiciones ambientales pueden incidir en los procesos relacionados con la diversidad de especies, así como con la estructura y dinámica de la comunidad de plantas (Bellinghami and Tanner 2000; Segura et al. 2003; Méndez-Toribio et al. 2016). La presencia o dominancia de plantas con ciertas estrategias ecológicas también pueden ser afectadas por este tipo de gradientes ecológicos (Pierce et al. 2013, 2017; Janssen et al. 2020).

Todo lo anterior sugiere que las especies de bosque tropical seco muestran patrones de distribución no aleatorios a lo largo de gradientes topográficos y de disponibilidad del agua (Quiséhuatl et al. 2023). No obstante, los estudios que abordan el efecto de la topografía sobre atributos comunitarios como la dinámica vegetal o las estrategias ecológicas de las especies en este ecosistema, aún son muy incipientes. En el caso del BTES de Tziritzícuaru, ubicado en la parte baja de la cuenca del Balsas en Michoacán-México, se sabe que en el sitio existen al menos 78 especies de plantas leñosas ($DAP \geq 1$ cm) distribuidas en 50 géneros y 24 familias. La familia Fabaceae es la que se encuentra mejor representada en la zona, contando con 24 especies y 14 géneros diferentes. Asimismo, las familias Burseraceae, Euphorbiaceae y Rubiaceae son importantes en cuanto al número de especies que albergan en la zona. En cuanto a la estructura del BTES, se sabe que es estructuralmente similar a otros bosques secos ubicados en el Neotrópico con una altura promedio de 5 m, un área basal de $18 \text{ m}^2 \text{ h}^{-1}$ y una cobertura del dosel de cd. 300% lo que indica una superposición considerable en las copas de los árboles (Méndez-Toribio et al. 2014).

Además, una parte importante del trabajo realizado en la zona de Tziritzícuaru, se ha relacionado con los gradientes ambientales, más específicamente la topografía, en donde a la orientación de a la ladera y a la posición topográfica, se les consideran como los factores topográficos más importantes. Actualmente sabemos que las laderas orientadas al sur en nuestro sitio de estudio son generalmente más secas y calientes [Temperatura Media Anual (MAT): 26,8 °C, Evapotranspiración Potencial (ET_0 del mes más húmedo: 224 mm e Índice de Humedad Topográfica (TWI): 5,1], que las laderas orientadas al norte (MAT: 25,8 °C, ET_0 :246, TWI: 5,7). Las partes altas de las montañas representan sitios más secos, menos calientes y son menos

propensos a la perturbación humana [MAT: 25,9 °C, ET₀: 231 mm y TWI: 4.1, Índice de Ganadería (CRI): 0.49], en comparación con las partes bajas (MAT:26.6 °C, ET₀: 245 mm: TWI: 6.9, CRI: 0.67) (Méndez-Toribio et al. 2016). Por lo tanto, la OP y la TP representan en nuestro sitio de estudio gradientes de disponibilidad de agua y riesgo de sequía para las plantas, que van desde sitios con alta humedad del suelo y evapotranspiración (por ejemplo, partes bajas y orientadas al N), hasta sitios con baja humedad del suelo y evapotranspiración (p. ej., partes altas y orientadas al S) (Méndez-Toribio et al. 2020). En relación con las características del suelo de nuestro sitio de estudio, las posiciones bajas presentan niveles más altos del Índice de Humedad Topográfica (TWI), en comparación con las partes altas, lo que se ha relacionado con un posible aumento de la profundidad del suelo y la reducción del contenido de roca en estos sitios, estas características del suelo en conjunto implicarían no sólo un mayor riesgo de sequía sobre el suelo en las partes altas, sino también debajo de él para las plantas que viven en estos microambientes (Méndez-Toribio et al. 2017).

Con relación al efecto que ejerce la topografía (OP y PT) sobre ciertos atributos comunitarios en el BTES de Tziritzicuaró. Lo que se sabe es que las especies presentes en las partes altas presentan rasgos funcionales que indican la presencia de estrategias “oportunistas” (presentando mayores niveles de contenido de agua de la corteza, grosor de la corteza, longitud del pecíolo y pubescencia de la hoja), del tal modo que, al desprenderse de sus hojas o al usar agua almacenada en sus tejidos las especies que coexisten en estos ambientes tienden a evitar la desecación. En contraparte, las especies en las partes bajas presentan rasgos relacionados con una estrategia de “tolerancia a la sequía” (presentando mayores niveles en la densidad de la madera, el pulvini de la hoja, el contenido de materia seca de la hoja y tiempo más prolongados de retención de la hoja), características que pueden representar para las especies de las partes bajas una ventaja adaptativa en entornos temporalmente heterogéneos con largos episodios de sequía y cortos períodos de crecimiento (Méndez-Toribio et al. 2017). Además, se ha encontrado evidencia de que estos rasgos funcionales están estrechamente relacionados con ciertas características del ambiente, como son: la humedad topográfica y el potencial de evapotranspiración; generando gradientes de riesgo de sequía para las plantas que van desde sitios más secos en las partes altas, hasta sitios más húmedos ubicados en las partes bajas. Este desacoplamiento de las condiciones estresantes causadas por la aridez del suelo y la atmósfera en conjunto con las diferentes adaptaciones presentadas por

las especies a estas condiciones ambientales podrían explicar los patrones de estrategias funcionales presentados por la vegetación de nuestro sitio de estudio (Méndez-Toribio et al. 2020).

Estrategias ecológicas en las plantas

Las plantas vasculares representan uno de los reservorios más importantes de materia y energía que existen en todos los ecosistemas terrestres (Field et al. 1998). La lucha darwiniana a la que se ven sometidas la gran variedad de especies por crecimiento, reproducción y supervivencia, han dado origen a una gran variedad de formas y funciones (Díaz et al. 2016). Sin embargo, durante los últimos dos siglos se ha pensado que pese a esta notable variación en las características de las plantas vasculares, pueden existir notables patrones de radiación evolutiva, y que, algunos conjuntos de rasgos son viables y exitosos, mientras que otros no lo son (Díaz et al. 2016; Grime 1974; Niklas 1997; Warming 1909).

Dentro de las teorías que se centran en las estrategias ecológicas de las plantas, destacan por su importancia la selección del continuo r (colonización) versus k (explotación) (Southwood 1977), la selección de adversidad o “selección A” (Greenslade 1983), el continuo adquisitivo-conservador (Lavorel et al. 2004; Reich et al. 1997), el espectro económico de la hoja (Wright et al. 2004) y las estrategias CSR de Grime (1974). En ese sentido, la teoría CSR, ha sido propuesta como un marco de referencia para la clasificación de las estrategias funcionales de las plantas que existen en los diferentes ecosistemas a nivel mundial. Esta teoría propone que la clasificación funcional vegetal se puede predecir y explicar por medio de las diferencias en la intensidad del estrés (condiciones que restringen la producción de biomasa) y la perturbación (destrucción parcial o total de la biomasa) a las que están expuestas las plantas en un sitio determinado (Grime 1977).

Originalmente, Grime (1974) clasificó a las tres estrategias funcionales de plantas (C, S y R) con base en una larga lista de atributos funcionales, entre los cuales destacan (por su importancia): la altura del dosel, la dispersión lateral, la acumulación de hojarasca y la tasa de crecimiento relativa en la etapa de plántula. Por un lado, las especies clasificadas en la dimensión C, se ordenan en los gráficos ternarios de acuerdo con un índice de “competencia” o “morfología” compuesto por la altura del dosel, dispersión lateral y acumulación de la hojarasca. Las especies de la dimensión S, se ordenan de acuerdo con la tasa máxima de crecimiento relativo en la fase de plántula. En el caso de las especies de la dimensión R, originalmente no se intentó una ordenación explícita, sin embargo, se caracterizan por destinar la mayor cantidad de recursos en altas tasas de reproducción (Hodgson et al. 1999).

Posteriormente, el esquema CSR sufrió algunas modificaciones, lo cual dio como resultado una clave dicotómica para clasificar a las especies en una de las tres estrategias primarias (C, S o R), o una de las cuatro secundarias (CR, SR, SC o CSR), o una de las doce terciarias (C/CR, C/CS, C/CSR, CR/CSR, CS/CSR, CS/CSR, R/CR, S/CS, R/CSR, S/CSR, SR/CSR, R/SR y S/SR), dando como resultado un total de 19 tipos funcionales diferentes de plantas (Grime 1974, 1977; Hodgson et al. 1999). Además, a los cuatro atributos principales de selección original se le sumaron la fenología y el recambio de las hojas de las especies (Grime et al. 1988).

Posteriormente se propuso una segunda versión del esquema CSR la cual fue denominada “estándar de oro”, debido a que las subsecuentes ordenaciones se supeditaron a coincidir al máximo con las puntuaciones CSR propuestas por Grime et al. (1997). De esa manera, el “estándar de oro” para la dimensión C, se estructuró con base en la abundancia relativa de las especies, presentando los valores más altos de esta dimensión en hábitats productivos y no perturbados. En el caso del “estándar de oro” de la dimensión R, se basó en la abundancia relativa media de especies monocárpicas (geófitas, anuales y bianuales). El “estándar de oro” de la dimensión S, fue determinado por las cargas y puntajes del primer eje del PCA de 67 rasgos en 43 especies de plantas británicas, relacionados con características adquisitivas de recursos frente a una estrategia conservadora (Li and Shipley 2017).

Con el objetivo de simplificar el “estándar de oro”, se planteó una tercera versión del modelo CSR, en la cual Hodgson et al. (1999) usando ecuaciones de regresión, propusieron seleccionar solamente variables relevantes y fáciles de medir. Por lo tanto, los 67 rasgos que se consideraban para predecir los puntajes del PCA se redujeron a solo 7 (altura del dosel, extensión lateral, peso seco de la hoja, contenido de materia seca de la hoja, área foliar específica, período de floración y punto de inicio de la floración). Sin embargo, este nuevo método contaba con ciertas inconsistencias, quizás la más importante, era que no permitía la comparación directamente de formas de vida de árboles altos con formas de vida más pequeñas (Pierce et al. 2013). Y, además, requería de datos fenológicos que son difíciles de obtener en especies diferentes a las europeas, lo cual complicaba su uso/aplicación en floras de otros continentes.

Considerando todo este contexto, Pierce et al. (2013) propusieron un nuevo método de ordenación CSR más asequible y general, basado en solo tres rasgos foliares fáciles de medir (área foliar: LA, área foliar específica: SLA y contenido de materia seca de la hoja: LDMC). Por un lado, al LA se le definió como un determinante de la capacidad para interceptar luz y representaba el

espectro del tamaño de la planta; al LDMC y al SLA se les asoció con la retención de nutrientes y con las tasas de asimilación/crecimiento, que representaban la estrategia conservadora vs economía adquisitiva de los recursos. Esta nueva herramienta “StrateFy” propuesta por Pierce et al. (2013, 2017) se calibró globalmente, lo cual implicaba que los valores CSR no se calculaban directamente de los rasgos foliares. Es decir, a partir de la relación entre estos rasgos en comparación con el espectro global (posición a lo largo de los ejes multivariados basados en los rangos globales de valores de rasgos), es como se calcula cada valor CSR, proporcionando de esta manera una comparación cuantitativa con respecto a la flora global (Pierce et al. 2017).

Actualmente, la clasificación CSR (Pierce et al. 2013, 2017) se ha utilizado para describir las estrategias ecológicas que presentan las plantas en diferentes escalas espaciales, que van desde lo regional (Novakovskiy et al. 2016, 2021; Rosenfield et al. 2019; Han et al. 2021), a lo local (Rosado and de Mattos 2017; Rosenfield et al. 2019; Araujo da Costa et al. 2020; Janssen et al. 2020). Asimismo, el método de clasificación CSR Grime (1974) propuesto por Pierce et al. (2013) (StrateFy), se ha utilizado para caracterizar las estrategias funcionales de las plantas en diferentes ecosistemas, como el bosque costero de planicie de arena (Araujo da Costa et al. 2020), la selva tropical de tierras bajas (Chen et al. 2022; Wen et al. 2022), el bosque de coníferas (Han et al. 2021), y los bosques subtropicales (Rosenfield et al. 2019), así como en diseños experimentales de laboratorio (Li and Shipley 2017). También se han explorado las relaciones entre las estrategias ecológicas de las plantas con respecto a algunos gradientes ambientales, como la sucesión ecológica (Zanzottera et al. 2020; Chen et al. 2022; Wen et al. 2022), la fertilidad y perturbación del suelo (Li and Shipley 2017), y la elevación e inundación (Janssen et al. 2020).

No obstante, hasta la fecha aún no existen estudios que aborden puntualmente, por un lado, el dominio y la variación de las estrategias ecológicas (CSR) en los bosques tropicales secos. Y, por otro lado, tampoco se ha explorado la fuerza que tiene el filtrado ambiental en la estructuración de las estrategias ecológicas (CSR) a través de gradientes ambientales a mesoescala impuestos por la topografía (i.e. orientación y posición). En este estudio, se determinó el efecto que tienen algunos elementos topográficos del paisaje (orientación de la ladera y posición topográfica) sobre la dinámica de la comunidad y sobre el dominio o variación de las estrategias ecológicas de la comunidad arbórea de un bosque tropical estacionalmente seco (BTES) de Michoacán. Esta región ubicada en la parte Baja de la Cuenca del Balsas al Occidente de México, presenta una amplia variedad de características fisiográficas, geológicas y topográficas que a su vez generan una

variación tanto a nivel macro como microclimática a la cual las especies arbóreas responden (Martínez-Cruz et al. 2013).

La tesis está dividida en 8 secciones (Resumen general, Abstract, Introducción general, Objetivos, Hipótesis, Discusión general y conclusiones, Bibliografía general y Anexos); y 2 capítulos principales, los cuales se describen a continuación:

Capítulo 1. “*La topografía influye en la dinámica arbórea de un bosque seco tropical en el occidente de México*”. En este capítulo se muestra el efecto que ejercen dos condiciones topográficas (OP y PT) sobre tres atributos de la dinámica vegetal (composición, estructura y diversidad), siete atributos de la estructura (altura, área basal, cobertura, número de tallos e individuos, porcentaje de individuos multitallos y diámetro de a la altura del pecho), y tres atributos de la diversidad (número efectivo de especies del orden q_0 , q_1 y q_2), así como los cambios porcentuales temporales (Δ) de las variables de estructura y diversidad; en una comunidad de plantas leñosas localizada en la parte baja de la Cuenca del Balsas Michoacán, México. En este capítulo explicamos la importancia de los estudios a larga plazo, especialmente en un ecosistema poco estudiado como es el caso del BTES, así como la forma en como la topografía impone el filtrado ambiental y esto modifica los patrones relacionados principalmente con la dinámica comunitaria del BTES anteriormente mencionado.

Capítulo 2. “*Los rasgos restringidos vs no restringidos gobiernan el ensamblaje comunitario en un bosque tropical estacionalmente seco*”. En este capítulo se exploró el efecto que ejercen los gradientes ambientales asociados a dos condiciones topográficas (OP y PT), sobre la estructuración de las estrategias ecológicas relacionadas con dos conjuntos de rasgos funcionales, “rasgos restringidos” (contenido de materia seca de la hoja, área foliar, área foliar específica, masa de semillas, altura, contenido de agua de la corteza y xilema, densidad de la madera y el tiempo de retención de la hoja); versus “rasgos no restringidos” (tiempo de desarrollo y tamaño del fruto, viabilidad y germinación de las semillas y la fenología frutal). Asimismo, se exploró el efecto que tiene la topografía sobre otros atributos comunitarios como la diversidad filogenética y la riqueza funcional, y las relaciones que se establecen entre estos dos atributos con respecto a las estrategias ecológicas (C, S y R) y los rasgos funcionales individuales. Como modelo de estudio se utilizó una comunidad de plantas de bosque tropical estacionalmente seco ubicada en la parte baja de la cuenca del Balsas, en Michoacán- México. En este capítulo destacamos la importancia de los rasgos funcionales relacionados con el manejo del estrés hídrico para las plantas que desarrollan su ciclo

de vida, y resaltamos la importancia de los filtros ambientales en la estructuración de patrones relacionados con las estrategias ecológicas, la diversidad filogenética y la riqueza funcional de las plantas de un BTES.

4. OBJETIVOS

A continuación, se presentan los objetivos particulares de los dos artículos originales (capítulos I y II), en los cuales se centran los aspectos de investigación más significativos de esta tesis:

➤ **Capítulo I:**

1. Evaluar el efecto que ejercen los filtros ambientales impuestos por dos condiciones topográficas (OP y PT) sobre la mortalidad, el crecimiento y el reclutamiento de plantas en un BTES ubicado en la parte baja de la cuenca del Balsas, Michoacán,
2. Examinar el efecto de la topografía sobre los cambios temporales de la diversidad y estructura de la comunidad de plantas de un BTES ubicado en la parte baja de la cuenca del Balsas, Michoacán.

➤ **Capítulo II:**

1. Determinar las relaciones entre los rasgos funcionales que involucran cantidades de materia economía/tamaño ('rasgos restringidos'), los rasgos que no involucran cantidades de materia ('rasgos no restringidos') y las estrategias ecológicas (C, S y R), y la forma en cómo varían estas relaciones con respecto a los filtros ambientales impuestos por dos condiciones topográficas (OP y PT); en una comunidad de plantas leñosas de BTES ubicada en la parte baja de la cuenca del Balsas, en Michoacán, México.
2. Determinar las relaciones que existen entre la dominancia y subordinación de las especies, la diversidad filogenética y riqueza funcional, las estrategias ecológicas CSR y los rasgos funcionales únicos, con respecto a los filtros ambientales impuestos por dos condiciones topográficas (OP y PT); en una comunidad de plantas leñosas de BTES ubicada en la parte baja de la cuenca del Balsas, en Michoacán, México.

5. HIPÓTESIS

Dadas las anteriores consideraciones teóricas, en el presente estudio establecemos las siguientes hipótesis para cada capítulo:

Capítulo I: Debido al mayor estrés hídrico que representan los sitios ubicados en posiciones altas y en pendientes con orientación sur, se presentarán mayores niveles de mortalidad, menor crecimiento y reclutamiento en estos sitios en comparación con su contraparte ambiental, es decir, los sitios más húmedos ubicados en las posiciones bajas y con pendientes orientadas al norte. Asimismo, debido a la alta heterogeneidad ambiental dada por la posición topográfica, en las partes altas de las montañas se presentarán mayores ganancias porcentuales en los valores de diversidad de especies y la densidad total de tallos e individuos.

Capítulo II: Debido a que los rasgos funcionales que involucran un intercambio importante de materia y energía (rasgos restringidos) son esenciales en la presencia de determinadas estrategias ecológicas en las plantas de manera global, en el BTES que utilizamos como modelo de estudio, estos ‘rasgos restringidos’ se correlacionarán con los valores C, S y R; mientras que los rasgos ‘no restringidos’ serán independientes de estos. Con respecto a la topografía, dadas las condiciones de estrés hídrico por encima y debajo del suelo asociadas a las partes altas y laderas orientadas al sur en estos sitios, se presentará una mayor cantidad de especies subordinadas en comparación con las dominantes. También se presentará mayor diversidad filogenética y riqueza funcional en los sitios que representan mayor heterogeneidad ambiental, es decir, posiciones altas y laderas orientadas al sur. Las estrategias CSR ofrecerán un mejor resumen del funcionamiento de la comunidad de plantas que los rasgos funcionales únicos por separado.

Topography influences the tree dynamics of a tropical dry forest in western Mexico

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Abstract

In seasonally dry tropical forests (SDTF's) drought risk driven by topography-related factors determines vegetation structure, functional composition, and species diversity; however, the effect of slope aspect and topographic position on tree community dynamics are still poorly explored. In this paper, we studied the dynamics and structural attributes of the tree community of a Mexican SDTF. Plots were established in a combination of two topographic conditions: slope aspect (north/south) and topographic position (upper/middle/lower). Differences among these conditions were assessed through (i) community dynamics' parameters, (ii) species dynamics, (iii) vegetation structure, and (iv) species diversity. We analyzed community attributes for each of our study years (2012–2020) and rates of change between this period for the entire community (DBH ≥ 1 cm), small-sized trees (DBH ≤ 3 cm), and large-sized trees (DBH > 3 cm). Multivariate analyses were also used to examine the relationship between vegetation and topography. In upper positions, trees showed higher mortality (mean $mr \pm SE = 3.1 \pm 0.2\% \text{ yr}^{-1}$) and lower recruitment rates (mean $rr \pm SE = 6.3 \pm 0.9\% \text{ yr}^{-1}$) than those from the lower positions (mean $mr \pm SE = 1.7 \pm 0.1\% \text{ yr}^{-1}$; mean $rr \pm SE = 7.7 \pm 0.7\% \text{ yr}^{-1}$). The relative change (%) in the number of individuals for the entire community and small-sized trees increased towards the lower positions. The entire community showed a temporary loss of stems on south-facing slopes, but temporary gains in number of stems in lower positions for the small-sized trees. We did not find any temporary changes in species diversity attributes. The drought risk gradient imposed by topographic position influences the tree dynamics with a higher mortality of stems/individuals towards upper positions, but species diversity was maintained.

KEYWORDS

community dynamics, drought risk gradients, environmental filters, slope aspect

1 | INTRODUCTION

Topographic variability plays a determining role in the distribution of woody species in tropical forests. In the Northern Hemisphere, the slopes oriented towards the Equator (south-facing) generally have higher levels of drought and evapotranspiration, which are a consequence of greater insolation than the north-facing slopes (Galicia et al., 1999). Because these microclimatic conditions can represent inherent barriers to environmental filtering, it has been suggested that there may be a delimitation of species distribution towards a specific habitat (Olivero & Hix, 1998; Quisehuatl-Medina et al., 2023). Hence, plant species established on south-facing slopes tend to exhibit lower rates of growth, recruitment, and higher tree mortality than those established on north-facing slopes (Bellinghami & Tanner, 2000; Hu et al., 2018; Yang et al., 2006), which thus affects community dynamics and vegetation attributes.

This same principle applies to topographic position (TP), with the upper mountain sites being colder and drier with shallower soils and greater exposure to natural disturbances (e.g., slope exposure to wind currents and hurricanes) than those of lower topographic positions (Bellinghami & Tanner, 2000; Ferry et al., 2010; Méndez-Toribio et al., 2016). Therefore, in general, trees at the upper sites show higher mortality, lower recruitment rates, and slower growth (Adams et al., 2014; Bentos et al., 2013; Fortunel et al., 2018; Gale & Hall, 2001; Segura et al., 2003). For the case of the Central Amazon, recent research suggests that the water table, defined in part by the topographic position, plays a central role driving the species diversity, structure, and the functional traits of the tree community. According to Costa et al. (2023), forests with shallower water tables harbor resource-acquisitive and hydrologically vulnerable species, shorter canopies forests, and lower biomass than forest with deep water tables, which demonstrates different dynamics as a function of water availability. During normal climatic years, forests with shallow water tables show higher mortality and lower productivity than those with deep water tables. During moderate droughts, however, mortality is buffered, and productivity increases (Costa et al., 2023).

