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SAN NICOLÁS DE HIDALGO

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Dinámica de la comunidad y estructura filogenética de la comunidad arbórea en la selva seca de Álamos, Sonora

TESIS

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Biól. Sebastian Vargas Rumbo

Tutor de tesis:

Dr. Leonel López Toledo

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El éxito es la suma de pequeños esfuerzos, que se repiten día tras día -
Robert Collier

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Resumen

A lo largo de la historia, la ecología de comunidades se ha centrado en analizar el origen y mantenimiento de la diversidad biológica, a partir de dos grandes teorías: la primera, conocida como la teoría de nicho ecológico, establece que son las diferencias ecológicas entre las especies y las condiciones ambientales lo que influye directamente el ensamblaje de la comunidad. Por otro lado, la teoría de ensamble por dispersión postula que todos los individuos de todas las especies presentan una neutralidad en los procesos ecológicos. Son estos procesos los factores que determinan el ensamblaje de la comunidad, incluyendo los procesos de dispersión, extinción local y eventos históricos como la especiación. No obstante, existen factores a escalas locales que influyen directamente la distribución y diversidad de especies. Uno de esos factores es la topografía, entre los que destacan la orientación y la posición topográfica. De esta manera, la dinámica de la comunidad es altamente influenciada por los filtros ecológicos, estos pueden ser factores bióticos, abióticos e históricos (historia natural) que actúan u operan seleccionando a las especies que conformarán la comunidad. Estos determinarán los índices de reclutamiento, mortalidad y recambio de especies. Es así, como esta tesis se basó en analizar el efecto de la orientación y la posición topográfica sobre la diversidad, la dinámica y la estructura filogenética de la comunidad de leñosas de la selva seca de Álamos, Sonora para determinar los procesos que subyacen el ensamblaje de la comunidad. Para esto, se establecieron. 16 subparcelas de 20 x 40 m a principios del 2017 con diferente orientación topográfica (N y S) en la reserva Sierra de Álamos Rio Cuchujaqui ubicada en Álamos, Sonora. En cada una de estas parcelas se marcaron e identificaron todos los arboles con un DAP $\geq$ 1 cm, para así, caracterizar la estructura taxonómica y filogenética en dos categorías de tamaño (juveniles y adultos). El trabajo de campo de esta investigación consistió en volver a hacer el censo de los individuos marcados en el 2017 marcando e identificando dos categorías de tamaño (plántulas y brinzales) en cuadrantes de 5 x 5 m que se establecieron en cada una de las esquinas de las 16 subparcelas. De esta manera, se obtuvieron las tasas de mortalidad, reclutamiento, crecimiento y recambio de especies para cada subparcela, así como la estructura filogenética para cada categoría de tamaño: plántulas, brinzales, juveniles y adultos. Los resultados indicaron un efecto significativo de la interacción de los factores topográficos sobre la mortalidad de especies en estadios juveniles, siendo la condición sur alto y norte alto la que presentó mayor (0.14 ± 0.10 %) y menor mortalidad (0.01 ± 0.002%) respectivamente. Asimismo, el recambio de especies fue mayor para la condición norte bajo (8.5 ± 1.71), siendo 1.6 veces mayor que norte alto (5.3 ± 1.18). Por otro lado, para la riqueza de especies encontramos diferencias únicamente en brinzales, siendo norte alto el que presentó los valores más altos (9.25 ± 1.03). Mientras que en número de individuos, tallos y área basal los adultos mostraron diferencia para la orientación topográfica, donde los valores más altos se presentaron en las orientaciones sur para todas las variables (Individuos: 214.0 ± 16.6 ind/0.08 ha^{-1}), (749.3 ± 42.6 tallos 0.08 ha^{-1}), (25.5 ± 2.7 m2/0.08 ha^{-1}) respectivamente. Por otro lado, los patrones filogenéticos observados con el índice NRI fueron del agrupamiento (0.61) en plántulas a la sobredispersión (-0.21) en orientaciones sur, contrastando con las orientaciones norte, donde el patrón fue de la sobredispersión al agrupamiento. El resultado del efecto diferencial de los factores topográficos a lo largo de las categorías de tamaño y de las condiciones topográficas podría deberse a un efecto de filtros ambientales sobre las comunidades vegetales que genera una diferenciación en su composición y estructura.