The distinctive plant structure of the seasonally dry tropical forests (SDTF) has developed under specific environmental conditions, such as high evapotranspiration rates, several months of severe or absolute drought, and large spatial variation in water availability (Dexter et al., 2015; Méndez-Toribio et al., 2020; Pineda-García et al., 2015). Because of the marked drought faced by SDTF trees, soil water availability is one of the main factors explaining floristic composition, species phenology, plant survival, and functional trait variation (Balvanera et al., 2011; Cortés-Flores et al., 2017; Markesteijn et al., 2011; Méndez-Toribio et al., 2017; Quisehuatl-Medina et al., 2023; Suresh et al., 2010).

The relationships between topographic factors and community dynamics have been a topic mostly addressed in tropical rainforests but not in dry forests (Bellinghami & Tanner, 2000; De Toledo et al., 2011; Frey et al., 2007; Tai et al., 2017;

Tsujino et al., 2006). Usually, the mortality and recruitment rates for SDTF fluctuate around 4% per year (Carvalho & Felfli, 2011; Silva & de Araújo, 2009), while in rainforests these rates are lower and do not exceed 2% per year (Korning & Balslev, 1994; Lang & Knight, 1983; Manokaran & Kochummen, 1987). The higher mortality rates experienced by trees in dry forests may be caused by the marked climatic seasonality and periods of water stress within the wet season (dry spells) (Murphy & Lugo, 1986; Swaine et al., 1990). Currently, studies about SDTF communities are still scarce and have mostly focused on the floristic and structural description in a spatial context, and, to our knowledge, the effect of topographic factors on community dynamics has been significantly little studied within SDTF (de Souza et al., 2021; Dryflor et al., 2016; Méndez-Toribio et al., 2014; Pineda-García et al., 2007; Quisehuatl-Medina et al., 2023).

Regarding the spatial organization of tree communities in tropical dry forests, there seems to be no clear pattern. In Alamos, in the state of Sonora in northeastern Mexico, no differences in structural attributes were found among topographic positions (Quisehuatl-Medina et al., 2023), while in Chamela SDTF, under mesic conditions as those in lower positions, larger trees were found more frequently. Furthermore, the total stand density was lower, but the basal area was higher (Segura et al., 2003). The opposite occurred in the Brazilian Caatinga forest, however, where diversity, stem density, and individual density were higher in upper positions (Ramos et al., 2020). This latter pattern is consistent with previous findings at our study site in the Balsas River basin, with a similar structure between topographic positions but higher diversity in the upper positions (Méndez-Toribio et al., 2016).

The most drastic changes in plant community dynamics usually occur during the early life stages (small-sized trees) (Harcombe, 1987). According to Nagamatsu et al. (2002), the dynamics of small-sized trees can be strongly influenced mainly by environmental factors, such as soil moisture (Ashton & Gunatilleke, 1995), microscale disturbances (Kobayashi & Kamitani, 2000), canopy cover (Denslow & Guzman, 2000), and deep litter layers (Seiwa, 1997). Similarly, biotic processes, such as herbivore incidence, pest infection (Seiwa, 1997), and intra- and inter-specific competition (Callaway, 1992), may play a decisive role in the dynamics of this stage. These two classes of ecological factors (biotic and abiotic) can vary with topography and its associated environmental conditions (Gallardo-Cruz et al., 2009; Méndez-Toribio et al., 2016; Segura et al., 2003). Therefore, the variability imposed by topography can significantly influence the recruitment and mortality of small-sized trees (Gómez-Aparicio et al., 2005). Thus, there has been lower mortality and higher recruitment of small-sized trees in the lower positions of mountains, as they mainly represent sites with less exposure to drought and environmental disturbances (Ashton & Gunatilleke, 1995; Nagamatsu et al., 2002). In the case of SDTF, studies that address the dynamics and structure of small-sized trees are practically nonexistent. Most studies have focused on the static relationships between environmental measurements and the abundance or dominance of large-sized trees of species.

Because of the strong association between dynamics and community structure with topographic conditions are proxies for environmental gradients (drought risk), our aims in this paper are as follows: (1) to evaluate the effects of slope aspect and topographic position on tree dynamics (mortality, growth, and recruitment) in a tropical dry forest in the Mexican state of Michoacán and (2) examine the effect of such topography-related factors on vegetation structure and species diversity changes from 2012 to 2020. We expected that in sites representing higher water stress for plants (with upper positions and south-facing slopes), higher mortality, lower growth, and recruitment occurred, as compared with more mesic sites of lower positions and north-facing slopes. We also expect greater gains in species diversity and the total density of stems and individuals in upper positions as a result of the high environmental heterogeneity caused by topographic position.

2 | METHODS

2.1 | Study area

The study area is geographically located in Ejido Tziritzicuaró (19° 01'30.1 " N, 101° 58'58.1 " W), in the lower part of the Balsas River basin in Michoacán, western Mexico. The entire Balsas River basin covers an altitudinal gradient ranging from 200 to 1000 m.a.s.l. The geographic area is characterized by a very complex orography, including hills, a valley with ridges, a lava plateau, and mountain ranges with ravines and plateaus (Ferrusquia-Villafranca, 1993). The climate of the area is a warm, dry with a summer rainfall regime and an intertropical isotherm and heat wave (García, 2004). The average annual temperature is 27.1°C, and May is the hottest month of the year (30.2°C). Annual precipitation is 755.4 mm, of which 80% is concentrated between June and September, with a marked dry season from October to May (Méndez-Toribio et al., 2014). The vegetation type present in the area corresponds to tropical dry forests (Gentry, 1982) or seasonally dry tropical forests (Bullock et al., 1995). The SDTF in our study site is structurally similar to other dry forests located in the Neotropics, with an average height of 5 m, a basal area of 18 m² ha⁻¹, and a canopy cover of approximately 300%, which indicates a considerable overlap in the canopies of the trees (Méndez-Toribio et al., 2014). The predominant use of the vegetation in the area is for extensive livestock farming and wood extraction (Méndez-Toribio et al., 2017).

2.2 | Sampling vegetation design

In September–October 2012 (T_1 census), a total of 36 sampling plots (10 × 10 m) were established in three mountainous massifs (La Araña, El Ortigo, and El Tukuy) around Ejido Tziritzicuaró in Michoacán (Figure S1). The vegetation sampling units were established across two topographic factors (slope aspect and

topographic position) and their interaction to include a wide range of floristic and environmental variability in the area (Méndez-Toribio et al., 2014). The slopes were partitioned into three portions identified as lower (380–500 m), middle (480–540 m), and upper (560–780 m). The slopes facing north exhibited greater steepness (mean = 40%, range 15%–63%) as compared with those facing south (mean = 45%; range 14%–68%). Mean steepness (range) across topographic positions was 25% (14%–47%), 53% (40%–68%), and 48% (39%–58%) for the lower, middle, and upper sections, respectively.

In the T_1 census, all individuals within each sampling plot with a diameter at breast height (DBH) ≥ 1 cm were marked, recorded, and taxonomically identified to species level. Every individual's total height, cover, and stem number were recorded. The cover was estimated by measuring two crown diameters for each tree: the longest axis of the crown (d_1) and their perpendicular axis (d_2). We calculate the individual crown area using the following formula $C = 0.25 \times d_1 \times d_2$ and finally, C was summed for each plot to attain the total canopy cover. Given trees in these forests are short, total height was estimated using a steel tape measure from the base of the trunk to the highest leaf in the crown of each tree. In September–October 2020 the second vegetation census (T_2) was conducted in the 36 previously established plots. The surviving trees were recorded, and dead individuals were registered, as well as the recruits with DBH ≥ 1 cm. We categorized small- and large-sized trees by quantile analysis using the populations of each species present in the community, and we considered half of the lower limit as small-sized trees (DBH ≤ 3 cm) and the other half as large-sized trees (DBH > 3 cm). The tree community data were subsequently analyzed by considering three datasets: (i) the entire community (all tree stems ≥ 1 cm DBH), (ii) small-sized trees (tree stems ≤ 3 cm DBH), and (iii) large-sized trees (tree stems > 3 cm DBH).

2.3 | Environmental variation and disturbance

The sampling plots covered a gradient of water availability and drought risk for plants. South-facing slopes in our sampling plots are generally drier and hotter than north-facing slopes. The upper positions represent drier, cooler sites and are less prone to human disturbance as compared with the lower positions. Concerning the soil characteristics of our sampling plots, the lower positions present higher levels of the Topographic Wetness Index (TWI) compared with the upper positions, which have been related to a possible increase in soil depth and the reduction of rock content in these sites. These soil characteristics together would imply not only a greater risk of aboveground drought, but also below it for the plants living in these microenvironments (Méndez-Toribio et al., 2017). A complete environmental characterization describing the drought-risk gradient by topographic factors (mean daily air temperature, total incident radiation, potential evapotranspiration, topographic wetness index, maximum mineral soil depth, coarse fragments on superficial

horizon, and main rooting depth) in our sampling plots can be found in Méndez-Toribio et al. (2016, 2017, 2020).

2.4 | Dynamics at the community and species level

For each of the 36 plots, we calculated annual mortality (*mr*) and recruitment (*rr*) rates using standard exponential population change models that assume a constant probability of death and recruitment over the time period (% yr⁻¹) (Sherman et al., 2012). The equations for calculating these rates are as follows:

$$mr = \ln(NT_1) - \ln(Ns) / t \times 100$$

$$rr = \ln(NT_2) - \ln(Ns) / t \times 100,$$

where NT_1 and NT_2 is the number of trees per plot at time T_1 (2012) and T_2 (2020), respectively, Ns is the number of survivors at time T_2 , and t is the interval between censuses (8 years). We then estimated the relative growth rate for each tree (*rgr*) by using the following formula (Sherman et al., 2012):

$$rgr = \frac{\ln(\text{DBH } T_2) - \ln(\text{DBH } T_1)}{t},$$

where DBH is the average diameter at breast height of each tree at time 1 and 2, respectively, divided by t years between censuses. Mortality, recruitment rate, and relative growth rate were also calculated for the most abundant species that had individuals in all or most of the plots, and we compared among species. We acknowledge that this approach may underestimate mortality rates for small individuals that grew and died within the 8-year time period (Kohyama & Takada, 1998).

2.5 | Relative changes of vegetation attributes and diversity

Species diversity in the plant community was calculated using additive and multiplicative decompositions based on Hill numbers: the effective number of species (Chao et al., 2012; Hill, 1973; Jost, 2007). We calculated them (q^D) by including species richness (q^0), the Shannon entropy exponential (q^1), and the inverse Simpson concentration (q^2) (Chao et al., 2012) with the “*entropart*” package (Marcon & Hérault, 2015) in R software version 4.2.2 (R Core Team, 2022).

The percentage change (delta Δ) of the vegetation attributes (average height, total basal area, average cover, number of individuals, proportion of multitemmed individuals and number of stems) and species diversity variables (q^0 , q^1 , and q^2) per plot was calculated as follows:

$$\Delta x = \left(\frac{x_{T_1} - x_{T_2}}{x_{T_2}} \right) \times (100),$$

where x refers to each of the community attributes, T_1 and T_2 are the first ($T_1=2012$) and second censuses ($T_2=2020$), respectively, multiplied by 100 to express them as a percentage (%).

2.6 | Statistical analysis

To assess the effect of topographic factors on the tree dynamics of the Tziritzicuario seasonally dry tropical forest, we conducted four groups of analyses: (i) on the community dynamics, (ii) on the dynamics of the most abundant species, (iii) on vegetation structure and species diversity for the 2012 and 2020 censuses, and (iv) on relative changes (“ Δ ” in %) of community attributes within the study period ($\Delta=2020-2012$). All analyses were conducted separately for the entire community, small-sized trees, and large-sized trees. The response variables for the community dynamics and species dynamics included mortality (*mr*), recruitment (*rr*), and growth (*gr*) rates, while for the vegetation structure they addressed height, basal area, canopy cover, number of individuals, multitemmed trees, the number of stems and DBH. For species diversity, we included q^0 , q^1 and q^2 , and the relative change (“ Δ ” in %) of community attributes, which refers to differences in each of the variables within the study period ($\Delta=2020-2012$). For all analyses, the slope aspect (SA), topographic position (TP), and the interaction between both terms (SA \times TP) were used as fixed factors (explanatory variables) in the models. Generalized linear models (GLM) were employed to test for the effect of topographic-related factors on response variables (Crawley, 2012). For discrete variables (number of individuals and stems, q^0 , q^1 and q^2), a log link and Poisson-type error were set. For mortality and recruitment, we used a binomial error and a logistic link function. For the case of continuous variables (basal area, height, cover, DBH, growth, and delta “ Δ ” for all variables), an identity link with a Gaussian-type error was used. We previously checked the normality and homogeneity of variance in continuous variables. For Poisson and binomial models, when overdispersion problems occurred, an empirical scaling of quasi-Poisson or quasi-binomial type was performed, and the data were adjusted to an approximate F-distribution (Crawley, 2012). For those models with significant terms, we then conducted post hoc tests (Crawley, 2012; Everitt & Hothorn, 2010). Analyses were conducted using R software version 4.2.2 (R Core Team, 2022), and the “*gmodels*” package in R were used for post hoc tests (Warnes et al., 2018).

A PERMANOVA was used to analyze the topography-related effects on percent changes (Δ) of structure (height, basal area, cover, number of individuals, multitemmed trees, and number of stems and DBH) and species diversity (q^0 , q^1 and q^2) using the Manhattan method with 49,999 permutations. The model included topographic position, slope orientation, and the interaction term (SA, TP, and SA \times TP) as factors (Anderson, 2001). A PCA was also employed to analyze the variation of percent changes in structure and diversity across the topographic gradient. We performed separate analyses for each of our three datasets (entire

community, small- and large-sized trees). All statistical analyses were conducted in R software ver. 4.2.2 (R Core Team, 2022) with the packages *ade4*, *car*, *ggplot2*, *maptools*, *plyr*, and *vegan* for the multivariate analyses (Bivand et al., 2023; Jombart et al., 2023; Simpson et al., 2022).

3 | RESULTS

Overall, we found 1066 individuals corresponding to 69 species of trees. The 10 most abundant species were *Randia nelsonii*, *Cordia elaeagnoides*, *Euphorbia schlechtendalii*, *Senegalia picachensis*, *Handroanthus impetiginosus*, *Apoplanesia paniculata*, *Lippia umbellata*, *Mimosa arenosa*, *Lysiloma divaricatum*, and *Lysiloma tergeminum*. These 10 species comprised 67% of the total abundance; however, only the first seven are widely distributed in most of the topographic conditions analyzed, while the last three species are restricted to

specific conditions. We also found 26 species with very low abundance (1–2 individuals), which comprise only 3% of the total abundance in the community (Table 1).

3.1 | Dynamics at the community and species level

Regarding community dynamics at the plot level, for the entire community, the highest mortality was found in the South-Upper condition (mean \pm SE = $3.2 \pm 0.5\%$ yr⁻¹), while the lowest was in the South-Lower (mean \pm SE = $1.4 \pm 0.1\%$ yr⁻¹), as seen in Figure 1a and Table S1. A similar pattern was found for small- and large-sized trees (Table 1 and Table S1). The GLM indicated that for the three data-sets (the entire community, the small-sized trees, and large-sized trees), mortality was only influenced by the topographic position, with the highest mortality in the upper position (Figure 1, Table 1 and Table S1).

TABLE 1 Statistics for GLM's used to assess the community dynamics (mortality, recruitment, and growth) and the relative changes in structural attributes (Δ in % for the number of individuals and stems) of the tropical dry forest at Tziritzicuaru Western, Mexico.

Variables	Factors								
	Slope aspect (SA)			Topographic position (TP)			SA xTP		
Data set	χ^2/F	d.f.	p	χ^2/F	d.f.	p	χ^2/F	d.f.	p
Community dynamics									
Mortality rate									
Entire community	0.4	1	.54 ^{ns}	23.5	2	<.001	2.0	2	.40 ^{ns}
Small-sized trees	2.8	1	.09 ^{ns}	10.3	2	<.01	4.8	2	.09 ^{ns}
Large-sized trees	0.4	1	.49 ^{ns}	12.9	2	<.01	0.2	2	.91 ^{ns}
Recruitment rate									
Entire community	0.9	1	.46 ^{ns}	3.7	2	.36 ^{ns}	17.1	2	<.01
Small-sized trees	0.3	1	.42 ^{ns}	2.0	2	.10 ^{ns}	0.01	2	.99 ^{ns}
Large-sized trees	0.1	1	.50 ^{ns}	0.4	2	.43 ^{ns}	1.25	2.30	.08 ^{ns}
Growth rate									
Entire community	0.3	1.33	.09 ^{ns}	0.01	2.32	.94 ^{ns}	0.07	2.30	.70 ^{ns}
Small-sized trees	0.001	1.33	.99 ^{ns}	0.01	2.31	.27 ^{ns}	0.001	2.29	.66 ^{ns}
Large-sized trees	0.001	1.34	.51 ^{ns}	0.01	2.32	.25 ^{ns}	0.001	2.30	.73 ^{ns}
Changes in structure (Δ in %)									
Number of individuals									
Entire community	0.8	1.30	.37 ^{ns}	10.1	2.30	<.001	1.0	2.30	.37 ^{ns}
Small-sized trees	0.1	1.30	.72 ^{ns}	6.3	2.30	<.01	3.9	2.30	<.05
Large-sized trees	1.5	1.30	.21 ^{ns}	2.1	2.30	.14 ^{ns}	0.2	2.30	.79 ^{ns}
Number of stems									
Entire community	0.5	1.30	.49 ^{ns}	3.8	2.30	<.05	2.2	2.30	.13 ^{ns}
Small-sized trees	0.4	1.30	.53 ^{ns}	4.8	2.30	<.01	3.7	2.30	<.05
Large-sized trees	0.1	1.30	.70 ^{ns}	1.4	2.30	.25 ^{ns}	2.1	2.30	.14 ^{ns}

Note: For each response variable, the analyses were conducted for the entire community (DBH \geq 1 cm), the small-sized trees (DBH \leq 3 cm) and large-sized trees (DBH >3 cm). Slope aspect, topographic position and their interaction were the terms included in the models. Chi-square is the statistic for variables with Poisson and binomial distribution, while F is for variables with normal distribution error, d.f. = degrees of freedom and p = probability. The significant effects are marked in gray and the nonsignificant (ns) effects are indicated (see Figures 1 and 2). The relative changes in structural and diversity variables were not-significant and can be found in the Appendix S1. The grey shade area indicates the significant terms on the statistical analysis.

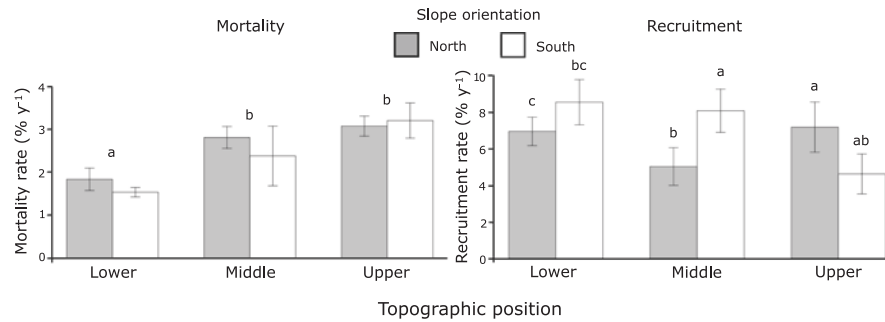


FIGURE 1 Community tree dynamics over 8 years (2012–2020) in a tropical dry forest from western Mexico. Mean (\pm SE) annual mortality and recruitment rates for the entire community (individuals ≥ 1 cm DBH) in plots with different topographic positions (Lower, Middle, and Upper) and slope aspect (North and South). Letters above the bars indicate differences based on post hoc contrasts between levels of the significant terms in the corresponding GLM ($p \leq .05$; see Table 1 and Table S1).

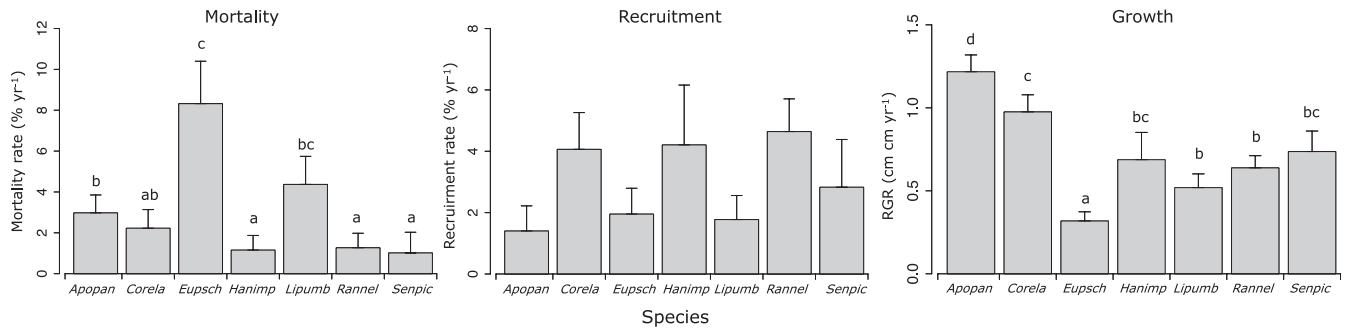


FIGURE 2 Dynamics for the seven most important species of the seasonally dry tropical forest of Tzirtzicuar, western Mexico. Mean (\pm SE) annual mortality and recruitment rates are shown for Apopan, *Apoplanesia paniculata*; Corela, *Cordia elaeagnoides*; Eupsch, *Euphorbia schlechtendalii*; Hanimp, *Handroanthus impetiginosus*; Lipumb, *Lippia umbellata*; Rannel, *Randia nelsonii*; Senpic, *Senna picachensis*. Letters above the bars indicate differences based on post hoc contrasts between levels of the significant terms in the corresponding GLM ($p \leq .05$). For recruitment no differences were found among species (see Section 3).

The tree recruitment for the entire community was not affected either by slope aspect (SA) or topographic position (TP) but by the interaction of these two factors (Figure 1, Table 1, and Table S1). Interestingly, recruitment for the entire community was the opposite of mortality in which the highest values (mean \pm SE = $3.5 \pm 0.2\%$ yr⁻¹) were found in the South-Lower positions (Figure 1). In contrast, no differences among slope aspect or topographic position were found for small and large individuals (Table 1 and Table S1). Overall, the diameter relative growth rate (RGR \pm SE) for the entire community was 1.6 ± 0.1 cm yr⁻¹, and it was not statistically influenced by the slope aspect, topographic position nor the interaction. Similarly, both for small- and large-sized individuals, RGR did not differ among topographic conditions (Table 1 and Table S1).

Considering the seven most abundant and widely distributed species, which comprised about 62% of the individuals, we found a large variation of mortality and significant differences among species ($\chi^2 = 56.1$, $df = 6$, $p < .001$; Figure 2). The lowest mortality rate was found for *Senegalia picachensis* with a mean (\pm SE) = $1.01 \pm 0.5\%$ yr⁻¹, while that of *Euphorbia schlechtendalii* was eightfold higher (Figure 2a). Regarding recruitment, *Randia nelsonii*, *Handroanthus impetiginosus*, and *Cordia elaeagnoides* showed the highest recruitment with values above 4.0% yr⁻¹ (Figure 2b), although statistically we did not find differences among the seven species (Figure 2; $\chi^2 = 10.9$, $df = 6$, $p = .09$). In terms of the relative growth rate in DBH, significant

differences were found among species ($F_{6,101} = 21.7$, $p < .001$). For example, *Apoplanesia paniculata* was the fastest species with a mean (\pm SE) of 1.2 ± 0.06 cm yr⁻¹, while *Euphorbia schlechtendalii* was the slowest growth species (Figure 2c).

For the rest of the species, which were poorly represented (<4 individuals), there were 17 species, such as *Erythroxylum mexicanum* and *Haematoxylum brasiletto*, *Bursera denticulata*, *Piscidia piscipula*, *Pterocarpus orbiculatus*, and *Karwinskia latifolia*, which did not show mortality during the 8 years of study (Table 2). Thus, the same individuals sampled in 2012 remained alive until 2020 (Table 2). For 38 species we did not record any recruitment at all during the study period (Table 2). There was also another group of nine rare species that in the first census were singletons (one individual), and by 2020 all those individuals had died. Additionally, these species had no recruitment, and thus they vanished from the sampled community. Among those species are *Sideroxylon celastrinum*, *Gyrocarpus jatrophifolius*, and *Coursetia glandulosa* (Table 1).

3.2 | Vegetation structure and diversity and changes among censuses (Δ)

Comparing the six conditions resulting from the slope aspect (SA) and topographic position (TP), we found no differences in structure

TABLE 2 Community tree dynamics of a tropical dry forest from western Mexico.

Species	N _{T1}	N _{T2}	Death	Recruited
Anacardiaceae				
<i>Amphipterygium adstringens</i>	24	21	8	5
<i>Cyrtocarpa procera</i>	15	13	2	0
<i>Spondias purpurea</i>	6	4	2	0
Apocynaceae				
<i>Plumeria rubra</i>	7	5	3	1
Bignoniaceae				
<i>Handroanthus impetiginosus</i>	64	67	21	24
Bixaceae				
<i>Cochlospermum vitifolium</i>	2	1	1	0
Boraginaceae				
<i>Boraginaceae sp1</i>	2	2	1	1
<i>Boraginaceae sp2</i>	1	1	0	0
<i>Boraginaceae sp3</i>	1	1	0	0
<i>Cordia alliodora</i>	2	2	0	0
<i>Cordia elaeagnoides</i>	80	109	12	41
<i>Cordia morelosana</i>	2	1	1	0
<i>Cordia nelsonii</i>	1	0	1	0
Burseraceae				
<i>Bursera copallifera</i>	5	8	1	4
<i>Bursera coyucensis</i>	26	14	14	2
<i>Bursera crenata</i>	9	8	1	0
<i>Bursera denticulata</i>	1	1	0	0
<i>Bursera fagaroides</i>	11	9	3	1
<i>Bursera grandifolia</i>	15	12	4	1
<i>Bursera heteresthes</i>	3	3	1	1
<i>Bursera inferdinalis</i>	3	3	1	1
<i>Bursera sp</i>	3	3	0	0
<i>Bursera trimera</i>	9	7	3	1
Cactaceae				
<i>Stenocereus queretaroensis</i>	1	1	1	1
Capparaceae				
<i>Capparis indica</i>	2	1	2	1
<i>Morisonia americana</i>	1	0	1	0
<i>Forchhammeria pallida</i>	0	1	0	1
Caricaceae				
<i>Jacaratia mexicana</i>	3	2	1	0
Erythroxylaceae				
<i>Erythroxylum mexicanum</i>	4	4	0	0
<i>Erythroxylum rotundifolium</i>	5	2	3	0
Euphorbiaceae				
<i>Adelia oaxacana</i>	1	0	1	0
<i>Cnidocolus inferdinalis</i>	11	5	6	0

(Continues)

TABLE 2 (Continued)

Species	N _{T1}	N _{T2}	Death	Recruited
<i>Cnidocolus multilobus</i>	1	0	1	0
<i>Croton morifolius</i>	35	11	24	0
<i>Euphorbia schlechtendalii</i>	93	86	75	68
<i>Manihot tomatophylla</i>	5	3	2	0
Fabaceae				
<i>Apoplanesia paniculata</i>	41	34	12	5
<i>Bauhinia divaricata</i>	5	1	4	0
<i>Brogniartia sp</i>	10	7	7	4
<i>Coulteria platyloba</i>	1	3	0	2
<i>Coursetia glandulosa</i>	1	0	1	0
<i>Diphysa floribunda</i>	8	7	3	2
<i>Haematoxylum brasiletto</i>	3	5	0	2
<i>Lonchocarpus balsensis</i>	2	2	1	1
<i>Lonchocarpus constrictus</i>	10	8	2	0
<i>Lonchocarpus longipedunculatus</i>	11	11	3	3
<i>Lysiloma divaricatum</i>	40	27	16	3
<i>Lysiloma tergeminum</i>	23	25	6	8
<i>Mariosousa coulteri</i>	7	6	4	3
<i>Mimosa arenosa</i>	21	51	5	35
<i>Mimosa rosei</i>	9	3	7	1
<i>Mimosa sp</i>	1	1	0	0
<i>Piscidia piscipula</i>	1	1	0	0
<i>Pithecellobium dulce</i>	1	0	1	0
<i>Poincianella eriostachys</i>	1	0	1	0
<i>Pterocarpus orbiculatus</i>	1	1	0	0
<i>Senegalia macilenta</i>	2	2	0	0
<i>Senegalia picachensis</i>	72	81	14	23
<i>Vachellia campechiana</i>	2	1	1	0
Hernandiaceae				
<i>Gyrocarpus jatrophifolius</i>	1	0	1	0
Malpighiaceae				
<i>Bunchosia palmeri</i>	6	8	1	3
<i>Malpighia mexicana</i>	4	6	2	4
Malvaceae				
<i>Ceiba aesculifolia</i>	3	7	0	4
<i>Heliocarpus occidentalis</i>	21	22	9	10
<i>Malvaceae sp.</i>	3	1	2	0
Polygonaceae				
<i>Coccoloba acapulquensis</i>	4	2	2	0
<i>Ruprechtia fusca</i>	7	2	5	0
Rhamnaceae				
<i>Colubrina triflora</i>	5	5	0	0
<i>Karwinskia latifolia</i>	1	1	0	0
Rubiaceae				
<i>Genipa americana</i>	3	3	1	1

(Continues)

TABLE 2 (Continued)

Species	N _{T1}	N _{T2}	Death	Recruited
<i>Guettarda elliptica</i>	6	7	3	4
<i>Hintonia latiflora</i>	24	14	12	2
<i>Randia aculeata</i>	9	13	2	6
<i>Randia echinocarpa</i>	1	2	0	1
<i>Randia nelsonii</i>	138	197	33	92
Urticaceae				
<i>Pouzolzia occidentalis</i>	4	1	4	1
<i>Sideroxylon celastrinum</i>	1	0	1	0
Verbenaceae				
<i>Lippia umbellata</i>	45	41	21	17
Unknown family				
Unknown	1	47	1	47
TOTAL	1014	1067	385	437

Note: The total number of individuals registered at the study site for each species. N_{T1}, N_{T2} are the number of individuals in 2012 and 2020, and deaths and recruited individuals within the period.

(height, basal area, cover, and DBH) and only minor differences for species diversity (q^0 , q^1 , and q^2) for both the first (2012) and second censuses (2020) for the three datasets analyzed. A description of these results and the details can be found in Appendix S1 and Tables S3–S5. Therefore, in this section, we focus on the percentage of changes (Δ) in variables of the vegetation structure and species diversity.

Overall, regarding the changes between censuses ($\Delta=2020-2012$) and without considering the topographic conditions, the plant community showed a slight increase in DBH, basal area, and individual density (1.2%, 8.2%, and 6.2%, respectively), as well as a decrease in the percentage of multistemmed individuals, cover, height, stem density, and species richness: 21.6%, 15.9%, 11.4%, 6.1%, and 3.2%, respectively. These changes, however, did not differ significantly between slope aspects (SA) and topographic positions (TP), and the interaction between these factors (SA \times TP) was not significant. The only exceptions were the number of individuals and the number of stems (Figure 3, Tables S3 and S4). Specifically, for the entire community, we found a significant variation with a large increase in individuals (62.0%) in South-Lower and a large decrease in individuals in the South-Upper position (–18.9%; Figure 3). These differences were significant among topographic positions, regardless of slope aspect (Table 1). For small-sized trees, we found similar differences (Figure 3), and both the topographic position and the interaction were significant (Table 1). Thus, overall, there was a greater temporal gain of individuals in lower positions. For the number of stems in the entire community, we also found increases at the South-Lower position (29.3%) but negative changes in the South-Upper (–29.6%; Figure 3); moreover, we found significant differences among topographic positions (Table 1). Similar results were revealed for small-sized individuals (Figure 3), and significant differences were found for topographic position and the interaction term (Table 1). In the case of large-sized trees, there were no temporary changes (Δ) in any of the variables analyzed (Table S5).

Regarding diversity, there were no significant temporal percent changes (Δ) in the species richness (q^0), common species (q^1), and dominant species (q^2) concerning topography (SA, TP, and SA \times TP) for any of the three datasets (Tables S3–S5).

According to the PERMANOVA, the topographic position significantly influenced temporal percent changes (Δ) in the entire community ($F_{2,34}=2.24$, $p<.05$) and small-sized trees ($F_{2,34}=3.2$, $p<.01$), representing 11% and 15% of the variation, respectively (Table S2). The PCA showed that the percentage change of the basal area and the number of stems/individuals increased positively in the entire community and the small-sized trees in the lower positions (Figure 4a). On the contrary, the percentage changes of height, cover, and multistemmed trees seemed to increase towards the upper and middle positions in the complete community and small-sized trees, respectively (Figure 4b,d).

4 | DISCUSSION

In this study, we analyzed the effect of two topographic factors (topographic position and slope aspect) as proxies of environmental filters (drought stress) on the community dynamics and the structure of the vegetation in a seasonally dry tropical forest located in the lower part of the Balsas-River basin, in Michoacán, Mexico. The results show that higher mortality occurs towards the upper positions of the mountains (Table 1 and Figure 1). This agrees with the results previously reported for the Mexican tropical dry forest of Chamela (Segura et al., 2003), for a tropical lowland forest located in northern Borneo (Gale & Hall, 2001), for a mixed deciduous forest located in southern New England (Frey et al., 2007), and for a tropical wet forest in Puerto Rico (Schwartz et al., 2020). The results, however, contrast with the trends reported for other regions and ecosystems where mortality is due to other environmental factors, such as richer nutrient soils at upper positions and/or flooding at lower positions (Ferry et al., 2010; Lieberman & Lieberman, 1987; Rocha et al., 2003).

In our study site, the upper positions of the mountains are cooler with drier soils and less exposure to radiation than the lower positions. The shallow soils in the upper positions have a low water retention capacity and dry rapidly after rainfall (de Toledo et al., 2012; Méndez-Toribio et al., 2017). This implies a higher mortality risk for trees in prolonged periods of drought, as well as during the growing season and in the dry season (Méndez-Alonzo et al., 2013; Méndez-Toribio et al., 2017; Pineda-García et al., 2011; Segura et al., 2003). The high mortality in the upper positions can be caused by the high levels of hydric stress that plants undergo, as has been described in some localities where the greater occurrence of standing dead trees is related to species vulnerability to drought (de Toledo et al., 2012; Gale & Hall, 2001). In the lower parts of the mountains, these more humid microsites could serve as refuge sites for species less tolerant to stress, reducing the demographic impact associated with drought. Under future climate change scenarios, these “hydrologic microrefugia” will likely prove essential for the persistence of certain plant species (McLaughlin et al., 2017). Additional studies and field experiments on seed dispersal and seedling establishment, the effects

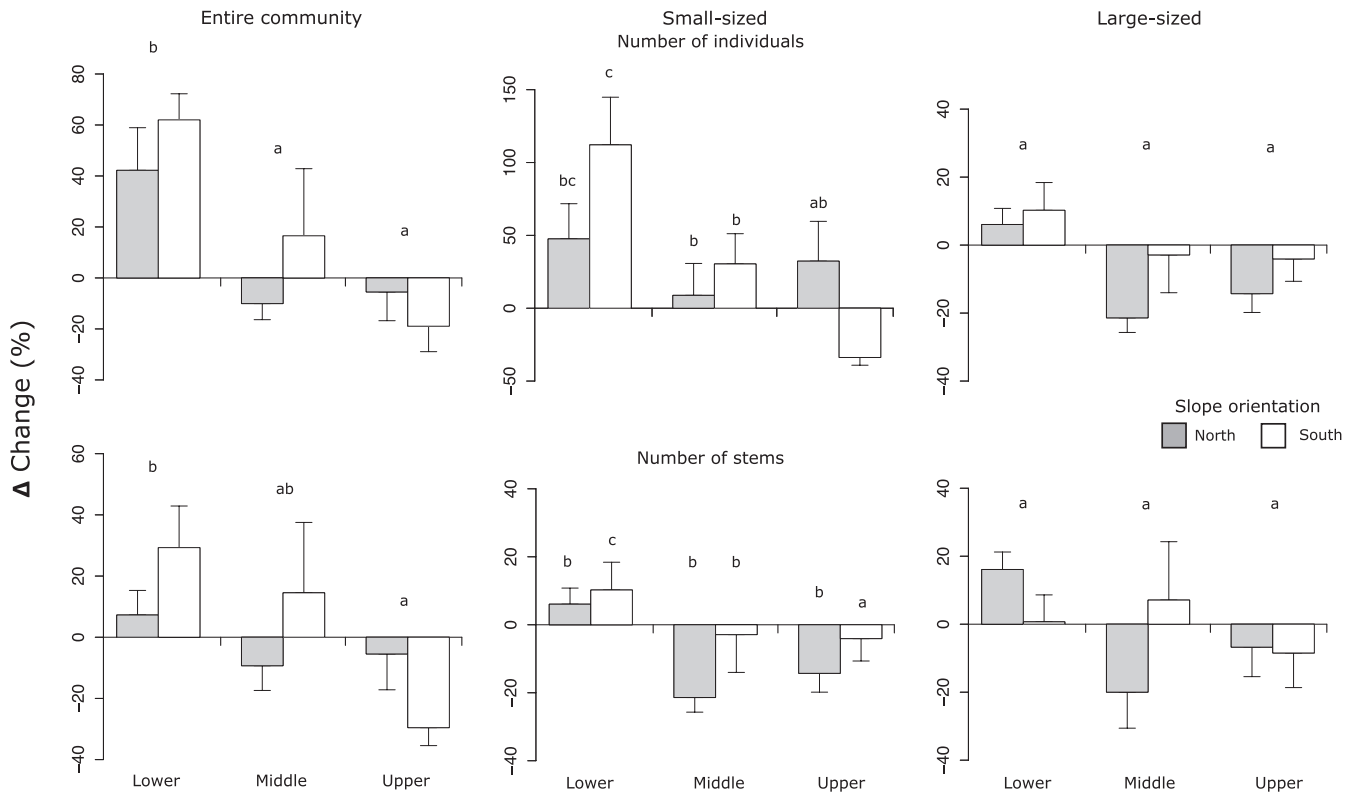


FIGURE 3 Relative changes (Δ) in vegetation attributes for the entire community (tree stems ≥ 1 cm DBH), small (tree stems ≤ 3 cm DBH), and large-sized trees (tree stems > 3 cm DBH) in a tropical dry forest from western Mexico. Upper plots show data for individuals, while lower are for number of stems. Letters above the bars indicate differences based on post hoc contrasts between levels of the significant terms in the corresponding GLM ($p \leq .05$; see Table 1 and Table S1).

of pathogen attack, competition, and herbivory, together with the interaction effect of these biotic factors with environmental conditions, may provide valuable insight for fully understanding the dynamics of these tree communities (Muscarella et al., 2013).

The highest values of recruitment occurred in the lower positions of the mountains (Table 1 and Figure 1). This contrasts with other sites, such as the tropical rain forest in northeast Queensland, Australia, where a higher recruitment of trees has been found in the upper positions (Herwitz & Young, 1994). This pattern has been explained because of a higher frequency of strong winds in upper positions, which increases the turnover rates of trees, and, therefore, the recruitment in these sites (Lawton, 1982). Our findings of higher recruitment in the lower positions agree with those from following research: a study on mixed deciduous forests of southern New England (Frey et al., 2007), a study on a mixed coniferous forest in the Sannoko Forest Reserve in Japan (Nakamori et al., 2009), and a work on a humid forest in the Brazilian Amazon (Bentos et al., 2013).

The environmental differences among topographic positions may affect the capacity of trees to accumulate resources required for growth and/or reproduction and hence recruitment rates. Soil moisture plays a fundamental role in the establishment and survival of new trees across the topographical gradient (Nagamatsu et al., 2002). In this sense, the lower positions, which are more mesic sites, have been related to higher levels of recruitment as compared with upper positions (Bentos et al., 2013) mainly because these lower

sites may represent more suitable areas that guarantee the survival and establishment of recruits. This may be a plausible explanation for our study site, considering that the plots in low positions represent sites with higher soil moisture (Méndez-Toribio et al., 2017). This can generate adequate microenvironments and temporary windows with low levels of water stress (especially during the dry season) so that new trees can establish themselves in the community.

Another possible explanation for the occurrence of higher recruitment in lower positions is related to vegetation structure and competition. It has been postulated that the increase in basal area, stem density, and the ability to cast shade are directly related to the decrease in plant recruitment rates (sensu Käber et al., 2021). Combined, they indicate the competitive situation of a forest stand: the oldest stands tend to exhibit higher values of basal area, which increases competition between plants and reduces the recruitment of new trees (Käber et al., 2021; Zell et al., 2019).

In our study site, topographic position, which is a proxy of environmental variation, influences the community dynamics and the establishment of trees of certain ecological strategies across this drought risk gradient. Thus, the topographic position creates clear gradients of environmental variation, with higher temperature and evapotranspiration in the top positions. Detailed studies on the climatic variation in our study site across the topographic gradients and the effects on species association have been published elsewhere (Méndez-Toribio et al., 2017, 2020). The same effect has also

Entire Community

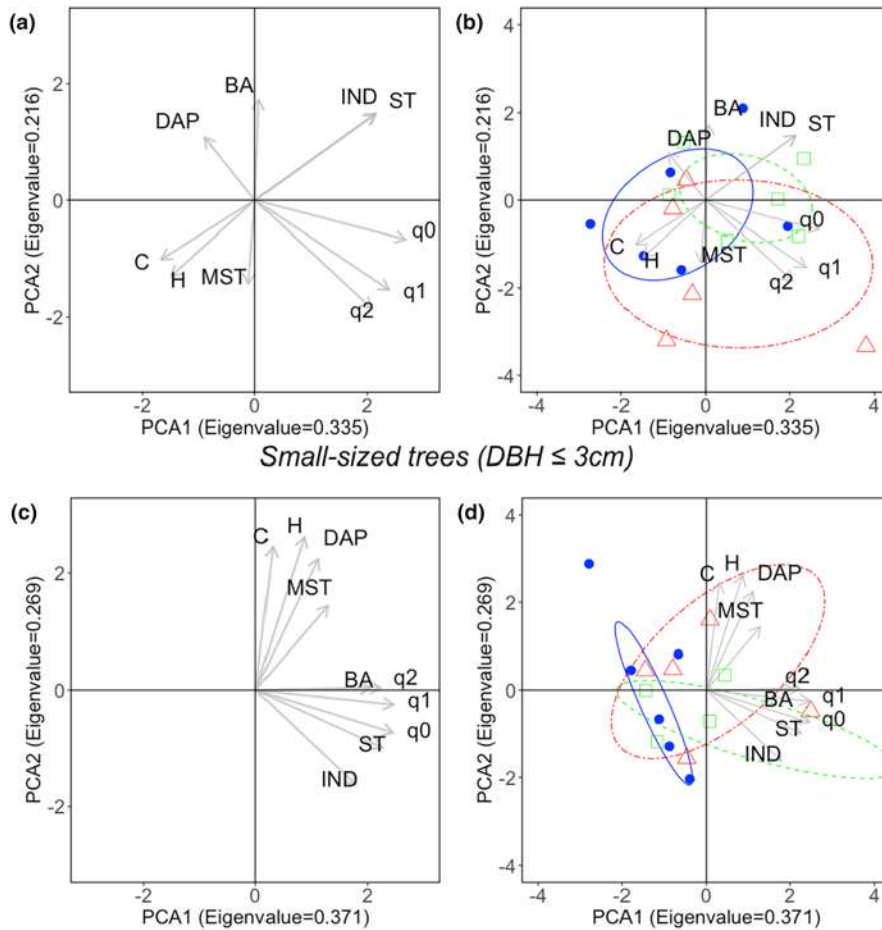


FIGURE 4 Principal component analysis on delta (Δ) values in a tropical dry forest from western Mexico. The top charts correspond to attributes of vegetation structure in the entire community, while the bottom charts are for small-sized trees (DBH \leq 3 cm), (a) and (c) structure and diversity attributes, (b) and (d) PCA plots of three topographic positions, green squares = lower position, red triangles = middle position, blue circles = upper position. BA (basal area); C (cover); DBH (Diameter at Breast Height); H (height); IND (number of individuals); MST (number of multi-stemmed trees); ST (stems density); q0, q1, and q2 (effective number of species of order 0, 1 and 2, respectively). Ellipses were drawn with a confidence level of 95%.

been described in other tropical ecosystems. These studies have identified topography and elevation as key drivers of forest structure, composition, and productivity, which constrain local nutrient and hydraulic conditions that drive tree growth and other community dynamics (Homeier et al., 2010; Jucker et al., 2018).

In our research, we found no difference in growth across the gradient imposed by topography (Table 1), which coincides with the results reported for a tropical montane forest in Jamaica (Bellinghami & Tanner, 2000). It has been reported, however, that towards the lower positions and slopes facing north, the trees tend to show higher growth. Explanations for these results revolve around the presence of lower drought levels in these sites (Fortunel et al., 2018; Hu et al., 2018; Schwartz et al., 2020; Yang et al., 2006).

Although in the upper positions of our study sites, there were trees with lower wood density (Méndez-Toribio et al., 2017), an intuitive result related to the above could be the presence of higher growth rates in those positions. Nevertheless, this generalization of the relationship between wood density and growth rates has been supported by research performed mainly in tropical moist forests (Chave et al., 2009; King et al., 2006; Poorter et al., 2008). This relationship has not been found for the tropical dry forest because in this ecosystem the presence of soft tissues in the plants has been mainly associated with a functional strategy drought-avoidance (Méndez-Toribio et al., 2020; Prado-Junior et al., 2017). Therefore, soft tissue

species present in higher positions could allocate more resources to store water and starches for reproduction during the dry season and not for growth. This could explain the apparent homogeneity of tree growth along the topographic gradient for the studied SDTF.