Palabras clave: Filtrado ambiental, asociación de hábitat, diversidad filogenética

Abstract

Throughout history, the ecology of communities has focused on analyzing the origin and maintenance of biological diversity, this is how two great theories arise, the first known as the ecological niche theory establishes that is the ecological differences between species and environmental conditions that directly influence the assembly of the community. On the other hand, the dispersal assembly theory postulates that all individuals of all species in the community present a neutrality in the processes of the same. The assembly of the community are determined by processes of dispersion, local extinction and historical events such as speciation. However, there are factors that directly influence the distribution and diversity of species on a local scale, one of these factors is the topography, among which orientation and topographic position stand out. In this way, the dynamics of the community is highly influenced by the ecological filters, these can be biotic, abiotic and historical (natural history) factors that act or operate by selecting the species that will make up the community, these Will determine the recruitment rates, species mortality and turnover. Thus, this Project was based on analyzing the effect of orientation and topographic position on the diversity, dynamics, and phylogenetic structure of the Woody community in the Alamos region, Sonora.

In this way, analyzing the dynamics and phylogenetic structure of the community allows us to determine the processes that underlie the assembly of the community, for which our work was carried out in a permanent plot of 50 ha. Established in the dry forest of Alamos, Sonora Within this plot, 16 subplots of 20 x 40 m were established at the beginning of 2017 with different topographic orientation (N and S), in each of these plots,all tres with a DBH > 1 cm were marked and identified, in order to characterize the taxonomic and phylogenetic structure in two size categories (juveniles and adults). The field work of this research consisted of the survey of the marked individuals in 2017 ad additionally two size categories (seedlings and saplings) were marked and identified in 5 x 5 m quadrants that were established in each of the corners of the 16 subplots. In this way, the rates of mortality, recruitment, growth and turnover of species were obtained. As well as the phylogenetic structure of the plant community in four size classes: seedlings, saplings, juveniles and adults. The results indicate a positive effect of the interaction of the topographic factors on the mortality of species in juveniles, being the south high condition and the north high the one that presented the highest (0.14 ± 0.10 %) and lowest mortality (0.01 ± 0.002%), respectively. In the same way, the turnover species was higher fot the north low condition (8.5 ± 1.71), being 1.6 greater tan the north high condition (5.3 ± 1.18). On the other hand, for the species richness we found differences only in saplings, being the north high condition the unic that presented the highest values (9.25 ± 1.03). While in number of individuals, stems and basal área, the adults showed difference for the topografic orientation, where the highest values were presented in the southern orientations for all the variables (214.0 ± 16.6), (749.3 ± 42.6), (25.5 ± 2.7) respectively. On thw other hand, the phylogenetic patterns observed were from clustering (0.61 ± 0.50) in seedlings to overdispersion (-0.21 ± 0.21) in southern orientations, costrasting with north orientations, where the pattern was from overdispersion to clustering. The resulto f the differential effect of topographic factors along the size categories and topographic conditions could be due to an enviromental filter effect on plant communities that generates a differentiation in their composition and structure.

Key words: habitat filtering, habitat association, phylogenetic diversity

Capítulo I

Introducción general

El bosque tropical seco, también conocido como selva baja caducifolia o selva seca, se caracteriza por presentar una marcada estacionalidad de sequía y temperaturas cálidas muy constantes (Balvanera et al., 2002; Pennington et al., 2009). A nivel mundial este tipo de ecosistema tiene su mayor extensión en el continente americano, abarcando desde el norte de México hasta Sudamérica y conforma el 54.2% de la vegetación tropical del continente (Miles et al., 2006). En México, este ecosistema se extiende sobre la vertiente del Pacífico desde Sonora hasta la Depresión Central de Chiapas (Pennington et al., 2000; Balvanera et al., 2002; Miles et al., 2006) . En general, la selva seca se sitúa en suelos fértiles y la cantidad de lluvia anual es muy variable (190-1200 mm) aunque no excede los 1600 mm anuales (Velez-Ruiz et al., 2020).

La importancia del bosque tropical seco no solo radica en su extensión, sino también en el gran número de especies que alberga. Así, en un décimo de hectárea de selva seca se pueden encontrar entre 50-70 especies de árboles (Balvanera & Aguirre, 2006; Méndez-Toribio et al., 2014) . Debido a esta gran diversidad de especies, las selvas secas representan una gran fuente de recursos forestales maderables y no maderables para el hombre, extrayendo plantas medicinales, alimentos, madera, material para construcción y elaboración de artesanías (Balvanera & Aguirre, 2006; Osorio Beristain et al., 2006). Por estas razones, este ecosistema presenta grandes amenazas antropogénicas, entre las que destacan la ganadería y la deforestación. Por ejemplo, para el caso específico de la selva seca en México se deforestan alrededor de 300 mil hectáreas de selva por año, ya sea por la extracción de madera o el cambio de uso de suelo (Osorio Beristain et al., 2006; Balvanera et al., 2017) .

La fisionomía de la selva seca se caracteriza por presentar un estrato arbóreo dominante de un tamaño generalmente pequeño (4-10 m). La mayoría de las especies no presenta hojas enteras y contienen espinas. Además, pierden sus hojas como respuesta al estrés hídrico generado por la sequía lo que les permite afrontar la pérdida de agua (Balvanera & Aguirre, 2006; Osorio Beristain et al., 2006) . Por lo tanto, la dinámica de la comunidad y la fisionomía están determinadas directamente por la cantidad total de precipitación pluvial y la temperatura. Por lo general, las especies de plantas florecen y fructifican durante la época de lluvias. (Miles et al., 2006; Osorio Beristain et al., 2006). Por otro lado, la germinación está fuertemente limitada, no solo por la marcada ausencia de agua durante la época seca, sino también por la elevada insolación que presenta la superficie del suelo, generada por la pérdida del follaje arbóreo. Por lo tanto, el agua determina directamente los ciclos fenológicos y la dinámica de las comunidades vegetales en estos ecosistemas (Méndez-Alonzo et al., 2013).

En el Continente Americano, la selva seca presenta su distribución más norteña en la región de Álamos, Sonora en México. Esta zona es de gran importancia biológica ya que convergen los elementos florísticos neárticos y neotropicales (Martinez-Yrizar et al., 2000). Además, la accidentada topografía presente en la región le confiere gran diversidad de condiciones abióticas, generando así una multitud de microclimas idóneos para las especies de la selva seca (Van Devender et al., 2000). Por lo tanto, este ecosistema juega un papel importante para estudiar el papel de las condiciones bióticas y abióticas en el establecimiento de nuevos individuos en una comunidad. Este proceso conocido es metafóricamente como un filtro ambiental en donde solamente las especies con ciertas características morfológicas o fisiológicas pueden pasar estos filtros (Kraft et al., 2015). Para el caso de la selva seca, los filtros ambientales están principalmente relacionados con la disponibilidad de agua y su importancia radica en identificar el papel que estos desempeñan en la estructuración de las comunidades (Balvanera et al., 2011; Quisehuatl 2019).

Una comunidad se define como el ensamblaje de poblaciones de diferentes especies que viven en un ambiente e interaccionan, formando así un sistema con su propia composición, estructura, relación ambiental, desarrollo y función (Whittaker, 1972; Begon et al. 2005). La dinámica de la comunidad es altamente influenciada por los filtros ecológicos que pueden ser factores bióticos, abióticos e históricos que actúan u operan seleccionando a las especies que conformarán la comunidad. Estos factores o filtros ecológicos determinarán los índices de reclutamiento, mortalidad y recambio de especies (Letcher et al., 2012; Swenson et al., 2012; Wiegand et al., 2017). Como resultado, las especies responden a estos filtros mediante variaciones en sus rasgos funcionales, lo que les permite su establecimiento y el ensamblaje de la comunidad (Kraft et al., 2007; Cavender-Bares et al., 2009; Chun & Lee, 2019).

No obstante, existen factores que influyen directamente la diversidad y la distribución de especies a una escala local, tal es el caso de la topografía. Diversos estudios han reportado un efecto de la topografía sobre la distribución, establecimiento y supervivencia de las plantas. Este factor no solo afecta a las comunidades vegetales, sino también a las características microclimáticas claves para los organismos, como por ejemplo, la temperatura, humedad, la capacidad de absorción de agua del suelo y la evaporación del agua (Chun & Lee, 2019; Méndez-Alonzo et al., 2013; Méndez-Toribio et al., 2016). Específicamente, la orientación de la ladera genera condiciones ambientales contrastantes, debido a que en latitudes norte, las laderas orientadas hacia el sur reciben mayor incidencia solar, presentando temperaturas más altas, menor porcentaje de humedad y mayor evaporación, contrastando con laderas orientadas hacia al norte, las cuales reciben menor radiación solar, por lo tanto presentan temperaturas más frías, mayor porcentaje de humedad y menor evaporación (Segura et al., 2003; Bennie et al., 2008). La posición topográfica es otro componente de la topografía que influye directamente en las condiciones abióticas del ecosistema. Este factor afecta la capacidad de absorción de agua del suelo y la formación del mismo, dado que los niveles de escorrentía y movimiento de partículas del suelo es mayor en posiciones altas. En cambio, las posiciones topográficas bajas reciben el agua y la materia orgánica proveniente de las partes altas, generando suelos más ricos, mayor humedad y mayor capacidad de absorción del agua (Bellinghamz & Tanner, 2000; Segura et al., 2003; Balvanera et al., 2011; Méndez-Toribio et al., 2016) .