The percent changes of most of the vegetation attributes (height, basal area, cover, DBH, and multistemmed trees) showed no association with topography (Tables S3–S5). Generally, however, the percent changes in the number of individuals and stems increased negatively in South-facing sites located in upper positions, which represents tree losses under these conditions (Table 1). Similarly, the largest percentage of increases usually occurred in North-facing sites located in lower positions: there is a greater gain of trees in these conditions. This phenomenon is mainly remarkable in small-sized trees (Table S4).

The upper positions of our study site experience an apparent acceleration of the processes related to community dynamics, which results in high mortality rates, low levels of recruitment, and limited growth. This is directly reflected in the structure of the vegetation at the community level through the topographic gradient, which causes greater percent losses of stems and individuals to occur in upper positions, as well as greater gains of these same attributes in the lower positions. Even though the vegetation structure in this tropical dry forest seems to be homogeneous over time and for the topographic gradient, we do not discard that other vegetation attributes such as aboveground biomass may respond to these factors.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Dryad Digital Repository: [10.5061/dryad.nvx0k6f0w](https://doi.org/10.5061/dryad.nvx0k6f0w)

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Constrained vs. unconstrained traits govern community assembly in a Mexican seasonally dry tropical forest

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Running head:

Community assembly in a Mexican dry forest

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Abstract

In seasonal plant communities, topography-related variation in water availability and drought risk is recognized as determining specific sets of traits and functional strategies; however, the effects on species dominance/subordination, phylogenetic diversity, functional richness, the occurrence of CSR ecological strategies, and the relationships between restricted and unrestricted functional trait sets are not well understood. This study examines the effects of slope aspect and topographic position on community functioning and species dominance-subordination in a seasonally dry tropical forest landscape, and explores the relationships between phylogenetic diversity, functional richness, and CSR strategies and the water stress gradient created by the interaction of these two topographic factors. The study was conducted in the Balsas River basin in western Mexico. Fifty-five species (≥ 2.5 cm diameter at breast height) were evaluated in plots located in three topographic positions (lower, middle and upper) and two slope orientations (north and south). Eleven functional traits related to the plants' ability to avoid or tolerate water stress and describing the reproductive ecology of the species, three CSR ecological strategies and three demographic attributes were used. Eight dominant species were presented in the entire plant community and 47 subordinate species, their identity changed across positions and orientations, highlighting *Cordia elaeagnoides* as the only species that dominates in all conditions. Phylogenetic diversity was affected only by orientation, presenting the highest values on the northern slopes. Functional richness was affected only by position, presenting decreasing values towards the lower positions. Most species presented CSR strategies related to positions C to S of the Grime triangle, which represents a mostly stress-tolerant vegetation. The main axis of variation that potentially explains plant community functioning is represented by sets of traits related to water use and storage (water content in bark and xylem), wood density, and leaf retention time. CSR ecological strategies function as a secondary axis of variation, especially for slope orientation, in this Mexican dry forest.

Keywords: Drought, functional traits, phylogenetic diversity, functional richness

Introduction

The classical theory that tries to explain the spatial variation of community patterns is based on two main approaches, deterministic and stochastic processes (Hubbell 2001; Kraft, Valencia, and Ackerly 2008; Chase 2010). On the one hand, the deterministic approach has an argumentative support based on the niche theory (Hutchinson 1957; Hutchinson 1959), which states that each species has a range of environmental characteristics within which it can have an optimal population performance, highlighting the role that abiotic factors and biotic interactions have in the distribution patterns of species. On the other hand, the approach based on stochastic events (Hubbell, 2001), which involves unpredictable disturbances, probabilistic dispersion and random demographic events in the modelling of species distribution patterns (Chase & Myers, 2011). Currently, one of the central objectives in the field of ecology is to determine how different mechanisms involving deterministic and stochastic factors influence and act on community assembly across different space-time scales.

At regional and mesoscale levels, topography presents a wide range of floristic and environmental variability, and has been associated with the generalized niche differentiation assembly theory driven by deterministic processes (Brown et al., 2013). As such, topography represents gradients of water availability and drought risk for plants; ranging from sites with high soil moisture and evapotranspiration (e.g., lower N-facing topographic positions) to sites with low moisture and evapotranspiration (e.g., higher S-facing topographic positions) (Gallardo-Cruz et al., 2009; Méndez-Toribio et al., 2016). Topographic gradients play a determining role in structuring the patterns of functional traits and phylogenetic diversity of plants at the community level, which, in turn, has been related to the assembly and functioning of ecosystems (verbi gratia: Brown et al., 2013; Dubuis et al., 2013; Méndez-Toribio et al., 2020; Schmitt et al., 2020).

Due to this environmental heterogeneity associated with topography, it has been proposed that functional traits, that is, morpho-physiological, biochemical, structural or phenological characteristics (in the case of plants) that are relevant in the response of organisms to the environment and/or their effects on the properties of ecosystems (Violle et al., 2007); present predetermined sets of these that set patterns for the occurrence of functional strategies of plants in different types of ecosystems (Apaza-Quevedo et al., 2015; Méndez-Toribio et al., 2017; Sanaphre-Villanueva et al., 2017; Cheesman et al., 2018).

For example, in the case of seasonally dry tropical forests (SDTF), the presence of species with ‘conservative traits’ (dense tissues and late deciduous leaves) has been reported more frequently in sites with greater availability of water resources in the soil (lower parts of the mountains). At the other extreme, that is, in places with drier soils (higher parts of the mountains), species with ‘acquisitive traits’ (water storage tissues and thin, light leaves with short retention periods) have been reported to occur more frequently, highlighting topography as a factor imposing water stress gradients above and below ground that condition the appearance of these two types of functional strategies (Méndez-Toribio et al., 2017, 2020). However, this type of characterization of functional strategies based on single traits has certain important inconsistencies. First, the results of this type of studies always lead to pre-established strategies, which can make it difficult to identify intermediate (secondary or tertiary) strategies of plants. Second, and as pointed out (Li & Shipley, 2017; Pedraza & Martorell, 2019), when trying to demonstrate the theoretical links between the presence of unique traits and functional strategies, it is almost inevitable to fall into conclusions that generate circular reasoning around the functional performance of plant species in a community. Hence the importance of developing studies with comprehensive approaches, which consider, on the one hand, the development of ecological strategies in plants, but which also take into account other attributes of vegetation such as diversity or phylogenetic structure; constituting elements of analysis that

can help to explain with greater breadth and clarity the assembly patterns at the community level of plant species in different environmental contexts.

Currently, ecologists use combined information on functional traits and species' phylogenetic relationships to draw more robust conclusions about community assembly patterns in plants (Webb et al., 2002; Cadotte et al., 2009; Cavender-Bares et al., 2009; Coyle et al., 2014). One of the most frequently used components to describe community-level evolutionary relationships is phylogenetic diversity (PD), which, conceptually represents the sum of branch lengths in the evolutionary tree connecting species within a given assemblage, often defined by geographic proximity (Davies & Buckley, 2011). PD has been mainly associated with regional altitudinal gradients (Kluge & Kessler, 2011; Manish, 2021; Manish & Pandit, 2018; Qian et al., 2014; W. Zhang et al., 2016; Zhu et al., 2019), where, the main findings point towards a monotonically decreasing pattern of phylogenetic diversity with respect to increasing elevation, or, in several cases, a “hump” pattern is also reported, presenting the highest PD values in the intermediate elevation zones. However, the exploration of the relationships established between mesoscale environmental gradients, such as topography, and the phylogenetic relationships between species that live in this type of microenvironments, are topics that are still very little studied, especially for the SDTF (Quisehuatl et al., 2023).

Many studies have attempted to classify species present in plant communities taking into account the importance of functional groups (H. Poorter & Navas, 2003), ecosystem engineers (Yeakel et al., 2020), functional traits (Kimball et al., 2016), keystone species (Garibaldi & Turner, 2004), relative abundance (Grime, 1998; Sonnier et al., 2010), among other components of biodiversity. These different community attributes can have direct effects on ecosystem functioning, generating complex interrelationships between different ecosystem components (Hooper et al., 2005; Mariotte, 2014). One of the simplest yet elegant approaches

that attempt to explain ecosystem functioning was proposed by Whittaker (1965), who postulated that species in a given community can be ranked according to their relative success in competition, which can be estimated through productivity. This categorization of species with respect to productivity curves gave rise to the classification of dominant, subordinate and transitional species (R. H. Whittaker, 1965). Later, Grime (1998) incorporated this categorization of species based on the degree of dominance in the "biomass proportion hypothesis", in which he states that dominant species, due to the large amount of biomass they represent, significantly influence the structuring of important ecosystem processes, such as the functional performance of species in ecosystems, which was subsequently corroborated experimentally by Garnier et al., (2004). Although the way in which dominant and subordinate species vary with respect to environmental gradients has been very little explored, research in this field has focused its attention on productivity and disturbance gradients (Tahmasebi Kohyani et al., 2009; Mariotte et al., 2013; Alvarez-Diaz et al., 2016), leaving aside the effect that other environmental gradients such as topography can exert, which have been closely linked to productivity and biomass in ecosystems such as the SDTF (Mohamed et al., 2014; Salinas-Melgoza et al., 2018), and which in turn, could represent a determining factor of variation for the degrees of dominance or subordination presented by the species that coexist through the gradients of drought risk imposed by the orientation of the slope and the topographic position.

Decades of study of plant functional traits have confirmed that plant functioning can be constrained by adaptive trade-offs or by a differential balance or investment of resources between incompatible traits (Grime, 1965; Grime & Mackey, 2002; Cerabolini et al., 2010; Pierce et al., 2012). However, trade-offs are not always obvious and functional traits can be conceptually divided into two classes. Traits involved in resource (matter and energy) capture, use and acquisition (e.g., leaf area, leaf mass per area, leaf dry matter content, seed mass,

height, stem specific density) are critical to biological functions and the balance between each other (“primary traits”) and, when considered as integrated sets of traits, can also be interpreted as “adaptive strategies” (Díaz et al., 2016; Pierce et al., 2017; Wright et al., 2004). Essentially, trait values are constrained by the trade-off in resource investment. In contrast, some individual traits or subsets of traits affect fitness during very specific times in the life cycle, particularly traits involved in reproductive ecology (‘proximal traits’; Grime & Pierce, 2012), which are therefore not constrained by the balance between primary resources.

Indeed, empirical studies demonstrate a primary spectrum of trade-offs (the ‘global spectrum of plant form and function’; Díaz et al., 2016), but that some traits are only loosely associated with this spectrum and exhibit additional, weaker trade-offs (Pierce et al., 2014), or specific character states that do not vary along a spectrum (e.g., flower colour states, C3 vs. C4, or CAM photosynthesis; Grime & Pierce, 2012). Because they do not represent quantities of resources but rather how resources are qualitatively deployed, proximate traits are largely unconstrained by the primary global spectrum of plant functioning. Indeed, Grime and Pierce (2012) proposed a model whereby primary (constrained) and proximal (unconstrained) traits are sequentially filtered during plant community assembly, resulting in overall convergence but local divergence of traits (see also Grime, 2006). Studies of native plant communities from harsh environments provide an extreme test that generally supports this view, finding that primary adaptive strategies of plants can be highly convergent, with species coexistence and community assembly explained by divergence in unconstrained traits (Rosado & de Mattos, 2017; Tameirão et al., 2021).

In less extreme environments, community assembly is likely to represent a balance between constrained traits (adaptive strategies) and proximal unconstrained traits, as suggested by Grime & Pierce (2012), although studies in the field of plant functional ecology tend to belong to different schools of thought focusing on either “strategies” or “traits”, and the relative

importance of restricted versus unrestricted functional traits during local community assembly is not considered. As unrestricted traits are particularly evident in harsh environments, the balance between restricted and unrestricted traits is also likely to shift along environmental gradients such as topography, although this remains to be investigated.

The only current theory of plant strategy that agrees with (and can potentially explain) the primary spectrum of resource economy and size is Grime's (2001, 1974) CSR theory of plant strategy, for which a globally applicable method for vascular plants is available (Pierce et al., 2017). In summary, Grime's CSR theory (Grime, 1974, 1977, 2001; Grime & Pierce, 2012) suggests that plants can be classified according to their life strategies in a triangular scheme. On the one hand, species with highly competitive ability (component C), survive using traits that maximize resource acquisition and control in constantly productive environments. Stress-tolerant species (component S), survive by maintaining metabolic performance in environments with high levels of environmental stress. While ruderal species (R component) are characterized by having accelerated life cycles with high seed production rates, and proliferate in environments exposed to high levels of disturbance.

The CSR classification has been currently used to describe plant ecological strategies at different spatial scales, ranging from regional (Novakovskiy et al., 2016; Rosenfield et al., 2019; Han et al., 2021) to local scale (Rosado & de Mattos, 2017; Araujo da Costa et al., 2020). This classification has also been used to characterize ecological strategies in different plant ecosystems, such as: laboratory experimental designs (Li & Shipley, 2017), coastal sandy plain forest (Araujo da Costa et al., 2020), lowland tropical forests (Chen et al., 2022; Wen et al., 2022), coniferous forests (Han et al., 2021) and subtropical forests (Rosenfield et al., 2019). However, the use of this type of tools for characterizing ecological strategies in widely extended ecosystems such as the SDTF, as well as the way in which these adaptative strategies

vary through the imposition of environmental filters inherent to topographic gradients, are topics that are still very little explored.

The general idea tested in this study (expressed as specific hypotheses, below) is that community assembly is associated with convergence on restricted traits (related to ecological strategies) and divergence (niche differentiation) on unrestricted traits. In this study, we tested the following specific hypotheses: (1) PD will be higher at middle and/or upper positions compared to lower mountain sites; (2) dominant species will occur more frequently at lower positions, whereas subordinate species will occur dispersed across both gradients imposed by elevation and slope aspect; (3) dominant species exhibit convergence toward one end of the strategy but are divergent from each other (i.e., they occupy a portion of the CSR triangle but do not overlap); subordinate species exhibit greater divergence across CSR strategies and differ in terms of individual traits or subsets of traits not directly related to CSR strategies (e.g., reproductive ecology traits); (4) Traits that involve amounts of matter ('constrained traits') will be correlated with C, S, or R values in the SDTF (i.e., they are constrained by trade-offs), whereas traits that do not involve amounts of matter ('unconstrained traits') are independent of CSR (and should be analyzed separately); (5) Environmental gradient responses identified solely from traits are also evident in CSR strategies.

Methods

Study area and sampling design

The study area is geographically positioned in the ejido of Tziritz'cuaro, which is located in the lower part of the Balsas Basin within the state of Michoacan in western Mexico (19 ° 01'30.1" N, 101 ° 58' 58.1"W). The vegetation in the area corresponds to tropical dry forest (Gentry, 1982), which develops mainly on low-lying mountains, whose altitude oscillates between 300- 800 meters above sea level (Ferrusquia-Villafranca, 1993). The vegetation

structure of the Tziritzícuaro TDF presents a medium height, canopy cover, and a basal area of 5 m, c. 300% and 18 m²/ha respectively, which are similar to those of other TDFs located in the Neotropics (Méndez-Toribio et al., 2014; Murphy & Lugo, 1995). The climate of the area is warm-dry and has a marked seasonality, with a drought that lasts from October to May, and a rainy season that goes from June to September (Méndez-Toribio et al., 2017).

In order to cover a greater range of floristic and environmental variability, 36 10 × 10 m (100 m²) sampling plots of forest dynamics were established along three topographic positions (TP: lower, middle and upper) and two slope aspects (SA: north and south), of three mountainous massifs (El Ortigo, La Araña and El Tukuy). The conditions imposed by these two topographic factors (TP and SA), represents in our study site, gradients of water availability and risk of drought for plants, ranging from sites with high soil moisture and evapotranspiration (e.g., lower N-facing slopes), to sites with low soil moisture and evapotranspiration (e.g., upper S-facing slopes; Méndez-Toribio et al., 2020). The plots were established in sites without apparent disturbance; however, the extraction of firewood and extensive livestock are common activities in areas surrounding the sites (Méndez-Toribio et al., 2016).

Functional traits and ecological strategies

A total of 14 traits and 3 demographic attributes of 55 plant species from seasonally dry tropical forests were used in this study: mean values of leaf area (LA, mm²), specific leaf area (SLA mm²/mg), leaf dry matter content (LDMC, mg/gram), height (H, m), bark thickness (BT, mm), bark water content (Bwc, %), leaf retention time (LRT, days), xylem water content (Xwc, %) and wood density (WD, g cm⁻³), we used these nine functional attributes published in (Méndez-Toribio et al., 2014, 2017). These nine vegetation attributes were sampled during the rainy

season in 2014 and come from the species present in the 36 sampling plots located at the study site (Table 1).

In addition, we used phenological data published in Cortés-Flores et al., (2019) that correspond to the fruit development time (FruitDev, days), fruit phenology (FruitPhen, degrees, measurements are expressed in these units because circular statistics were used to calculate the mean angle of fruit ripening) and fruit size (FruitSize, mm²). These data come from plant species from a dry forest present in Churumuco, a site also located in the Balsas Depression (approximately 40 km away from Tzitzucuaró). Likewise, viability (Viab, %) and seed germination (Germ, %) data were used, from the global seed information database (SID), provided by the Society for Ecological Restoration (SER) in collaboration with Royal Botanic Gardens Kew (RBGK) (data available at: <https://ser-sid.org/>) (Table 1). Additionally, three demographic rates which come from data published in Arriaga-Ramírez et al., (2024) in the same 36 sample plots were used: mortality (MR, %year⁻¹), recruitment (RR, %year⁻¹) and growth (RGR, %year⁻¹).

Finally, we calculated the values of the ecological strategies: competitive (C), stress tolerant (S) and ruderal (R) for each species using the 'StrateFy' tool proposed by Pierce et al., (2017). The calculation of the C, S and R scores are inferred through the analysis of the average values of three traits: leaf area (LA, mm²), specific leaf area (SLA, mm²/mg) and leaf dry matter content (LDMC, mg/gram), integrated and compared with offsets encompassing more than 3,000 species in a wide variety of biomes around the world. High values of SLA and LDMC represent the spectrum of fast and slow leaf economics, while LA has been correlated with the height of the plant and the mass of the seed, and they serve as an orthogonal axis with respect to the economics spectrum (Díaz et al., 2016). Thus, despite the fact that this classification of ecological strategies only uses three traits, it actually represents in a broader way the spectrum of plant functioning (Dayrell et al., 2018).

TRAITS	ABBREVIATION	UNITS	FUNCTIONAL ROLE	DATA PROVENANCE
LEAF AREA	LA	cm ²	Leaf cooling, light capture efficiency (self-shading)	Méndez-Toribio et al., (2017)
SPECIFIC LEAF AREA	SLA	cm ²	Leaf cooling, light capture efficiency (self-shading)	Méndez-Toribio et al., (2017)
LEAF DRY WATER CONTENT	LDMC	mg/g	Water-stress tolerance, leaf longevity	Méndez-Toribio et al., (2017)
BARK THICKNESS	BT	mm	Desiccation resistance (water storage/ water loss avoidance)	Méndez-Toribio et al., (2017)
BARK WATER CONTENT	Bwc	%	Lagging of water-stress, resistance to desiccation	Méndez-Toribio et al., (2017)
XYLEM WATER CONTENT	Xwc	%	Lagging of water-stress, resistance to desiccation	Méndez-Toribio et al., (2017)
WOOD DENSITY	WD	g cm ⁻³	Drought tolerance	Méndez-Toribio et al., (2017)
LEAF RETENTION TIME	LRT	days	Drought avoidances	Méndez-Toribio et al., (2017)
PLANT HEIGHT	H	m	The ability to pre-empt light resources and disperse diaspores	Méndez-Toribio et al., (2014)
DEVELOPMENT TIME OF THE FRUIT	FruitDev	days	Affects subsequent life cycle events including dispersal and establishment	Cortés-Flores et al., (2019)
FRUIT PHENOLOGY	FruitPhen	degrees	Affects subsequent life cycle events including dispersal and establishment	Cortés-Flores et al., (2019)
FRUIT SIZE	FruitSize	mm ²	Reflects a tradeoff between seedling survival versus colonization ability in space and time	Cortés-Flores et al., (2019)
SEED VIABILITY	Viab	%	Increased regenerative capacity	Global seed information database (SID)
SEED GERMINATION	Germ	%	Increased regenerative capacity	Global seed information database (SID)

Table 1. Table 1. List and description of the eight functional traits of leaves and branches (leaf area, specific leaf area, leaf dry matter content, water content in bark and xylem, wood density, leaf retention time and plant height), three phenological traits (development time and fruit size, and fruit phenology) and two seed traits (germination and viability); measured in 57 species of seasonally dry tropical forest trees in western Mexico.

Data analysis

Ternary graphs and range-abundance curves were constructed in the SigmaPlot program. In both cases, the following species dominance index was implemented:

$$D_{index} = Cob * H * Abun$$

where 'Cob' corresponds to the sum of the canopy cover, 'H' corresponds to the average height and 'Abun' corresponds to the abundance of a species in a given community. Likewise, rescaling of the data from 1 to 0 was used to "smooth" the graphs and help to have a better visual presentation of them.

In order to reduce the dimensionality and assess the magnitude of the relationships between the different functional traits, principal component analyses (PCA) and Spearman rank correlations were performed using the packages 'ade4', 'vegan' and 'Hmisc'. These analyses were performed for the entire community, topographic position, and slope aspect. Subsequently, using the 'FD' package and using the mean values of the functional attributes and the abundance of the species, the values of the community weighted means (CWM) of each of the 36 sampling plots were calculated (Lavorel et al., 2008). Similarly, using the 'FD' and the full set of functional traits, functional richness values (FRic) were calculated for each sample plot (Villéger et al., 2008).

To calculate the phylogenetic diversity (PD) of the plots, a reconstruction based on the rcbL gene was used for 60 species and data on their abundance through the topographic gradient. Sequence information alignment and filtering was carried out in the MUSCLE online tool (available at: <https://www.ebi.ac.uk/Tools/msa/muscle/>), while the best model of nucleotide substitution was selected using the Akaike Information Criterion (AIC) in the jModelTest program. Phylogenetic reconstructions were carried out using the 'raxml' program (available at: <https://raxml-ng.vital-it.ch/#/>), using the maximum likelihood procedure. The calculation of PD values in each plot was performed using the 'picante' package (Faith, 1992)

To test whether the values of CWM, FRic, and PD varied significantly along the environmental gradient imposed by the topography (SO, TP, and SO x TP), we used a generalized linear model (GLM). Since the values of all the variables were continuous data, we used a Gaussian error identity link. The graphs corresponding to the PCA, the relationships between CWM vs FRic and PD, Spearman rank correlations, as well as all the statistical analyses of the different variables were constructed using the Rstudio program (version 4.05).