A lo largo de la historia, la ecología de comunidades se ha centrado en explicar la diversidad, dinámica, el establecimiento y el ensamble de las comunidades. Es así como surgen teorías e hipótesis para entender y analizar dichos patrones (Hubbell et al., 1999; Engelbrecht et al., 2007). Las principales son la teoría de ensamble por nicho ecológico y la de ensamble por dispersión. La primera establece que son las diferencias ecológicas entre las especies y las condiciones ambientales lo que influye directamente en el ensamblaje de la comunidad (Whittaker, 1972; Hubbell et al., 1999). La segunda, que es la teoría de ensamble por dispersión postula que los individuos de todas las especies en la comunidad presentan una neutralidad en la dinámica de la misma (reproducción, muerte y especiación). Así, el ensamblaje de las comunidades depende de procesos neutrales tales como procesos de dispersión, extinción local y eventos de especiación (Clark & Clark, 1984; Bell, 2000; Webb et al., 2002; Rosindell et al., 2011) .

Con la finalidad de entender los procesos y patrones que determinan la estructura y el ensamblaje de las comunidades han surgido diversos métodos que permiten analizar la dinámica de la vegetación. Esto ha generado un gran avance en el esclarecimiento de las hipótesis que se postularon para explicar la coexistencia de las especies en estos ecosistemas. Tal es el caso del establecimiento de parcelas permanentes de 50 ha y las herramientas proporcionadas por la ecología filogenética (Webb, 2000; Rosindell et al., 2011).

El uso de filogenias en ecología surge a partir del año 2000, en el que Webb desarrolló dos índices de diversidad filogenética que permiten analizar y cuantificar relaciones conespecíficas entre especies. Esto permite comprender de una mejor manera los procesos evolutivos y ecológicos que influyen directamente en el ensamblaje de las comunidades (Webb *et al.,* 2002, 2008; Cavender-Bares et al., 2009). Consecutivamente, se generó un amplio campo en la ecología de comunidades que utiliza las herramientas filogenéticas para dilucidar si son los procesos estocásticos y deterministas o las reglas de ensamblaje las que determinan la estructuración de las comunidades (Webb et al., 2002, 2008). De esta manera, analizar la información filogenética de una determinada comunidad proporciona una visión más profunda de los procesos ecológicos que dan estructura a la composición de las comunidades (Webb 2000). Es así como surge la estructura filogenética de la comunidad como un concepto y análisis que hace referencia a las relaciones filogenéticas compartidas entre las especies coexistentes, de esta manera nos permite examinar y comprender los procesos que gobiernan el ensamblaje de las comunidades, si son los factores basados en el nicho o si son los procesos neutrales (Swenson & Enquist, 2009; Freilich & Connolly, 2015; Miller et al., 2017; Davies, 2021). Debido a lo anterior, en los últimos años el conocimiento de la estructura filogenética de las comunidades ecológicas, se ha convertido en una herramienta crucial para dilucidar los posibles factores que determinan el ensamblaje de las especies dentro de las comunidades (Webb et al., 2002, 2008; Helmus et al., 2007). Así, el enfoque filogenético ofrece herramientas poderosas para responder preguntas fundamentales sobre la manera en que los organismos se relacionan con su ambiente y como los filtros ecológicos y los factores neutros influyen en el ensamblaje de las comunidades ecológicas (Cavender-Bares et al., 2009; Maire et al., 2012; Ndiribe & Guisan, 2013).

Este enfoque filogenético en la ecología de comunidades postula tres posibles escenarios. El primero es un patrón filogenético aleatorio que sugiere que el establecimiento de una comunidad es resultado de la acción de procesos neutrales tales como eventos estocásticos de mortalidad y reclutamiento. Bajo este supuesto, ningún proceso relacionado con el nicho o procesos deterministas tienen relevancia para la estructuración de la comunidad, pero si los mecanismos de migración, dispersión y extinción locales son los que presentan un papel preponderante (Webb et al., 2002, 2008; Ndiribe & Guisan, 2013). Por el contrario, los patrones no aleatorios en una comunidad (agrupamiento o sobredispersión filogenética) están determinados principalmente por dos fuerzas ecológica que son los filtros ambientales y la competencia. El resultado de este filtrado ambiental es un patrón de agrupamiento filogenético. No obstante, también se puede presentar un patrón de sobredispersión filogenética por filtro ambiental, ya que en ocasiones esta fuerza genera convergencia evolutiva en los atributos que les permiten atravesar el filtro y lograr su establecimiento, obteniéndose así un patrón de sobredispersión (Lasky et al., 2013; Kraft et al., 2015; Chun & Lee, 2019). Por el contrario, la competencia intraespecífica, definida como la competencia entre especies fenotípicamente similares que genera exclusión competitiva, da como resultado un patrón de sobre-dispersión filogenética (Webb et al., 2002; Kraft et al., 2007)