Results

Dominant and subordinate species

Eight dominant species (*Cordia eleagnoides*, *Cyrtocarpus procera*, *Randia nelsonii*, *Senegalia picachensis*, *Lysiloma divaricatum*, *Euphorbia schlechtendalii*, *Apoplanesia paniculata* and *Handrohantus impetiginosus*) and 47 subordinate species (list of subordinate species available in appendix x) were found in a SDTF plant community located in the lower part of the Balsas basin, Michoacán-Mexico.

Rank/abundance curves (calculated using the dominance index rather than abundance per se) indicated different degrees of dominance and species richness for the different topographic positions (lower, middle and upper sites), with the lower site characterized by the lowest species richness (35 species) and the highest degree of dominance (i.e., a small number of species were particularly dominant, with fewer species subordinated with respect to the middle and upper sites; Fig. 2). In contrast, the upper sites included three prevalent species with a much lower degree of dominance with respect to the degree of dominance at the lower sites, accompanied by a higher species richness (44 species). Indeed, the identity of the dominant species also changed, with *Cordia eleagnoides* being one of the most dominant species at all sites, but *Senegalia picachensis* and *Randia nelsonii* being the most dominant at the lower positions and *Lysiloma divaricatum* and *Apoplanesia paniculata* becoming dominant at the upper positions.

There were different degrees of dominance, but not species richness, on both slopes (north and south). On the southern slopes there were 46 species and a higher degree of dominance (dominant species: *Cordia eleagnoides*, *Randia nelsonii*, *Lysiloma divaricatum* and *Euphorbia schlechtendalii*), in relation to the northern slopes where 44 species were present, but a lower degree of dominance (dominant species: *Senegalia picachensis*, *Randia nelsonii*, *Cordia eleagnoides*, *Handrohantus impetiginosus*, *Apoplanesia paniculata* and *Lysiloma*

divaricatum). However, the identity of the most dominant species on both slopes was very similar, with the exception of *Euphorbia schlechtendalii*, which functioned as a dominant species only on the southern slopes.

Phylogenetic diversity and functional richness

Phylogenetic diversity (PD) was significantly higher on north-facing slopes than on south-facing slopes ($F=4.36$, $p=0.04$) (Fig. 6), but did not change significantly with position. Changes in phylogenetic diversity were not correlated with changes in the degree of selection on C, S, or R, and did not vary significantly with SA (Fig. 6A–C; Table S2). Individual traits decreased on south-facing slopes along with PD, however, only WD showed significant relationships with SA ($F=9.95$, $p<0.01$; Fig. 6F). Likewise, other individual traits less important in plant functioning showed statistical relationships with SA (Viab: $F=32.9$, $p<0.01$; Germ: $F=13.57$, $p<0.01$; FruitSize: $F=4.85$, $p=0.03$; Table S4).

Functional richness (FRic) (the range of values for all traits) increased from lower to higher topographic positions ($F=4.17$, $p=0.02$) (Fig. 5), but not with different slope aspects (non-significant data not shown; Table S5). With topography, the extent of community- and individual-trait-weighted mean CSR strategies were related to FRic: S- and R-scores (but not C-scores) also changed with topography (S: $F=3.54$, $p=0.04$; R: $F=3.4$, $p=0.04$), with higher functional richness of higher sites associated with significantly higher R-selection and less S-selection (Fig. 5A–C). Individual traits showed different relationships with topographic position and FRic, with CWM leaf retention time (LRT) and wood density (WD) decreasing with FRic (LRT: $F=7.2$, $p<0.01$; WD: $F=17.9$, $p<0.01$) (Fig. 5D, F) and CWM bark water content (Bwc) increasing concomitantly with FRic ($F=9.4$, $p<0.01$) (Fig. 5E).

Ecological strategies and plant functional traits

The CSR strategies of the dominant species (*Cordia alliodora*, *Cyrtocarpus procera*, *Randia nelsonii*, *Senegalia picachensis*, *Lysiloma divaricatum*, *Euphorbia schlechtendalii*, *Apollonia paniculata*, and *Handrohantus impetiginosus*) were convergent (i.e., restricted to the SC to S region of the CSR triangle), but each species diverged from each other (Fig. 1A). Subordinate species occupied a wider range of the CSR triangle (i.e., convergence was less extreme), and the only highly competitive species was a subordinate species (*Plumeria rubra*) (Fig. 1A; Table 2).

The entire community was characterized by variation primarily between the extremes of C and S selection, with most species trending toward stress tolerance (Fig. 1A; Table 2). Some variation in R-selection was evident towards the centre of the CSR space (i.e., there were no ruderal species in an absolute sense, although differences in the extent of R-selection were apparent) (Fig. 1A; Table S1). Despite the evident variation in CSR strategies, the main axis of variation (PCA1; Fig. 1B) was not determined by CSR strategies, as it is not related to C, S and R selection. It was primarily an axis of variation: tissue water content (Xwc and Bwc), leaf retention time (LRT) and wood density (WD); and weaker with bark thickness (BT), germination (Germ) and seed viability (Viab).

LRT was significantly (positively) associated with WD, as were Bwc and Xwc. However, these two trait groups (tissue water content versus WD-LRT) were significantly (negative) associated in pairwise comparisons. On the other hand, Viab was positively correlated with Germ and BT was negative correlated with fruit phenology (FruitPhen). The second axis of variation (PCA2; Fig. 1B) was strongly related to CSR strategies, representing the balance between C and S selection, but weaker in plant phenology attributes (FruitDev and FruitSize). C and S selections were negatively associated, while fruit development time (FruitDev) was associated (also negative) only with Viab (Fig. 1B; Table S2).

The strong dominance of the lower topographic position by three species represented the dominance of three divergent CSR strategies (Fig. 3A), in contrast to the situation at the upper topographic position where dominance was shared not only by a larger number of species, but by a broader range of CSR strategies, across the CSR region, 'CS' to 'S' of the CSR triangle (Fig. 3C). The main variation in plant function (PCA1) occurred at the middle and upper sites, and was generally a water-related functional axis in tissue water content (Bwc and Xwc). In the case of the lower sites, there were no significant relationships between any of the variables used in this study (Fig. 3D). CSR strategies presented only significant (negative) association between C and S selection at the middle and upper positions (Fig. 3; Table S2), with the rest of the variables there were no significant associations at any of the three topographic positions. The top and middle sites (PCA1; Fig. 3E and 3F) were characterized by significant (positive) associations between Bwc and Xwc. At the top positions, tissue water content had significant (negative) relationships with WD and LRT (Fig. 3F; Table S2); furthermore, Viab was (negative) correlated and Fruitdev was (positive) correlated with PCA1, and Viab was (positively) correlated with Germ. The second axis of variation (PCA2) only had a significant (positive) association with recruitment rate (RR) at the top positions (Fig. 3; Table S2). The strong dominance on the S slope by three species represented the dominance of three divergent CSR strategies (Fig. 4B), in contrast to the situation observed on the N slope where dominance appears to be weaker and shared by a larger number of species and ecological strategies, ranging from the 'CS' to the 'S' region in the CSR strategy triangle (Fig. 4A). The main variation in plant function (PCA1) among slopes was generally a 'C' selection axis, with important extension and 'S' on both slopes; together with variation in WD, LRT, Xwc and Bwc. On the northern slopes, PCA1 was characterized by a C (negative) and Bwc, Xwc selection gradient for selection of single traits such as WD and LRT (positive); On the southern slopes, selection C and selection S maintained the same relationship as on the northern slopes,

however, they presented weak and non-significant associations with PCA1 (Fig. 4B; Table S3). In addition, on the S slopes, selection R and the rest of the individual traits (WD, LRT, Xwc, Bwc) presented changes in the convenient direction of these (Fig. 4). The second axis of variation (PCA2) was characterized by presenting significant relationships with selections C (negative) and S (positive) only on the northern slopes.

Table 2. Functional strategies (C, S, R scores) and traits of 55 species sampled in vegetation from seasonally dry tropical forest (SDTF) in the lower part of the Balsas basin in Michoacan-Mexico. The values correspond to the average of five repetitions per species. CSR Categories: classes of strategy categories according to Pierce et al., (2017); C: competitiveness (%); S: stress tolerance (%); R: ruderalism (%); LA: leaf area (mm²); SLA: specific leaf area (mm² mg⁻¹); LDMC: leaf dry matter content (%); D_{index}: dominance index (relative units).

Family	Species	CSR category	C	S	R	LA	LDMC	SLA	D _{index}
Anacardiaceae	<i>Amphipterygium adstringens</i> (Schltdl.) Standl.	S/CS	21.4	69.4	9.2	573.33	32.18	11.72	20004.99
Verbenaceae	<i>Lippia umbellata</i> Cav.	S/CSR	27.5	53.5	19.1	1239.80	31.24	15.65	14965.33
Fabaceae	<i>Bauhinia divaricata</i> L.	CSR	28.6	37.2	34.3	1705.99	27.59	26.23	1418.25
Boraginaceae	Boraginaceae sp	CS/CSR	33.7	48.4	17.9	2194.18	31.67	16.12	14.16
Fabaceae	Brongniartia sp.	S/CSR	13.5	56.9	29.6	382.75	32.07	20.04	3399.99
Malpighiaceae	<i>Bunchosia palmeri</i> S. Watson	CS/CSR	39.8	38.4	21.8	2600.61	26.75	17.20	1134.21
Burseraceae	<i>Bursera denticulata</i> McVaugh y Rzed.	S/CS	15.5	82.5	2.0	323.66	34.88	10.13	97.39
Burseraceae	<i>Bursera inferdinalis</i> Guevara y Rzed.	S	11.0	78.8	10.2	264.46	39.23	12.34	314.57
Burseraceae	<i>Bursera fagaroides</i> (Kunth) Engl.	S	3.8	96.2	0.0	133.17	20.92	6.11	555.16
Burseraceae	<i>Bursera copallifera</i> (DC.) Bullock	S	4.8	95.2	0.0	193.40	82.47	8.24	588.45
Burseraceae	<i>Bursera</i> sp	S	7.0	93.0	0.0	267.36	71.94	4.57	1096.69
Burseraceae	<i>Bursera grandifolia</i> (Schltdl.) Engl.	CS/CSR	37.6	49.3	13.0	2209.88	30.00	13.53	1845.95
Burseraceae	<i>Bursera trimera</i> Bullock	S/CS	19.0	81.0	0.0	401.19	32.98	9.62	2529.01
Burseraceae	<i>Bursera heteresthes</i> Bullock	S/CS	31.2	60.6	8.2	1727.15	35.52	12.10	2800.59
Burseraceae	<i>Bursera crenata</i> Paul G. Wilson	S/CS	26.2	73.8	0.0	957.03	36.30	8.63	11176.52
Burseraceae	<i>Bursera coyucensis</i> Bullock	S	10.7	86.7	2.6	255.08	42.78	10.35	12636.95
Fabaceae	<i>Poincianella eriostachys</i> Benth.	S/SR	0.8	79.8	19.4	34.18	39.74	15.26	233.17
Bombacaceae	<i>Ceiba aesculifolia</i> (Kunth) Britten y Baker f.	S/CSR	32.5	58.3	9.1	1460.57	31.48	12.02	700.14
Polygonaceae	<i>Coccoloba acapulquensis</i> Standl.	CS	40.1	58.3	1.6	2579.03	33.92	10.16	1411.20
Bixaceae	<i>Cochlospermum vitifolium</i> (Willd.) Spreng.	CS/CSR	46.4	34.1	19.5	5999.82	29.42	19.43	39040.12
Boraginaceae	<i>Cordia alliodora</i> (Ruiz y Pav.) Oken	S/CS	30.7	59.9	9.5	4449.82	31.91	12.11	179.81
Fabaceae	<i>Coulteria platyloba</i> S. Watson	S/CS	22.6	64.8	12.5	639.36	30.99	12.55	227.51
Euphorbiaceae	<i>Croton morifolius</i> Willd.	CS/CSR	44.0	42.1	13.9	198.82	31.78	11.22	17547.33
Fabaceae	<i>Diphysa floribunda</i> Peyr	S/SR	2.9	79.0	18.1	45.64	28.05	12.53	548.08
Erythroxylaceae	<i>Erythroxylum rotundifolium</i> Lunan	S/CS	18.3	77.2	4.5	522.28	37.25	10.77	574.97

Erythroxylaceae	<i>Erythroxylum mexicanum</i> Kunth	CSR	39.7	34.2	26.0	1964.39	23.87	17.44	812.43
Rubiaceae	<i>Genipa americana</i> L.	C/CS	61.7	30.5	7.8	13615.66	30.06	13.37	765.77
Fabaceae	<i>Haematoxylum brasiletto</i> H. Karst.	S/SR	10.9	60.6	28.5	181.25	27.51	16.03	179.74
Malvaceae	<i>Heliocarpus occidentalis</i> Rose	C/CSR	47.4	29.5	23.1	2264.72	34.38	11.76	32217.48
Rubiaceae	<i>Hintonia latiflora</i> (Sessé y Moc. ex DC.) Bullock	S/CSR	30.8	55.0	14.2	2004.40	35.51	14.72	19321.09
Caricaceae	<i>Jacaratia mexicana</i> A. DC.	C/CR	62.7	7.8	29.6	5351.75	18.15	20.17	2779.84
Rhamnaceae	<i>Karwinskia latifolia</i> Standl.	S/CSR	24.9	53.3	21.8	762.54	27.96	15.23	35.60
Fabaceae	<i>Lonchocarpus longipedunculatus</i> M. Sousa y J. C. Soto	CS/CSR	36.7	50.4	12.9	3152.26	35.24	14.63	6553.43
Fabaceae	<i>Lonchocarpus constrictus</i> Pittier	S	12.1	80.2	7.7	470.16	52.49	12.39	16789.02
Fabaceae	<i>Lysiloma tergeminum</i> Benth.	S/CSR	18.1	50.3	31.6	808.39	33.37	24.62	29646.51
Malpighiaceae	<i>Malpighia mexicana</i> A. Juss.	S/CSR	32.1	54.0	13.9	2365.39	36.46	14.94	746.07
Fabaceae	<i>Mimosa rosei</i> B. L. Rob.	S/SR	10.7	68.6	20.8	287.16	37.76	16.49	1412.67
Fabaceae	<i>Mimosa arenosa</i> (Willd.) Poir.	S	0.0	100.0	0.0	5.15	42.29	0.04	55531.89
Capparaceae	<i>Morisonia americana</i> L.	CS	39.9	60.1	0.0	5491.12	49.38	5.31	0.32
Fabaceae	<i>Piscidia piscipula</i> (L.) Sarg.	S/CS	34.6	63.0	2.3	1305.78	30.52	10.22	1.84
Fabaceae	<i>Pithecellobium dulce</i> (Roxb.) Benth.	S/CS	17.3	74.6	8.1	373.80	32.22	11.33	5.89
Apocynaceae	<i>Plumeria rubra</i> L.	C	90.0	8.4	1.6	12230.48	18.43	10.17	3418.66
Fabaceae	<i>Pterocarpus orbiculatus</i> DC.	S/CS	25.4	69.9	4.8	2012.35	52.12	11.54	477.84
Polygonaceae	<i>Ruprechtia fusca</i> Fernald	S/CS	23.6	73.5	2.9	1041.83	41.04	10.53	243.51
Anacardiaceae	<i>Spondias purpurea</i> L.	CS/CSR	50.1	37.8	12.1	717.96	19.78	10.97	737.35
Cactaceae	<i>Stenocereus queretaroensis</i> (F.A.C. Weber) Buxb.	S	9.0	91.0	0.0	377.76	30.54	0.61	465.80
Fabaceae	<i>Vachellia campechiana</i> Wight y Arn.	S/SR	0.0	81.2	18.8	1.27	41.83	15.36	206.45
Fabaceae	<i>Apoplanesia paniculata</i> C. Presl	S/CSR	14.4	62.3	23.3	329.54	30.68	15.79	155686.06
Boraginaceae	<i>Cordia elaeagnoides</i> DC.	CS	46.7	46.0	7.3	4449.82	31.91	12.11	721151.22
Anacardiaceae	<i>Cyrtocarpa procera</i> Kunth	S/CS	20.0	74.9	5.2	455.65	32.09	10.73	447062.35
Euphorbiaceae	<i>Euphorbia schlechtendalii</i> Boiss.	SR/CSR	13.6	52.1	34.3	290.20	27.30	19.40	170397.78
Bignoniaceae	<i>Handroanthus impetiginosus</i> (Mart. ex DC.) Mattos	CS	35.9	57.1	7.0	2264.72	34.38	11.76	101382.60
Fabaceae	<i>Lysiloma divaricatum</i> (Jacq) J.F. Macbr	S	0.0	100.0	0.0	4.19	43.70	4.01	294045.55
Rubiaceae	<i>Randia nelsonii</i> Greenm.	S/CS	17.5	79.4	3.1	535.76	39.89	10.49	333440.39
Fabaceae	<i>Senegalia picachensis</i> Brandegee	S	0.0	85.2	14.8	5.74	43.85	13.96	308561.80

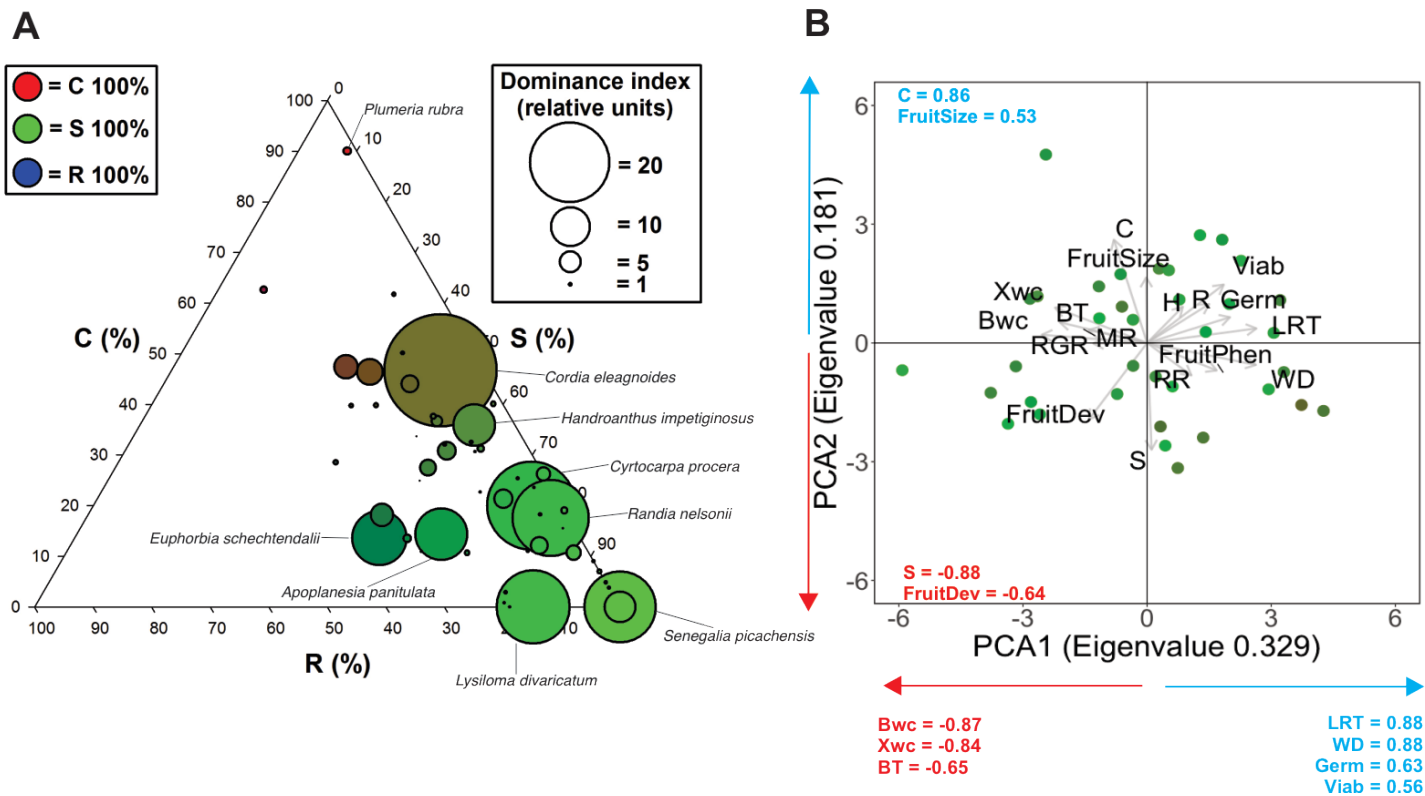


Fig. 1 Regional (mean, across-site) plant functioning in a seasonal dry forest in Michoacán, Mexico: A). the CSR strategies of single species (point size proportional to a 'relative dominance index' calculated as the square root of abundance (number of individuals) \times height (m) \times cover (m²), divided by a rescaling constant of 30), and B). multivariate analysis (principal components analysis; PCA) of CSR/trait relationships at 36 sites (color represents the median CSR strategy at each site). For B, significant correlations between the main axes of trait variability (PCA1 and PCA2) and either traits or the extent of competitive ability (C), stress-tolerance (S) and ruderalism (R) are shown, and were determined using Spearman's correlation coefficient (ρ), with significant correlations at the $P \leq 0.001$ level (point colors represent the median CSR strategy at each site). Traits are: Viability: Viab, Germination: Germ, Fruit Phenology: FruitPhen, Fruit Size: FruitSize, Fruit Development: FruitDev, Xylem water content: Xwc, Bark water content: Bwc, Bark Thickness: BT, Wood Density: WD, Leaf Retention Time: LRT, Height: H, Mortality Rate: MR, Recruitment Rate: RR, and Growth Rate: RGR. For full table of Spearman correlation coefficients between all traits, see Table S1.