Tanto los filtros abióticos como los bióticos (competencia) pueden actuar simultáneamente dentro de las comunidades, teniendo cada filtro distinta influencia en diferentes escalas espaciales (Shen et al., 2013; Wiegand et al., 2017; Davies, 2021). A nivel regional los patrones de agrupación filogenética pueden ser consistentes por los filtros abióticos, debido a que las especies no compiten por los recursos. En cambio, la sobre-dispersión puede ocurrir por el efecto de la competencia en escalas espaciales pequeñas, donde la semejanza en los requerimientos de las especies limitaría la coexistencia (Adler et al., 2007; Freilich & Connolly, 2015). Diversas investigaciones han documentado patrones de sobre-dispersión en escalas espaciales pequeñas, especialmente se ha identificado este patrón en comunidades locales que incluyen un único linaje filogenético. Esto es debido a que la competencia entre las especies es mayor a estas escalas, limitando la coexistencia de especies relacionadas filogenéticamente (Kraft et al., 2007; Emerson & Gillespie, 2008; Letcher et al., 2012; Swenson et al., 2012.

Actualmente la selva seca presenta grandes amenazas ecológicas originadas principalmente por actividades antropogénicas. Aunado al calentamiento global se prevé un cambio importante en la distribución y la posible re-estructuración de este ecosistema. Por lo tanto, resulta imprescindible conocer los procesos que rigen el ensamble de las comunidades en estos ecosistemas. Por lo cual, en el presente trabajo enmarcado en la selva seca de la región de Álamos, Sonora se planteó la siguiente pregunta de investigación: ¿Cómo afectan los filtros ambientales generados por la orientación de ladera y la posición topográfica los atributos, la dinámica y la estructura filogenética de diferentes categorías de tamaños de la comunidad arbórea? Por consiguiente, la información generada en la presente investigación permitirá comprender y predecir cambios en la diversidad y dinámica de las comunidades vegetales.

Objetivo

- Dilucidar el efecto de la orientación de ladera y la posición topográfica en los atributos, dinámica y estructura filogenética de las especies leñosas a lo largo de diferentes categorías de tamaño de la comunidad arbórea de la selva seca de Álamos, Sonora.

Hipótesis

Considerando que las condiciones ambientales y la disponibilidad de recursos varían a lo largo del gradiente impuesto por la orientación de ladera y la posición topográfica y bajo el supuesto de que estas características ambientales determinan la estructura taxonómica y el recambio de especies, entonces la dinámica de las comunidades, así como su estructura filogenética serán diferentes entre condiciones ambientales impuestas por el gradiente topográfico.

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Capítulo II

Diversity, dynamics and phylogenetic structure across ontogeny of the tree community at northernmost dry forest in the Americas

Sebastián Vargas-Rumbo[1], Abdieel Quisehuatl-Medina[1], Clementina González-Zaragoza[1],
Moisés Méndez-Toribio[2], Stephen P. Hubbell[3], Leonel Lopez-Toledo[1]

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

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

[3]University of California-Los Angeles,

Corresponding author; e-mail: Lopez-Toledo, L. (llopezt@umich.mx, leonellopeztoledo@gmail.com)

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Abstract

1. Biotic and abiotic factors have a direct influence on the community's species diversity and dynamics. Environmental heterogeneity generated by topography, not only influence the assembly and dynamics of communities, but also alter key microclimatic conditions for plant development and survival. Then, the study of size classes through the life cycle may allow us to identify the role of ecological filters and the vulnerable stages, which define the taxonomic and phylogenetic structure.
2. The main goal of this study was to evaluate the effect of topography on the community structure (individuals, stems, species diversity and basal area), community dynamics (survival, recruitment, growth and turnover rate community structure) and phylogenetic structure (NTI and NRI), considering different size categories (seedlings, saplings, juveniles and adults) in the woody plant coomunities of dry forest of Alamos, Sonora. For this, 16 20x40 m plots established in 2017 were re-surveyed to evaluate the influence slope orientation and topographic position (and their interaction) on the different size categories of the tree community.
3. Our results indicate a significant effect of the interaction between topographical factors on the species mortality in juvenile stages, being the South-High and the North-High the conditions that had the highest (0.14 ± 0.10%) and the lowest mortality (0.01 ± 0.002%), respectively. For species richness, we found differences only in seedlings, where the North-High had the highest values (9.25 ± 1.03). On the other hand, individuals at the southern orientation were highly branched (multi-stemmed) and had greatest basal area compared to those on the north. The observed phylogenetic patterns were from clustering in seedlings to overdispersion in adults at South orientations. By contrast, at North orientations, we found an opposite pattern.
4. The result of the differential effect of topographic factors along the size classes and topographic conditions may be due to an environmental filter effect on plant communities that generates a differentiation in their composition and structure of the community of trees of the northernmost tropical dry forest in the Americas.