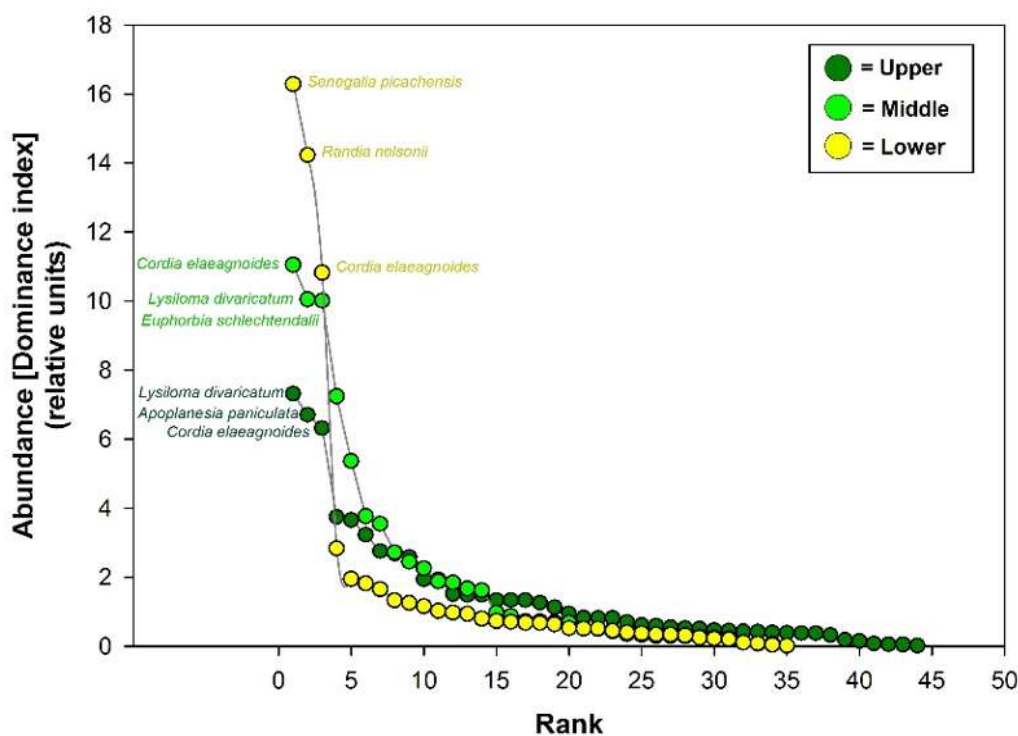


Fig. 2 Range/abundance curve, with abundance expressed as relative dominance taking into account the abundance, height and cover of the species present in three different topographic positions: lower (yellow), middle (light green) and upper (bright green).

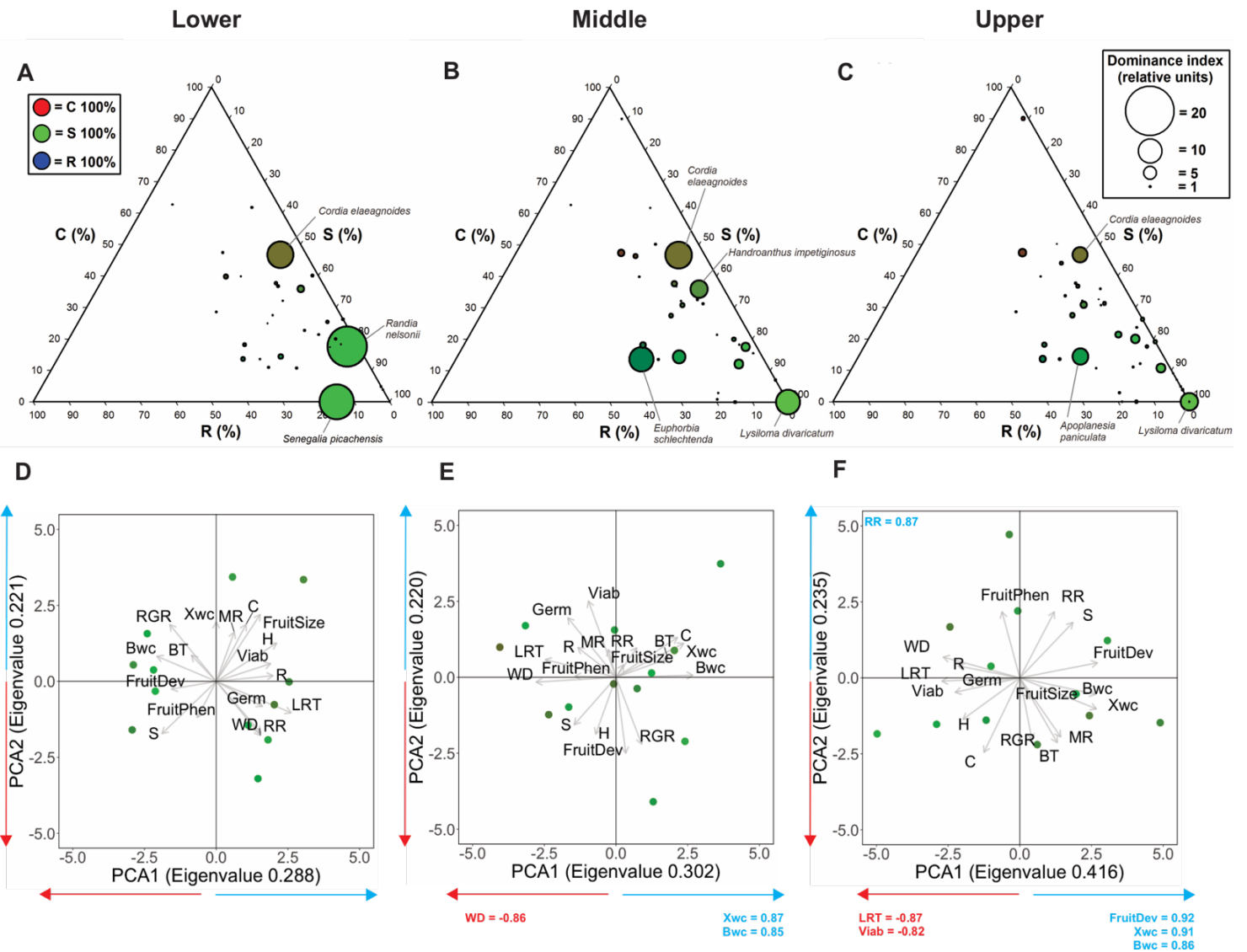


Fig. 3 Plant functioning along a topographic gradient in seasonal dry forest communities in Michoacán, Mexico: A-C). the CSR strategies of single species across Lower, Middle and Upper (respectively) topographic positions (point size proportional to a 'relative dominance index' calculated as the square root of abundance (number of individuals) × height (m) × cover (m²), divided by a rescaling constant of 30), and D-F). multivariate analysis (principal components analysis; PCA) of CSR/trait relationships at Lower, Middle and Upper topographic positions (respectively) (color represents the median CSR strategy at each site). For B, significant correlations between the main axes of trait variability (PCA1 and PCA2) and either traits or the extent of competitive ability (C), stress-tolerance (S) and ruderalism (R) are shown, and were determined using Spearman's correlation coefficient (ρ), with significant correlations at the $P \leq 0.001$ level (point colors represent the median CSR strategy at each site). Traits are: Viability: Viab, Germination: Germ, Fruit Phenology: FruitPhen, Fruit Size: FruitSize, Fruit Development: FruitDev, Xylem water content: Xwc, Bark water content: Bwc, Bark Thickness: BT, Wood Density: WD, Leaf Retention Time: LRT, Height: H, Mortality Rate: MR, Recruitment Rate: RR, and Growth Rate: RGR. For full table of Spearman correlation coefficients between all traits, see Table S1.

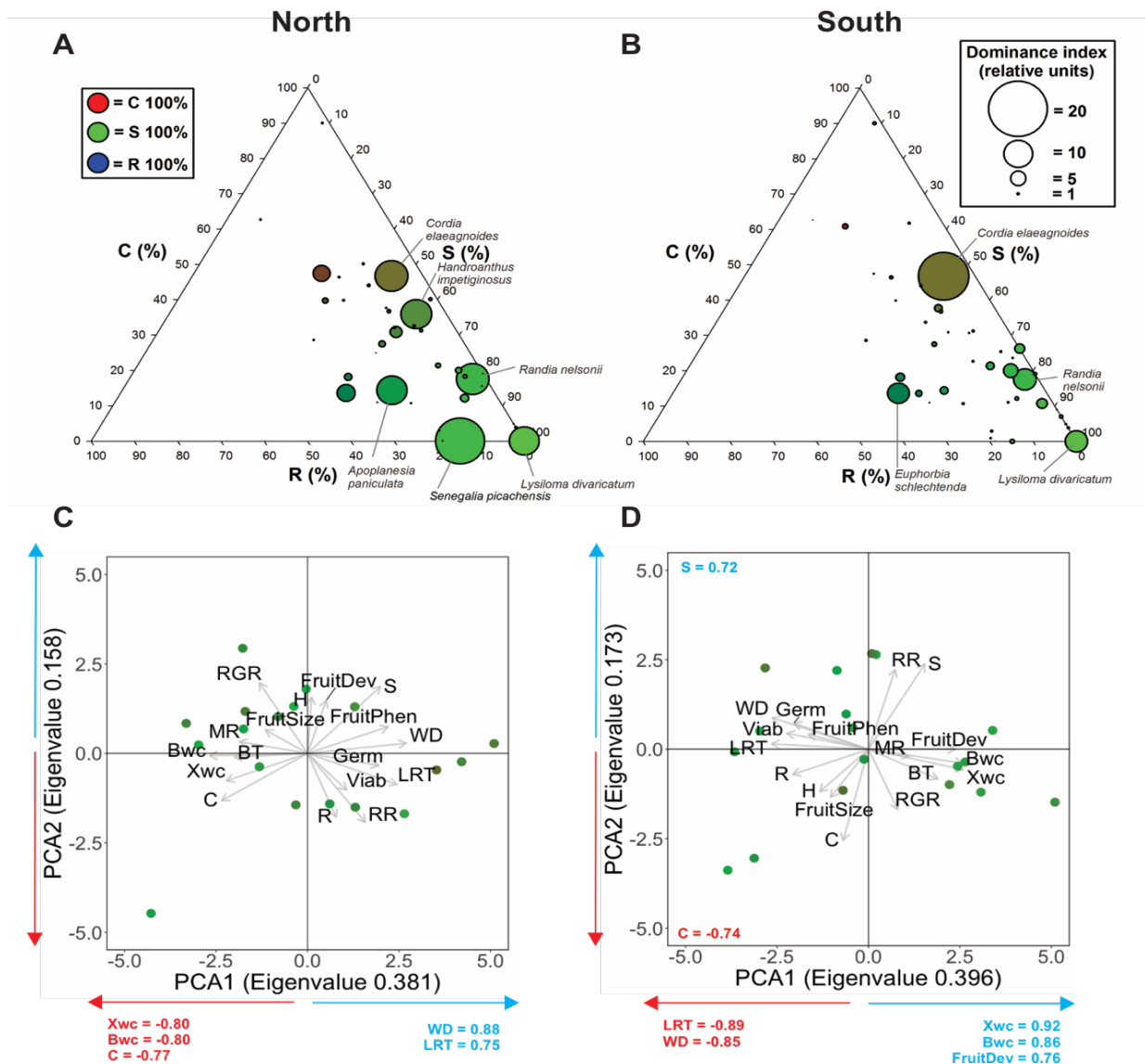


Fig. 4 Plant functioning in different slope aspects (north and south) in seasonal dry forest communities in Michoacán, Mexico: A,B). the CSR strategies of single species on Northern and Southern (respectively) slope aspects (point size proportional to a 'relative dominance index' calculated as the square root of abundance (number of individuals) \times height (m) \times cover (m²), divided by a rescaling constant of 30), and C-D). multivariate analysis (principal components analysis; PCA) of CSR/trait relationships on Northern and Southern (respectively) slope aspects (color represents the median CSR strategy at each site). For B, significant correlations between the main axes of trait variability (PCA1 and PCA2) and either traits or the extent of competitive ability (C), stress-tolerance (S) and ruderalism (R) are shown, and were determined using Spearman's correlation coefficient (ρ), with significant correlations at the $P \leq 0.001$ level (point colors represent the median CSR strategy at each site). Traits are: Viability: Viab, Germination: Germ, Fruit Phenology: FruitPhen, Fruit Size: FruitSize, Fruit Development: FruitDev, Xylem water content: Xwc, Bark water content: Bwc, Bark Thickness: BT, Wood Density: WD, Leaf Retention Time: LRT, Height: H, Mortality Rate: MR, Recruitment Rate: RR, and Growth Rate: RGR. For full table of Spearman correlation coefficients between all traits, see Table S1.

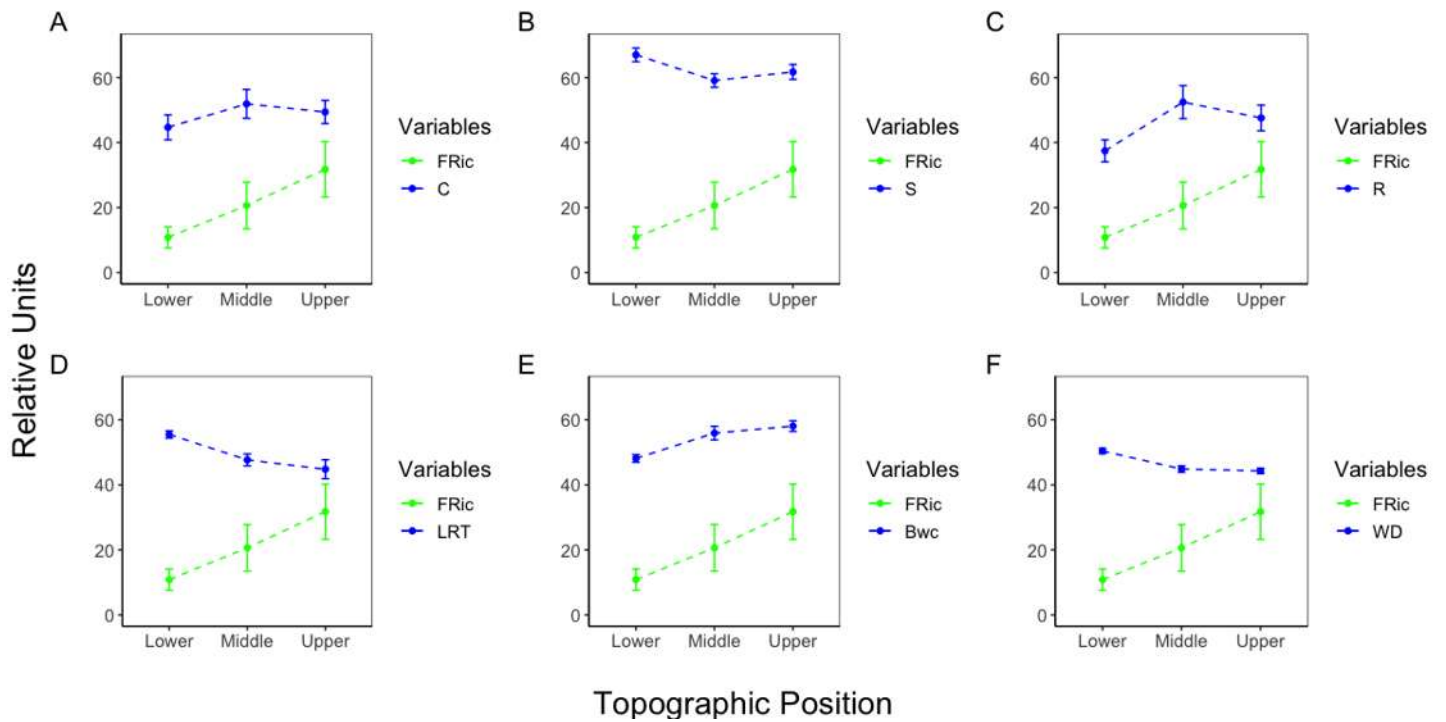


Fig. 5 Changes across topographic positions for overall functional richness (FRic; green), compared against a range of changes (blue) in community weighted mean (CWM) C, S, and R scores (A – C, respectively) and traits determined by PCA to be of primary importance: leaf retention time (LRT; D), bark water content (Bwc; E) and wood density (WD; F) in seasonal dry forest communities in Michoacán, Mexico. The data were transformed using multiplications and divisions with respect to the mean values of FRic at the different topographic positions, the values represent relative units.

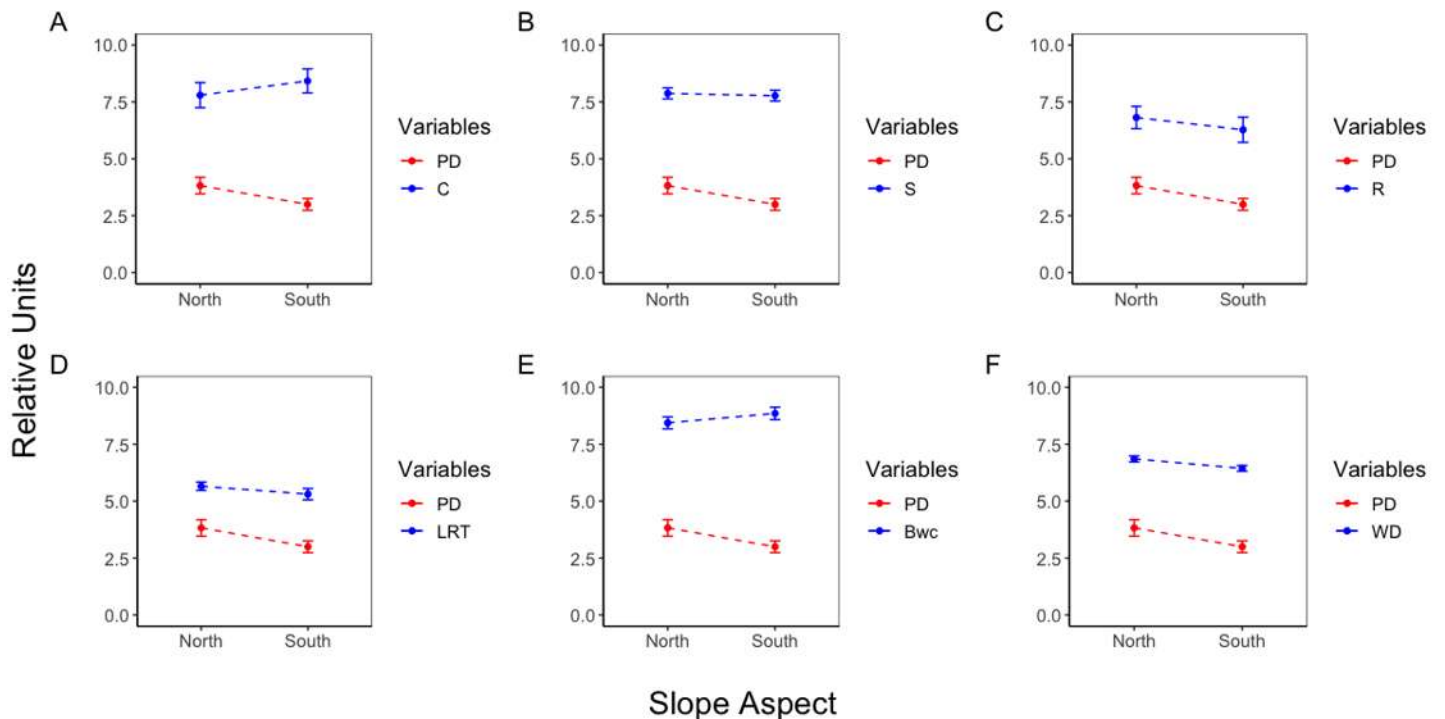


Fig. 6 Changes between slope aspects (north and south) in overall phylogenetic diversity (PD; red) and a range of plant characters (blue) including community weighted mean (CWM) C, S, and R scores (A – C, respectively) and traits determined by PCA to be of primary importance: leaf retention time (LRT; D), bark water content (Bwc; E) and wood density (WD; F) in seasonal dry forest communities in Michoacán, Mexico. The data were transformed using multiplications and divisions with respect to the average values of PD in the different slope aspects, the values represent relative units.

Discussion

Research on species categorization according to the level of dominance or subordination in a Mexican SDTF revealed the existence of eight dominant species and 47 subordinate species. However, the categorization according to the degree of dominance and subordination that the species present and that is framed in the theory proposed by (Grime, 1998; Whittaker, 1965), points to biomass as the fundamental factor of this categorization, as such, dominant species are more competitive since they present a greater amount of biomass, and on the other hand, subordinate species represent the most diverse community component (Garbin et al., 2016). In our study, dominance was expressed through the relationships established between cover, height and abundance of the species, trying to reflect both the horizontal and vertical competitive capacity of the species. Furthermore, these two vegetation attributes (cover and height) have been correlated with high levels of biomass production in different ecosystems (Zhang et al., 2016; Sanaei et al., 2018; Proulx, 2021; Shu et al., 2023), thus providing a strong theoretical link for the use of these variables as indirect estimators of aboveground biomass production. However, exploring aboveground biomass generation by species and how this attribute varies across the topographic gradient is a topic that remains open for future research at our study site.

Likewise, this research also revealed different identities and degrees of dominance of the species that coexist across the different microenvironments imposed by environmental gradients associated with topographic position (TP) and slope orientation (SA). Highlighting the role played by *Cordia elaeagnoides* as a species that presents high levels of dominance not only at the level of the entire community, but also across the metacommunities formed by the interaction of the two topographic factors (TP and SA) analysed. Some authors consider that these dominant species can appropriate the potential spatial niche of subordinate species (McNaughton & Wolf, 1970), and in this way, significantly influence the flows of matter and

energy experienced by ecosystems (Grime, 1998). *Cordia elaeagnoides* is an endemic tree of deciduous and semi-deciduous forests of the Pacific slopes of Mexico. It is of human interest due to its suitability as a biotic resource with timber potential (Van Groenendael et al., 1996). Its dense wood suggests that it is not a pioneer species, but its reproductive characteristics such as self-compatibility and anemochorous dispersal of pollen and seeds suggest a colonizing life strategy (Van Groenendael et al., 1996); these characteristics together could have a significant impact on the occupation of pollination niches for this species. There is specific scientific evidence that links the adaptation of pollinators and the evolution by reproductive isolation of plants. In turn, these microevolutionary processes impact the structuring of macroevolutionary patterns through adaptive radiations in pollination systems (Van der Niet & Johnson, 2012; Lagomarsino et al., 2017; Phillips et al., 2020). This is undoubtedly an extremely important area of research that remains to be explored in future research in our study site, as it could provide us with valuable information that puts into a broader context the panorama concerning the adaptive and dominance relationships established between the species that coexist in this Mexican SDTF.

In our research, we found significant relationships of phylogenetic diversity (PD) given by SA, but not by TP, presenting the highest values on the north-facing slopes. Changes in PD values have been associated with elevation, because altitude significantly influences local conditions (precipitation and temperature ranges, humidity below and above ground, atmospheric pressure, etc.), environmental filters associated mainly with precipitation and temperature influence the phylogenetic relationships of species (Qian & Sandel, 2017; C. Zhang et al., 2020; Pinto et al., 2023).

In the specific case of the dry tropical forest, it has been reported that in an altitudinal gradient located in the Andes, the lowest PD values occur in the lower positions, this in accordance with the presence of lower water availability and high temperatures that are the

main drivers of low levels of diversity and greater phylogenetic clustering in these sites (Cisneros et al., 2021). These results agree with what we reported in this research, that is, upper positions of our study site represent a greater water risk for plants compared to the lower positions of the mountains (Méndez-Toribio et al., 2017), which may influence the phylogenetic structure of the plant metacommunities formed by elevation. It is worth highlighting that despite the similarity in the PD value patterns presented across our shortest elevation gradient (mesoscale), there were no significant differences between treatments when statistical tests were applied. However, one aspect that remains to be explored at our site is the study of phylogenetic grouping across topographic positions, which can provide us with valuable information about the relationships that exist between the environment and the phylogenetic structure of these plant communities.