Introduction

Tropical ecosystems have been a study model for the analysis of plant communities due to the great diversity of flora that they harbor. However, most of these studies have been carried out in tropical humid forests (Engelbrecht et al., 2007; Gallardo-Cruz et al., 2009; Méndez-Toribio et al., 2016). Consequently, there is a poorly understanding in the processes and factors that determine the dynamics of tropical dry forest tree communities (Osorio Beristain et al., 2006; Engelbrecht et al., 2007; Balvanera et al., 2011; Pérez-García et al., 2012; Reis et al., 2017). Tropical dry forests are biologically and ecologically important ecosystem with a worldwide distributed (Miles et al., 2006; Balvanera et al., 2002). However, the greatest distribution is presented in the Americas, representing the 54.2% of the vegetation of the continent, and containing a high biological diversity (Miles et al., 2006). The most conspicuous characteristic of the dry forest is the marked seasonality of drought (6-8 months). Therefore, the availability of water is the most important factor for the establishment and distribution of plant species (Daws et al., 2002; Dyer, 2009; Balvanera et al., 2011). As a result, the dry forest represents an ideal ecosystem for the study of the response of plant species to the water availability in the community assemblages.

The structure and composition of communities are the result of ecological, evolutionary and biogeographic processes that have permeated throughout history, allowing the selection and establishment of the species that will assemble in the communities (Cavender-Bares et al., 2009). Two principal theories have been proposed to explain the processes involved in the community assembly: i) the theory of ecological niche and i) the theory by assembly. The first theory postulates that biotic and abiotic interactions are the main factors governing the dynamics of communities, for example the environmental restrictions and intra/interspecific competition are those that dominate the community's assembly (Whittaker, 1972; Hubbell et al., 1999; Swenson et al., 2012; Shen et al., 2013; Freilich & Connolly, 2015). The main core of the niche theory includes the concept of ecological filter, which is defined as the role of biotic and abiotic conditions on the establishment of new individuals in the community, acting metaphorically as a filter, where only species with certain morphological or physiological characteristics can pass through this filter (Cavender-Bares et al., 2009; Lasky et al., 2013; Kraft et al., 2015; Davies et al., 2021).

The second theory postulates that the species present a neutrality in the dynamics of the communities. Therefore, the assembly of communities depends on neutral processes such as dispersal, local extinction and speciation events (Clark & Clark, 1984; Bell, 2000; Webb et al., 2002; Adler et al., 2007; Engelbrecht et al., 2007; Palma, 2010;). At the moment, there are evidences of the effect of ecological filters on the diversity and dynamics of the community. Thus, biotic and abiotic filters operate by selecting species that will conform the community and consequently its rates of recruitment, mortality and species turnover (Letcher et al., 2012; Maire et al., 2012; Swenson et al., 2012; Wiegand et al., 2017). As a result, the species respond to these filters through their functional traits, driving the responses of species, which in turn may allow their establishment and assembly of the community (Kraft et al., 2007; Cadotte et al., 2009; Cavender-Bares et al., 2009; Chun & Lee, 2019).

Specifically, there are some factors that directly influence the establishment and assembly of species in the communities, which can be of paramount importance locally (Clark et al., 1999; Galicia et al., 1999; Daws et al., 2002). The topography, which has been widely documented, is one of these factors that directly influence the temperature, the incidence of solar radiation, the soil humidity and evapotranspiration and even processes of soil formation at mesoscale (Galicia et al., 1999; Daws et al., 2002; Badano et al., 2005; Bennie et al., 2008; Dyer, 2009; Méndez-Toribio et al., 2016). At higher latitudes the topography takes even more relevance, as opposed slopes greatly differ in the critical microclimatic conditions. Thus, at the northern hemisphere, south facing slopes receive higher solar incidence compared to north slopes, which generate differences in water availability and other key conditions and resources for the plant communities (Clark et al., 1999; Balvanera & Aguirre, 2006).

Nevertheless, the effect of topography on plant communities cannot be generalized, since this pattern is not constant throughout the planet, as in southern latitudes an opposite pattern is shown (Gallardo-Cruz et al., 2009; Maass & Burgos, 2011; Markesteijn et al., 2011; Méndez-Toribio et al., 2016). As a consequence, it is complex to extrapolate the results generated in other latitudes. Despite the interest on the factors and processes that determine biological diversity in dry forest, few studies have evaluated the effect of topography on the dynamics and diversity of species (Swaine et al., 1990; Segura et al., 2003; Appolinario, 2005; Lott & Atkinson, 2006; Maass & Burgos, 2011; Méndez-Toribio et al., 2014, 2017; Reis et al., 2017, 2018).

With the main goal to understand the patterns and processes that determine the structure and assembly of communities, several methods have emerged, among which the use of phylogenies stands out (Freilich & Connolly, 2015; Davies, 2021). Thus, examining the phylogenetic structure of the community allow us to elucidate whether stochastic processes or the postulates of the niche theory determine the assembly of the community (Webb et al., 2002, 2008; Helmus et al., 2007; Engelbrecht et al., 2007; Cavender-Bares et al., 2009; Maire et al., 2012; Ndiribe & Guisan, 2013)

In particular, the phylogenetic structure indices developed by Webb (2000) allow the analysis and quantification of conspecific relationships between species. These phylogenetic indices provide a better understanding of evolutionary and ecological processes, that directly influence the assembly of communities (Webb, 2000; Webb et al., 2002; Kraft et al., 2007; Emerson & Gillespie, 2008). Based on these indices, communities may exhibit a random, clustered or overdispersed pattern and the phylogenetic approach postulates that two forces determine these patterns. These forces are i) the interspecific competition and ii) the environmental filter. The first limits the coexistence of species, showing a pattern of phylogenetic overdispersion. Nevertheless, if competitive ability is trait-mediated, we can predict that competition may lead to phylogenetic clustering due a differentiation or specialization in the ecological niche (Kraft et al., 2007; Letcher, 2010; Pearse et al., 2014; Davies, 2021). The second force (the environmental filter) suggest that only those species with certain morphological or physiological characteristics can pass through this filter, generating a phylogenetic clustered pattern. However, the environmental filter can generate a convergent trait causing an overdispersed pattern (Baraloto et al., 2012; Lasky et al., 2013; Kraft et al., 2015; Chun & Lee, 2019). In the other hand, a random phylogenetic pattern suggests that the establishment of a community is the result of the action of neutral processes (Letcher, 2010; Letcher et al., 2012; Ndiribe & Guisan, 2013; Rosindell et al., 2011).

Comparison between different size classes is key and highly informative in determining whether there is or not an effect of the environmental filter on the establishment and survival of plant communities. Due to the relative abundance of trees is the result of biotic and abiotic processes affecting different size classes throughout the life cycle of species. Thus, different processes, such as natural enemies, climatic or edaphic condition, and competence between con and heterospecific neighbors (Bell et al., 2000; Kraft et al., 2007; Emerson et al.,: 2008; Freilich et al., 2015) throughout ontogeny may generate a different community assemblage (mainly at the earliest life cycle stages). Therefore, the study of size classes through the life cycle may allow us to identify the role of ecological filters and the vulnerable stages, which define the taxonomic and phylogenetic structure.

The dry forest of the Álamos region in Sonora, Mexico, the northernmost in the Americas represents a suitable ecosystem for studying and understand the evolutionary and ecological processes that directly influence the assembly of communities. The topography in the region gives a great environmental heterogeneity and microclimates that influence the establishment and mortality of plant species (Van Devender et al., 2000). Factors such as slope orientation and topographic position affect climatic conditions, generating contrasting microclimates. As a result, differences in composition and structure of the tree communities on different slope orientation may be expected ((Holland & Steyn, 1975; Bellinghamz & Tanner, 2000; Segura et al., 2003; Bennie et al., 2008). Under this phylogenetic and ecological context, in this study we addressed the following question: how does the environmental heterogeneity generated by slope orientation and topographic position affect the taxonomic structure, the dynamics and the phylogenetic structure of the woody plant communities? In this way, the present study focuses on studying the structure and dynamics of the community (trees and shrubs). We then identify the phylogenetic structure and the forces determining the assembly of the community in different size classes (seedlings, saplings, juveniles and adults).