Likewise, significant PD values were linked to SA in our study and occurred in areas with greater water availability and low temperatures, i.e., north-facing slopes. These results are consistent with environmental filtering in gradients that show high diversity and lower phylogenetic clustering in communities established in less warm and dry areas (González-Caro et al., 2014; Qian & Sandel, 2017; Liu et al., 2019; Cisneros et al., 2021). Although there are regional studies that point towards a non-random spatial and environmental distribution of phylogenetic diversity (e.g., plant communities in the Amazon Honorio Coronado et al., 2015, or the dry tropical forests of the Andes Cisneros et al., 2021), the effects of environmental filtering at smaller scales do not seem to follow a defined pattern given by the mechanisms proposed to explain this non-random variation in phylogenetic structure. Due to this substantial information gap, regional studies that evaluate the relationships of phylogenetic structure with slope orientation and elevation across different biogeographic regions, as is the case of the distribution of SDTF in Mexico, are of vital importance since these ecosystems are threatened

due to changes in land use and other human activities such as climate change, which directly impacts the distribution and adaptation patterns of the species present in this type of ecosystem.

In this study, we found a significant association between functional richness (FRic) and topographic position. FRic increases positively with elevation, presenting the highest values in the upper positions of the mountains. The same pattern of functional richness with elevation has been reported in other studies (Pakeman, 2011; Apaza-Quevedo et al., 2015), however, generalizations about the patterns involving functional richness with topography (mesoscale) are still sketchy and currently lack a strong theoretical support. A possible explanation for the presence of higher FRic in the upper and middle positions is related to the occurrence of environmental conditions that favor the coexistence of species with conservative and acquisitive functional strategies. This coexistence of species with different strategies in the upper positions would lead to an increase in the space of functional traits, resulting in higher levels of FRic in those sites (Apaza-Quevedo et al., 2015).

In our study site, the upper positions present environmentally more heterogeneous conditions than the lower positions. In general, these sites present more rugged microtopography, have shallower soils, are colder, drier and less exposed to radiation (especially during the dry season) than the lower positions, which represents a shorter and fluctuating window of water availability for the plants that live in these sites (Méndez-Toribio et al., 2017, 2020). This environmental heterogeneity associated with upper positions could promote coexistence between species with different types of functional strategies by providing different microhabitats, and therefore, a greater number of ecological or functional niches to the species.

The investigation on the functional strategies in a Mexican SDTF revealed a vegetation is characterized by species highly specialized to stress (S spectrum of the CSR triangle). The

fact that most of the species in the SDTF (an ecosystem which is subjected to high levels of water stress especially during the dry season of the year, and which to date had not been functionally characterized by CSR analysis) have been classified in this way, is a new proof of the notable reliability of the CSR theory and also of the 'StrateFy' tool (Grime, 1974; Grime & Pierce, 2012; Pierce et al., 2017). These results are consistent with those previously reported in other hydrologically hostile ecosystems for plants, such as a 'restinga' forest in Brazil (Rosado & de Mattos, 2017) and a *campo rupestre* vegetation also known locally as 'canga' in Brazil (Tameirão et al., 2021). Although the strategies reported for this Mexican SDTF suggest that there is greater variability of CSR strategies compared to the other dry ecosystems where this categorization was also used, and despite the fact that the risk of water stress is higher in the Mexican SDTF (annual average temperature: 27.1 °C; annual average precipitation: 755.4 mm) compared to the other two Brazilian dry forest sites (restinga, annual average temperature: 22.6 °C; annual average precipitation: 1200 mm; canga, annual average temperature: 19 °C; annual average precipitation: 1562 mm); these environmental variables could be important drivers of a wider range of ecological strategies for plants. As mentioned in other studies, water resources greatly influence the establishment of certain CSR strategies because high values of specific leaf area (SLA) can be linked to the presence of water resources (Lönnqvist et al., 2023).

The main axis of functional variation for the whole community and the metacommunities formed by TP and SA involved a variety of traits from the whole plant, fruits, seeds and seedlings, and was difficult to describe simply as “an axis of” a particular plant function. It is clear that trait sets changed along environmental gradients, and that this was associated with changes in the degree of expression of the CSR strategy, in this case with species generally selected from ‘S’ to ‘CS’ varying in the relative degree of ‘R’ selection. In the Mexican SDTF we studied, the most important variables explaining plant functioning are

associated with an axis of variation related to water resource use (Bwc and Xwc) and wood density in direct relation to leaf retention time (WD and LRT). In the sites that represent greater water stress for plants (high positions and south-facing slopes), plants with dense tissues predominate (high values of Bwc and Xwc), have soft woods (low WD values) and are highly deciduous (short LRT periods).

The importance of water storage in the stem and how these influences tree water relations has been recognized for several decades (Hinckley et al., 1991; Borchert, 1994). For tropical forests, the existence of two types of strategies to make efficient use of resources has been hypothesized. On the one hand, “drought-tolerant” species, which are less efficient at capturing resources and growing even when water is available (Chapin, 1993; Reich, 2014), within the functional traits presented by species with this type of strategy are dense wood (which helps reduce hydraulic failure), smaller specific leaf area (which implies less transpiration) (Chaturvedi et al., 2021); and on the other hand, the “acquisitive” species or those that avoid drought, which have high leaf decay, high SLA values, low LDMC and greater water storage capacity in the bark and wood, which gives them rapid transport and storage (Prado-Junior et al., 2016).

Specifically, water storage in the bark and stem have been positively correlated with the presence of these two types of strategies in dry tropical forests (Pineda-García et al., 2015; Fagundes et al., 2022). However, acquisitive species along drought gradients in dry forests have occurred in sites with greater environmental aridity (Méndez-Toribio et al., 2017; Pinho et al., 2019; Lima et al., 2021; Fagundes et al., 2022), which contrasts with the patterns reported in other ecosystems for most studies that have focused their attention on these aspects (Engelbrecht et al., 2007; Frenette-Dussault et al., 2012; Esquivel-Muelbert et al., 2017). These findings have been explained through trade-offs related to water use efficiency, i.e., low wood densities of trees present in drier areas could provide individuals with greater storage of this

resource, which would favour the maintenance of a much more stable physiological and metabolic activity, especially during the dry season (Borchert, 1994; Pineda-García et al., 2013; Ramírez-Valiente & Cavender-Bares, 2017; Pinho et al., 2019). This would offer a possible explanation for the presence of this type of water relations in plants established through the drought gradient imposed by the TP in our study site.

The CSR method currently calibrated for a global flora set (Pierce et al., 2017), involves trade-offs between extremes involving three easily measured leaf traits: leaf area (LA), specific leaf area (SLA) and leaf dry matter content (LDMC). LA is understood as an indicator of the size spectrum, i.e., a key determinant of light-intercepting capacity; SLA related to assimilation and growth rates; and LDMC associated with nutrient retention within the plant (Garnier et al., 2017). However, in dry forests it seems that the relationships between LA and light-intercepting capacity do not present similar patterns to those established in more humid ecosystems; the presence of longer internodes in dry forests help to expand the canopy of trees more quickly and thus eclipse their neighbours (L. Poorter, 2009). And the low SLA values in dry forests could be linked to an improvement in the water balance, since leaves with smaller areas lose less water through evapotranspiration (Poorter & Bongers, 2006; Prado-Junior et al., 2017). Consequently, these functional traits of leaves in this studied dry forest could be related to other types of compensations that do not necessarily involve assimilation and growth rates or be indicators of plant size, which does not offer a plausible explanation for the fact that CSR strategies were not the main variables explaining functioning in the studied plant community.

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6. DISCUSIÓN GENERAL Y CONCLUSIONES

La variabilidad ambiental impuesta por la topografía (orientación y posición) juega un papel determinante en la presencia de patrones relacionados con la estructura y diversidad de los bosques tropicales secos (Segura et al. 2003; Méndez-Toribio et al. 2016), la dinámica comunitaria (Bellinghami & Tanner, 2000; Frey et al., 2007; Segura et al., 2003) y las estrategias funcionales de las plantas (Jucker et al., 2018; Méndez-Toribio et al., 2020; Wang et al., 2022), especialmente en los bosques tropicales estacionalmente secos, en donde las plantas se ven sometidas a un constante estrés hídrico el cual condiciona fuertemente su desarrollo (Markesteijn et al., 2011). En gradientes ambientales a mesoescala, se ha postulado que las posiciones altas y orientadas hacia el sur representan sitios ambientalmente más hostiles para las plantas (con mayor evapotranspiración, más secos y fríos), que su contraparte, es decir, posiciones bajas y con orientación norte (Gallardo-Cruz et al., 2009; Méndez-Toribio et al., 2016).

Debido a lo anterior, en el presente proyecto de investigación se evaluó la importancia de dos condiciones topográficas (OP y PT) sobre la dinámica de la comunidad y los cambios temporales en la estructura/diversidad (Artículo I), y sobre la dominancia, la diversidad filogenética y riqueza funcional, y el desarrollo de estrategias ecológicas (Artículo II), de las plantas en un BTES ubicado en la parte baja de la Cuenca del Balsas- Michoacán, al Occidente de México. Una descripción detallada de las condiciones ambientales a través del gradiente topográfico y de su relación con la composición, la estructura, la diversidad y los rasgos funcionales de las especies presentes en este BTES michoacano puede encontrarse en Méndez-Toribio et al. (2014; 2016; 2017; 2020).

Como fue establecido en las hipótesis (Capítulo I), los cambios relacionados con la dinámica comunitaria (especialmente la mortalidad y el reclutamiento), así como los cambios temporales de la densidad de tallos e individuos; estuvieron íntimamente vinculados con la topografía. El gradiente de riesgo de sequía impuesto por la posición topográfica influye fuertemente sobre la dinámica de la comunidad de plantas, provocando que se acelere hacia las posiciones superiores, y esto tiene un impacto significativo en la estructura de la comunidad, ocasionando mayor pérdida temporal de

tallos/individuos hacia estas posiciones. Sin embargo, los patrones temporales relacionados con la diversidad y estructura comunitaria, en general, parecen ser bastante estables en el tiempo, como se ha observado también en otros bosques secos del continente americano (Segura et al. 2003; Santos et al. 2017; Reis et al. 2018; de Souza et al. 2021).

Con respecto a la dominancia y subordinación de las especies en el SDTF estudiado (Capítulo II), encontramos que 8 especies son dominantes, mientras que el resto (47 especies) son subordinadas. La identidad de estas especies cambia a través de las dos condiciones topográficas (PT y OL), pero, resalta el caso de *Cordia eleagnoides*, un árbol endémico de las regiones de bosques caducifolios y semicaducifolios presentes en la vertiente del Pacífico, el cual, presenta características reproductivas como la autocompatibilidad y la dispersión anemócora de polen y semillas, sugieren una estrategia de vida colonizadora (Van Groenendael et al., 1996). estas características en conjunto podrían repercutir de manera significativa en la ocupación de nichos de polinización para esta especie. Estas características en conjunto podrían repercutir de manera significativa en la ocupación de nichos de polinización para esta especie, y podrían representar una ventaja adaptativa que repercuta en una competencia mucho más favorable con relación a sus especies vecina en este bosque SDTF estudiado.

Por otra parte, la diversidad filogenética (PD), presentó valores más altos en sitios donde el estrés hídrico es menor, es decir, las laderas orientadas hacia el norte. Estos resultados son congruentes con el filtrado ambiental en gradientes que muestran una alta diversidad y menor agrupamiento filogenético en comunidades establecidas en áreas menos cálidas y secas (González-Caro et al., 2014; Qian & Sandel, 2017; Liu et al., 2019; Cisneros et al., 2021). Lo cual puede ofrecer una explicación plausible a la presencia de estos patrones de diversidad filogenética presentados en nuestro sitio de estudio.

La riqueza funcional (FRic) presentaron valores más altos en sitios donde la sequía es más intensa y la disponibilidad del agua presenta periodos más cortos, es decir, en posiciones altas (mayor FRic). Debido a esta heterogeneidad ambiental asociada a las posiciones altas, podrían presentarse diferentes microhábitats que representen un mayor número de nichos ecológicos o funcionales (Apaza-Quevedo et al., 2015), que, por ende,

faciliten la coexistencia de especies con diferentes tipos de estrategias funcionales en estos sitios.

El eje principal de variación funcional de la comunidad involucró una gama de rasgos relacionados con el almacenamiento de agua en los tejidos tales como el contenido de agua en la corteza (Bwc) contenido de agua en el xilema (Xwc), la densidad de la madera (WD), el tiempo de retención de la hoja (LRT), encontrándose especies con espectros de estrategia funcional ‘adquisitiva’, es decir, plantas con tejidos de almacenamiento densos, baja densidad de la madera y hojas altamente deciduas; este tipo de plantas predominaron principalmente en las partes altas. Por otro lado, se encontraron plantas con estrategia ‘conservadora’, es decir plantas con tejidos de almacenamiento suaves, alta densidad de la madera y hojas duraderas; estas plantas predominaron principalmente en sitios bajos. A pesar de que en otros ecosistemas se ha reportado la presencia de especies ‘adquisitivas’ en las secciones más húmedas a lo largo de gradientes de sequía (e.g. ,Engelbrecht et al. 2007; Frenette-Dussault et al. 2012; Esquivel-Muelbert et al. 2017); en los bosques tropicales secos se ha mostrado un patrón opuesto, en el que las plantas ‘adquisitivas’ se pueden encontrar en las secciones más secas (Méndez-Toribio et al. 2017, 2020; Pinho et al. 2019; Lima et al. 2021; Fagundes et al. 2022); o en su defecto, no mostrando relación clara con los gradientes hídricos (Sterck et al., 2011). Esto resalta la importancia de los rasgos funcionales relacionados con el almacenamiento y las estrategias para hacer frente a la sequía por parte de los árboles que viven en ambientes hidrológicamente hostiles, como es el caso del SDTF estudiado.

Por otro lado, tanto las estrategias ecológicas C y S y otros rasgos como el tamaño del fruto, representaron un eje de variación secundario para el funcionamiento de las plantas a nivel de comunidad. Además, no hubo patrones de correlaciones fuertes y constantes entre los valores CSR con respecto a los ‘rasgos restringidos’ y ‘no restringidos’ para la comunidad completa, la orientación de la pendiente y la posición topográfica. La vegetación puede caracterizarse de acuerdo al triángulo CSR propuesto por Grime (1977) como tolerante al estrés.

No obstante, en las comunidades de bosque tropical seco la variación en el

tamaño de las plantas es apenas evidente, debido a que cuentan con una estructura vertical bastante corta (en comparación con las selvas húmedas o los bosques de coníferas (Bullock et al., 1995), lo cual se ve claramente representado en la presencia casi nula de especies con estrategia ecológica ‘C’, y la cual ha sido identificada en otros ecosistemas menos secos (Pierce et al. 2017; Rosenfield et al. 2019; Novakovskiy et al. 2021). Este análisis a mesoescala de la variación a nivel comunitario de los rasgos funcionales y las estrategias ecológicas de las plantas implementa, y también valida, la observación reciente de intercambios que modulan las diferentes combinaciones de rasgos, no solo entre especies (Díaz et al., 2016), sino también entre comunidades vegetales (Bruehlheide et al., 2018; Zanzottera et al., 2020).

Sin embargo, encontramos evidencia de que los factores a escala local que sustentan el gradiente hídrico impuesto por la topografía (especialmente por la posición topográfica) seleccionan combinaciones de rasgos en las plantas para hacer frente a la sequía que también se encuentran representados en el marco de la teoría CSR, aunque para esta comunidad de bosque tropical estacionalmente seco las compensaciones CSR parecen jugar un papel secundario en la estructuración de las estrategias funcionales de las plantas. Como se ha mencionado en otras investigaciones en diferentes bosques secos del continente americano, el uso y aprovechamiento del recurso hídrico tiene implicaciones más importantes en la selección puntual de ciertas clases de rasgos/estrategias funcionales para las plantas que subsisten en este tipo de ambientes (Markesteyn et al. 2011; Pineda-García et al. 2011; Sterck et al. 2011; Fagundes et al. 2022).

Finalmente, es importante señalar que la exploración de la variación de la dinámica de la comunidad, los cambios temporales en la estructura-diversidad, el dominio o subordinación de las especies, la diversidad filogenética, la riqueza funcional, y la presencia de estrategias funcionales de las comunidades estacionalmente secas podrían ser tópicos mejor entendidos por medio de la inclusión de otros aspectos que se han usado para explicar la presencia de patrones relacionados con los ejes anteriormente mencionados, como: censos en periodos de sequía y lluvia, la variación de la distancia funcional y filogenética entre comunidades de plantas, o el análisis del ensamblaje de la

comunidad por selección de rasgos (CATS) (Gale and Hall 2001; Shipley et al. 2006; Cadotte et al. 2009).

En conclusión, los hallazgos reportados en este estudio permiten destacar la importancia de la topografía como un factor ecológico compuesto, que puede representar variación ambiental en varios aspectos, por ejemplo, en la disponibilidad de luz/agua, la exposición al viento y la fertilidad del suelo, y la resistencia al anclaje de los árboles; y por lo tanto, puede fungir como un factor determinante de la dinámica, los cambios temporales en la estructura, la dominancia de las especies, o los patrones de diversidad filogenética, riqueza funcional y la presencia estrategias funcionales a nivel comunitario, esto sin dejar de lado que aún quedan otros procesos ecológicos relacionados con la topografía por explorar en investigaciones a futuro, y principalmente en el bosque seco.

7. BIBLIOGRAFÍA COMPLEMENTARIA (Introducción y Discusión)

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8. ANEXO: ARTÍCULOS DE DIVULGACIÓN CIENTÍFICA

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Los árboles de México que sangran

Alexis Arriaga Ramírez, Leonel López Toledo y Moisés Méndez Toribio



Artículo publicado en la Crónica y el Portal Comunicación Veracruzana el 23 de agosto 2022

Apoplanesia paniculata es un árbol propio del bosque tropical caducifolio con características singulares al que habría que estudiar más. Una de éstas es que produce savia y resina roja parecida a sangre.

Palabras clave: *Apoplanesia paniculata*, llorasangre, antiplasmodial

En el bosque seco o boque tropical caducifolio, habita una especie de planta con características muy particulares. Se trata del “consangre”, “cansangre”, “llorasangre”, “palo de arco”, “chulul”, o “kiik-che”. Esta especie de árbol de la familia Fabaceae, llamada por los botánicos *Apoplanesia paniculata*, tiene un tamaño promedio que alcanza hasta los 15 m de altura, suele tener un tallo delgado y no mayor a seis cm de diámetro a la altura del pecho. Sus hojas son imparipinadas, es decir, se distribuyen en pares alrededor de un raquis o eje central en grupos de cinco a ocho pares de folíolos: hojitas más pequeñas (ver figura 1). Las flores del cansangre son blancas, pequeñas y muy numerosas, usualmente estas se encuentran amontonadas en forma de pirámide asemejando a un racimo de flores.

Este árbol se puede encontrar en la mayoría de los bosques secos de México, país en el que se ha documentado la mayor ocurrencia de registros especialmente sobre la vertiente sureste del Pacífico, en la Península de Yucatán y la Cuenca Baja del Río Balsas. Sin embargo, también se ha registrado en Guatemala, Honduras, Nicaragua y Costa Rica. Por lo que no se descarta su presencia en otras latitudes del continente americano, sobre todo en lugares con vegetación de bosque seco.

Propiedades curativas del llorasangre

En México, particularmente en el estado de Michoacán, se ha documentado el uso medicinal de esta planta para tratar “problemas del corazón”. La manera en que se procesa este “remedio”, es mediante la cocción de hojas del árbol y su posterior empleo como agua de “uso diario”, la cual cobra un color rojizo debido a que expulsa sustancias de las glándulas presentes en las hojas de estos árboles. En el estado de Guerrero, también se ha documentado el uso medicinal de esta planta para “curar el ombligo”. El remedio consiste en colocar en medio del vientre hojas machacadas y mezcladas con aceites de olivo, rosado y de almendras.

Además, en el año 2015 un grupo de investigadores de la Universidad Virginia Tech en Estados Unidos, evaluaron el efecto que tienen los extractos de la raíz de *Apoplanesia paniculata* para combatir al *Plasmodium falciparum*, parásito que causa la malaria en humanos. Los resultados del estudio fueron bastante positivos. Esto es muy prometedor en la búsqueda de opciones de medicinas que nos puedan ayudar a combatir la resistencia a los antibióticos que pudiera asociarse con la mayor presencia de malaria en un futuro cercano.

Los árboles que “sangran”

En el planeta Tierra existen muchos árboles que secretan resina roja o que tienen savia rojiza haciendo parecer que literalmente sangran cuando se les provocan lesiones. Probablemente el caso más estudiado es el de la especie *Croton draco* popularmente conocida como “sangre de drago”, la cual es una especie americana que produce resina roja. Sin embargo, también se conoce la existencia de otras especies como *Pterocarpus angolensis*, comúnmente conocida como “kiaat”, “mukwa” o “muninga”, la cual es una especie con savia roja de origen africano, o la especie *Corymbia terminalis*, árbol de origen australiano que también cuenta con savia rojiza.

El caso del cansangre aún no es claro, se sabe que estos árboles cuentan con glándulas parecidas a verrugas en el tallo y hojas que secretan un tipo de resina muy espesa de color rojo intenso (ver figura 2), sobre todo en épocas calurosas del año. Asimismo, al cortar el tallo de estas plantas, se vierte savia rojiza, la cual era utilizada en la época precolombina por los mayas para teñir telas. Sin embargo, las causas de la coloración rojiza en la savia y resinas de esta especie aún son poco claras, por lo que sería interesante tener información sobre la histoquímica, la organización estructural de las glándulas, su ontogénesis y los posibles usos que se puedan hacer de esta especie.

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Ana Luisa Gómez Sánchez1, Juan José Barrios Gutiérrez1, Carlos Daniel Pinacho Pinacho2, Sonia Gallina-Tessaro3, Andrés M. López-Pérez3

Actualmente [...]

**La diversidad taxonómica,
filogenética y funcional:
un acercamiento al caso
de “El Arca de Noé”**

***Taxonomic, phylogenetic
and functional diversity.
An approach to the case
of “Noah’s Ark”***



M. C. Alexis Arriaga Ramírez
Universidad Michoacana de San Nicolás de Hidalgo

Resumen:

Utilizando el evento bíblico de “El Arca de Noé” se hacen una serie de planteamientos enfocados en introducir al lector en diferentes conceptos utilizados en la actualidad en ecología de comunidades. También se introduce al lector una serie de planteamientos relacionados con la aplicación de estos temas en la conservación de la biodiversidad.

Palabras clave:

Rasgos funcionales, árboles filogenéticos, conservación, Arca de Noé

Abstract:

Using the biblical event of “Noah’s Ark”, a set of proposals are made focused on introducing the reader to different concepts currently used in community ecology. The reader is also introduced to the application of these issues in conservation of species issues.

Key words:

Functional traits, phylogenetic trees, conservation, Noah’s Ark

El Arca de Noé es uno de los relatos más populares de la Biblia, en el que se narra cómo, por orden de Dios (Yahvé o Jehová), el patriarca Noé decidió construir una embarcación para la salvación de aquellos que creyeran en la “promesa del diluvio universal”. No obstante, la narración del evento expone que solo fue Noé, su familia y siete parejas de cada animal “puro” (kosher, del hebreo ‘apto’ o ‘adecuado’) y una pareja de cada animal “no puro” (no kosher) quienes abordaron el arca. Todos ellos, preservados del diluvio universal, podrían repoblar la Tierra con su descendencia.

La Real Academia Española (RAE), ha definido el concepto de “biodiversidad” como la “variedad de especies animales y vegeta-

les en su medio ambiente”. Sin embargo, el concepto de biodiversidad tiene su origen en el año de 1980. Lovejoy, quien realizaba un estudio para el Fondo Mundial para la Naturaleza (WWF, por sus siglas en inglés), escribió en su reporte acerca de la diversidad biótica o biológica, y a pesar de que no dio una definición puntual de la misma, utilizó este concepto para referirse al número de especies presentes en un sitio (Núñez et al., 2003). Actualmente, el concepto de biodiversidad se ha utilizado ampliamente para hacer referencia a la variedad de la vida en todos los niveles de organización, clasificada tanto por criterios evolutivos (filogenéticos), como ecológicos (funcionales).

Históricamente, los esquemas de conservación en el mundo han tenido como meta la preservación del mayor número de especies en un área determinada, priorizando de esta manera a la diversidad de especies sobre otros componentes de la biodiversidad. En la actualidad, se presenta un interesante auge por tomar en cuenta otras dimensiones, como la funcional o la filogenética, o una combinación de estas. Dichos componentes de la biodiversidad se relacionan con la productividad primaria de los ecosistemas, el ciclaje de nutrientes y la resiliencia de las comunidades naturales a la invasión por especies exóticas, entre otros procesos. Además, estos componentes tienen implicaciones para diseñar acciones de conservación y manejo de recursos naturales, así como para seleccionar especies para la restauración ecológica de sitios perturbados.

En ese sentido, y tomando como modelo de estudio el acercamiento que tuvo Noé a la hora de seleccionar especies para contener la mayor biodiversidad posible en su arca (sensu lato Perry, 2010), surge el siguiente cuestionamiento: ¿cómo hubiese hecho Noé

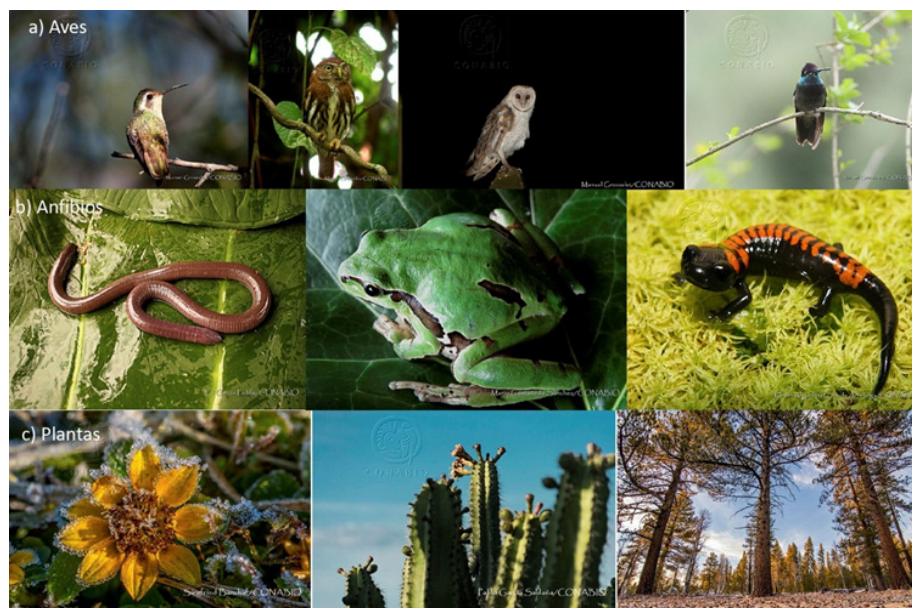


Figura 1. Representación de la diversidad biológica de diferentes grupos de organismos.

para llevar en su arca la mayor cantidad de diversidad taxonómica, funcional y filogenética? Bueno, pues tratemos de darle claridad a cada enfoque en las siguientes secciones.

1) De diversidades taxonómicas...

La diversidad taxonómica, ha sido definida por los científicos como la media y la varianza del número de especies por género, y de especies por familia (Neeson et al., 2013). Es decir, la diversidad taxonómica representa el número y la variedad de formas de seres vivos que habitan en un área geográfica determinada (ver figura 1).

La “diversidad” en biología, ha sido uno de los términos mayormente utilizados para hacer referencia a otro concepto importante, la “complejidad ecológica” presente en la estructura de una comunidad. Es decir, la presencia de diferencias entre los elementos que componen una colección de especies. Para medir la biodiversidad, se han utilizado una serie de índices que, en general, tratan de describir de manera matemática (y relativamente sencilla)

la complejidad ecológica que presenta un conjunto de especies. Entre los índices más populares utilizados por los ecólogos para medir la diversidad podemos encontrar: el Índice Shannon, el exponencial del índice de Shannon, el índice de Ginni-Simpson, el inverso del índice de Ginni-Simpson, la riqueza de especies, entre otros.

Sin embargo, dichas medidas no proporcionan información acerca de las relaciones a nivel evolutivo y con el medio ambiente que presentan las comunidades de organismos. En la taxonomía encontramos un marco normativo que nos permite identificar, cuantificar y evaluar el estado de la biodiversidad de una comunidad. Esto, a su vez, nos permite establecer prioridades de conservación, y, por lo tanto, se constituye como una piedra angular en la conservación de la biodiversidad.

En Levítico 11 y Deuteronomio 14, se describen una serie de mandatos taxonómicos supuestamente propuestos por Dios, el cual postula la existencia de animales “puros”

y “no puros”. En síntesis, los animales terrestres puros eran considerados aquellos rumiantes que tuvieran pezuña hendida (dividida), por lo que algunos ejemplos de animales puros se encontraban representados en la res, el antílope, la cabra, el venado; mientras que ejemplos de animales terrestres no puros podrían ser los conejos y los cerdos. Dentro de los animales acuáticos puros se consideraban aquellos que tenían aletas y escamas, por lo que ejemplos de animales acuáticos puros, dentro de esta construcción teocentrista (Dios como el centro del universo), serían los pargos, los róbalo, el bacalao, el salmón; mientras que ejemplos de animales acuáticos no puros podrían ser la langosta, el cangrejo y el camarón.

Esta diferenciación taxonómica inverosímil entre animales “puros” y “no puros”, según el relato bíblico, era bien conocida por Noé antes de que tuviera lugar el diluvio universal, el cual fue el criterio de selección con el que éste resguardó a las especies por mandato divino, ¿Cuántos seres vivos puros e impuros transportaría la supuesta arca? es en realidad un misterio. En ese sentido, uno de los debates creacionistas más destacados ha sido utilizar el concepto de “baramin” o “tipos” en lugar de especies. Un “baramin” (del hebreo bara: creado, min: tipo), según los creacionistas, es una unidad de vida originalmente creada por Dios, el problema fundamental que engloba este concepto es que dentro de cada “tipo” hay un potencial muy grande de variación (Moore, 1983). Este concepto conduce a una diferenciación muy abstracta entre las unidades bióticas que podrían abordar la supuesta arca, haciendo que se presenten estimaciones numéricas muy dispares entre creacionistas con respecto al número de “tipos” que podrían existir, que van desde los 1,544 hasta 50,000 tipos que se presume iban a bordo de la misma (Moore, 1983).

Actualmente sabemos que se han descrito taxonómicamente alrededor de 1.2 millones de especies eucariotas, y se predice la existencia de unas 8.7 millones en el planeta (Mora et al., 2011). Esto obviamente representa un problema mayúsculo en el mito de Noé, ya que se presume que el arca tenía una extensión limitada de 155 metros de largo por 26 de ancho y 25 m de alto, lo cual equivale aproximadamente al largo de un campo de fútbol y la altura de la gran esfinje de Giza. Una embarcación de estas dimensiones podría tener aproximadamente un volumen de 40,000 metros cúbicos (m³), la cual de ninguna manera podría albergar a 9 millones de especies, ni la combinación de siete parejas de organismos puros, por una pareja de no puros.

Solo para poner un poco de contexto, tomando las 1.2 millones de especies descritas taxonómicamente actualmente, considerando que la mitad fuesen “puras” (8,400,000 individuos), y la otra mitad fuesen “no puras” (1,200,000 individuos), nos da un total de 9,600,000 individuos, eso dividido entre los 40,000 m³ que es el volumen del arca, da como resultado un espacio de 0.0041 m³ para cada individuo (ignorando el hecho de que Noé debía destinar un espacio en la embarcación para un año de víveres con los que alimentaría a todos los pasajeros del arca). El volumen que ocupa una caja para transportar una cebra promedio es de aproximadamente 2.2 m³, el de una jirafa promedio es de 2.8 m³, el de un hipopotamo de 6.0 m³ (Moore, 1983). Bajo este contexto, el arca que diseñó Noé en aproximadamente 100 años, debería tener dimensiones mucho más amplias para albergar a quizás millones de individuos, tal vez el arca debería tener el tamaño de algunos países pequeños como San Marino o Tuvalu.

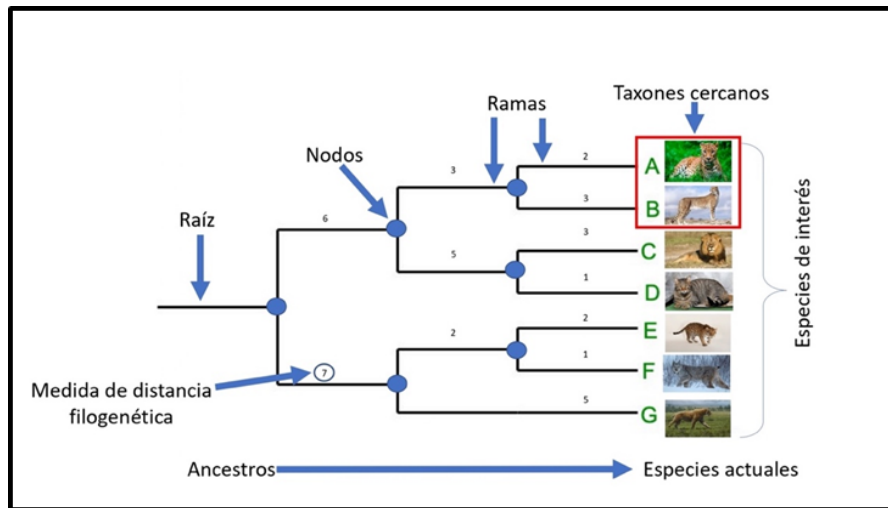


Figura 2. Ejemplo de un árbol filogenético y sus componentes principales para el caso de los felinos.

2) De diversidades filogenéticas...

A diferencia de la diversidad taxonómica, que nos permite conocer la variedad y el número de especies presentes en un sitio, la diversidad filogenética tiene como objetivo principal medir la biodiversidad tomando en cuenta el factor evolutivo, es decir, la diversidad de características que las especies han adquirido en términos de su historia evolutiva (Rivera, 2020).

Usualmente, los científicos determinan la diversidad filogenética mediante el uso de árboles filogenéticos, que son representaciones gráficas (parecidas a un tipo de cuadro sinóptico) en el que se muestran las relaciones de parentesco entre una agrupación de especies y/o taxones (ver figura 2). Un árbol filogenético es una hipótesis científica sobre las relaciones evolutivas de un conjunto de especies, no es un hecho definitivo. En ese sentido, la métrica de diversidad filogenética (PD) de Faith (1992, p. 4), la cual, es quizás la más utilizada actualmente; se calcula mediante la suma de las longitudes de las ramas del camino mínimo que une un conjunto de taxones en un árbol filogenético (ver figura 2). Es decir, esta métrica

mide la historia evolutiva compartida entre taxones que son parte de una muestra.

En los últimos 30 años, la biología de la conservación ha ampliado la calidad de sus horizontes de información para poder tomar decisiones puntuales, motivada principalmente por la grave crisis global de extinción de especies provocada por el hombre. Ante este escenario, la diversidad filogenética se ha presentado como una nueva herramienta para la conservación, que considera la evolución y la acumulación de características adquiridas a través del tiempo. Una de las principales ideas para usar a la diversidad filogenética como un criterio para la conservación de la biodiversidad, surge detrás de reconocer su valor intrínseco, en donde, al salvaguardar este componente se garantiza la protección de millones de años de evolución (Rivera, 2020). Además, se le ha relacionado con diversos procesos como la productividad de los ecosistemas y la resistencia de las comunidades a la invasión por especies exóticas, los cuales resultan criterios relevantes para llevar a cabo objetivos de conservación precisos.

Volviendo al punto de los baramines o “tipos”, como señala Moore (1983, p. 7), existen problemas genéticos puntuales detrás de esta clasificación con la cual Noé conformó su arca. Tomando el ejemplo de los caninos, en donde los creacionistas han puesto a lobos, perros, coyotes, dingos, fennecs, etc; se necesitarían conjuntos de cromosomas gigantes con una cantidad bestial de alelos (cada una de las formas en que puede manifestarse de un gen) que albergaran la inmensa variedad de rasgos como el tipo de pelaje, el color de los ojos, la forma de la cabeza, y/o el tamaño de la dentadura, que pudiesen manifestar las diferentes especies que se encontraban englobadas en una población de solo siete parejas de animales puros y una pareja de no puros, lo cual resulta prácticamente inviable.

En los milenios posteriores al diluvio, los animales que bajaron del arca debieron repoblar la tierra diversificando su descendencia en todas las especies de las comunidades naturales que conocemos hoy en día. Esto, como señala Moore (1983, p. 7) tiene como trasfondo, un dilema genético circunstancial a la hora de elegir a los individuos de cada “baramin”, es decir, ¿Qué individuos elegiría Noé del baramin canino para englobar la inmensa diversidad filogenética contenida en los caninos? ¿Un coyote macho y una hembra de lobo siberiano?, o en el caso del baramin felino, ¿un macho león y una hembra de gato doméstico? ¿Cómo podría Noé saber todo esto?

Las parejas de animales no puros (solo hembra y macho por baramin) debían contener toda la información genética de su grupo en solo dos individuos. Esto, obviamente, lleva consigo problemas filogenéticos y genéticos importantes como el entrecruzamiento consanguíneo entre los descendientes, la deriva genética (cambios en la frecuencia

de aparición de las variedades que puede tener un mismo gen), mutaciones deletéreas (alteraciones genéticas que aumentan la probabilidad de padecer ciertas afecciones), y problemas de cuello de botella (reducción de la variabilidad genética debido a un tamaño poblacional reducido).

En fin, en la actualidad el uso de la diversidad filogenética en la toma de decisiones relacionadas con la conservación aún sigue siendo un tema a discutir. Esto en gran medida, de la biodiversidad que hasta hace un par de décadas eran completamente ignorados. Seguro que este tipo de herramientas le hubiese sido de gran utilidad a Noé para conformar un arca con miras a preservar no solo un gran número de especies, sino también una serie de procesos evolutivos asociados a las mismas. Los científicos siguen trabajando para desarrollar mejores metodologías enfocadas en resolver las diferentes problemáticas que tiene el mundo actual, como es el caso de las grandes extinciones de especies.

En el futuro cercano, como señala Rivera (2020, p. 274), es casi seguro que seguirán surgiendo nuevas incógnitas a las cuales los científicos deberán enfrentarse, como: ¿Qué debemos priorizar como sitios destinados a conservación, áreas con alta concentración de especies o áreas con alta diversidad de características o historia evolutiva? ¿Qué componentes de la biodiversidad se ven salvaguardados con las legislaciones que buscan proteger los ecosistemas? ¿Qué debería ser prioridad para conservación, aquellas áreas en donde se han originado múltiples especies afines entre sí o aquellas en donde se refugian linajes antiguos y lejanamente emparentados?

3) De diversidades funcionales...

Recientemente, los científicos han introdu-

cido en ecología el concepto de “diversidad funcional”, para hacer referencia a otro componente de la biodiversidad. Este concepto, se centra en describir las funciones que desempeñan los organismos en una comunidad o ecosistema, por medio del estudio de la variedad de “rasgos funcionales”. En el caso de las plantas, los rasgos funcionales son características morfológicas (p. e. altura, diámetro a la altura del pecho, longitud de la raíz, etc.) (ver figura 3), fisiológicas (p. e. potencial hídrico de las hojas, carbohidratos solubles totales, conductividad electrolítica, etc.) y fenológicas (p.e. tiempo de retención de las hojas, peso de biomasa aérea, etc.); que impactan directamente sobre la capacidad de adaptación, sobrevivencia y la producción de descendientes de las especies.

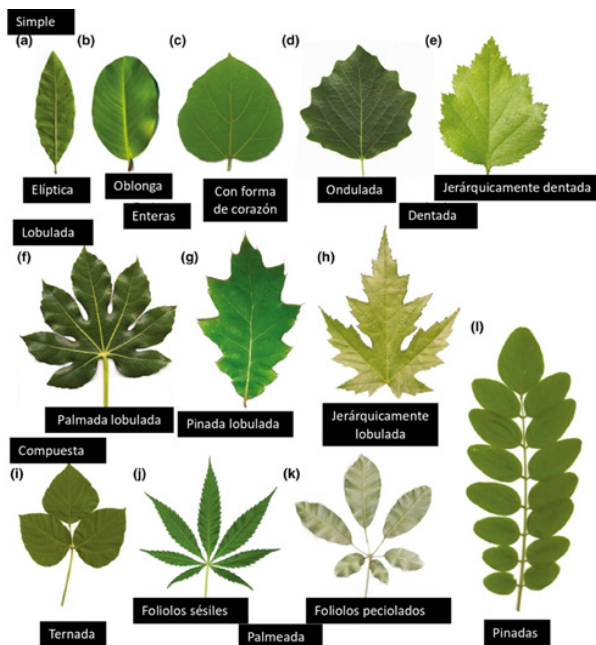


Figura 3. Ejemplos de diferentes formas y tipos de hojas, estas características pueden representar adaptaciones que les ayudan a las plantas a desarrollar diferentes funciones en el ecosistema, como: una mayor / menor captación de luz, mayor / menor retención de agua, mayor / menor captación de CO₂, etc. Imagen modificada de Runions et al., (2017, p. 2).

La manera más sencilla de describir la diversidad funcional de un sitio es separando a las especies por “grupos funcionales”. Es decir, se fragmenta un grupo de especies en subconjuntos o colecciones de organismos que comparten características que les hacen desempeñar funciones similares en el ambiente, por ejemplo: plantas, herbívoros y carnívoros. Además, existen al menos cuatro componentes principales de la diversidad funcional en ecología, que son: la riqueza, la equitatividad, la divergencia y la especialización. Estos cuatro componentes ayudan a los científicos a examinar con mayor detalle los mecanismos y procesos que relacionan a la diversidad con el funcionamiento de los ecosistemas (Córdova-Tapia & Zambrano, 2015, p. 81).

El funcionamiento del ecosistema, se ha vuelto una prioridad en asuntos relacionados con la conservación, debido a que muchos servicios ecosistémicos con valor de uso para el ser humano, como el almacenamiento de carbono y la producción de alimentos, se encuentran asociados directamente con el funcionamiento, y por lo tanto, existen fuertes incentivos económicos para conservarlos (Cadotte et al., 2011, p. 1085).

Para pensar en la metáfora del Arca de Noé desde esta perspectiva, hay que considerar que en la preservación de grupos funcionales existen especies que son decisivas, aquellas con funciones únicas que ninguna o muy pocas especies llevan a cabo. Estos grupos funcionales con una sola o muy pocas especies, son puntos estratégicos de conservación, y a menudo son conocidos como “especies clave”. Uno de los ejemplos más populares de especies clave es el caso de las abejas, las cuales utilizan el néctar de muchas flores e indirectamente transportan polen para ayudar al proceso de reproducción de muchas

plantas que el ser humano suele consumir en su alimentación. Por lo que, la conservación del grupo funcional de los polinizadores y en especial de las abejas, es de suma importancia desde el punto de vista económico y ecológico.

Esto, como señala Perry (2010, p. 479), implica para Noé la creación de un “ecosistema de funcionamiento” en el arca, en el cual estuviesen representadas todas las funciones que se desarrollan en los diversos ecosistemas que existen en el planeta Tierra. Por lo que, retornando al asunto de los baramines o tipos, ¿Noé habría construido el arca pensando en las diferentes funciones que presentarían los ecosistemas, luego de que los tipos puros y no puros que seleccionó bajasen del arca?, ¿Priorizaría Noé la preservación de especies funcionalmente clave a la hora de ponerlas a bordo?

Al tratar de responder estas preguntas, intuitivamente, el relato de Noé presenta muchos huecos de información desde el punto de vista de la diversidad funcional en ecología. Lo cual, por supuesto, debilita en muchos aspectos la creencia del relato bíblico de la conformación de un arca “perfecta”, que ayudase a Noé a preservar todas las especies y a los procesos ecosistémicos en las que éstas participarían.

Hoy en día y en la práctica, cada vez son más las estrategias de restauración y conservación que priorizan el uso de la diversidad funcional a nivel comunitario. El objetivo de estos proyectos es generar y/o mantener ecosistemas estables y funcionales (Cadotte et al., 2011, p. 1085). La diversidad funcional es una herramienta muy valiosa, la cual puede ayudarnos a resolver preguntas importantes con respecto a las diferentes problemáticas que pudie-

ran surgir en un futuro, a corto plazo, relacionadas con la pérdida de biodiversidad.

Conclusiones

La ecología de comunidades ha abierto las puertas para discutir nuevas visiones relacionadas con el manejo y conservación de la biodiversidad. A través de los años, la diversidad taxonómica ha cobrado una importante relevancia para diseñar herramientas orientadas a realizar acciones de conservación. Sin embargo, en la actualidad y debido al avance en diferentes campos de la ciencia como los sistemas de información geográfica, la ecofisiología, la bioestadística, y la genética, se ha logrado tener un panorama mucho más profundo acerca de los diferentes componentes de la biodiversidad, surgiendo de esta manera los enfoques filogenético y funcional.

La pérdida de biodiversidad que se encuentra íntimamente relacionada con el desarrollo de actividades humanas nos ha planteado nuevos retos de cómo entender la naturaleza. Las extinciones masivas de especies son un problema real al que nos enfrentamos como sociedad, no es un simple cuento popular o una saga surrealista de improbabilidades, como es el caso del Arca de Noé. Pero compareciendo ante las analogías, tal vez, si existiera un arca ésta sería el planeta Tierra, y solo tal vez, este barco que compartimos con las diferentes especies que coexistimos debiésemos conservarle y cuidarle mucho más para que llegue a buen puerto, porque al parecer el diluvio ya está ocurriendo

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