Therefore, under this scenario, it would be expected to observe a pattern of overdispersion in early stages (seedlings, saplings and juveniles) to phylogenetic clustering in advanced in adults, on south facing slopes. As a result of the hardest conditions presented, like the greatest solar radiation and temperatures that acting like environmental filter. In contrast to the northern slopes, where an overdispersion pattern will be maintained throughout all size classes due to, this slope presented a better environmental condition, thus the closely related species share similar trait that distantly relates species, hence the competition for limiting resources would tend to inhibit the coexistence of close relatives.

Materials and methods

Study site

The study was carried out in the Sierra Alamos Rio Cuchujaqui Reserve (SARC), which has an extension of 92,890 ha in the northern state of Sonora in Mexico. The SARC is part of the federal network of protected natural areas in Mexico and recognized by the UNESCO in the Man and the Biosphere (MAB) Program. Within SARC, elevations range from 300 to 1600 m. asl, generating a vegetation gradient that spans from seasonally tropical dry forest (TDF) to pine-oak forests. Specifically, our study site is located between 350-450 m. asl and it is widely covered by TDF within the Reserva Ecológica Monte Mojino (REEM). This is a ~8000 ha private reserve, established by Nature and Culture International and Naturaleza y Cultura Sierra Madre, A.C. to conduct conservation, applied research and community development (Figure 1).

Meteorological stations around the area have indicated that annual rainfall is highly variable with an average of 650 mm and minimum of 190 and a maximum of 1120 mm between 1940 and 2005 (López-Toledo et al., 2011). Data from an automatic micrometeorological station in the period 2013-2019 located within REMM, very close to the plot of study, registered a mean annual precipitation of 713.4 with minimum of 483.1 and a maximum of 595.9 mm. In general, most of the precipitation (74-95%) fall between June and September which results in a strong large dry season of 8 moths with 5-25% of the annual precipitation (Velez-Ruiz et al., 2020). Mean annual temperature is 21.5 °C with 10 °C and 41 °C as minimum and maximum temperatures, respectively.

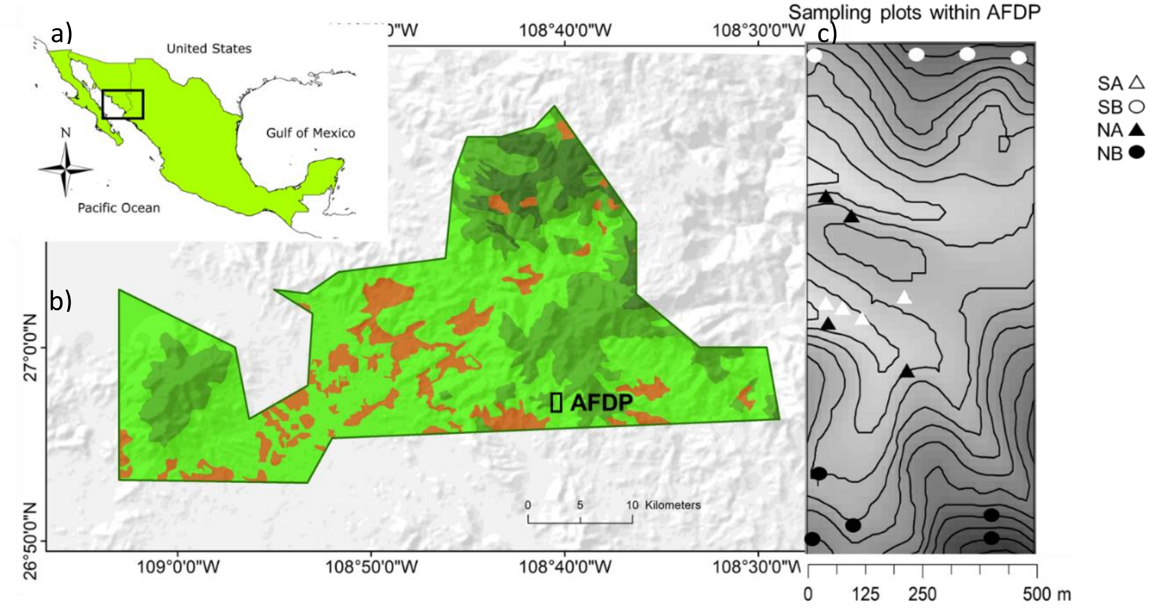

Figure 1. Map of the study area. The 50-hectare plot (AFDP) is located in the northernmost part of the dry forest distribution in America. a) the plot is located within the Monte Mojino Ecological Reserve within the Sierra de Álamos Flora and Fauna Protection Area in Sonora. Mexico. b) the 16 study subplots are randomly distributed throughout the 50 hectare plot. C)

Sampling design and data collection

The study was carried out within the Alamos Forest Dynamic Plot (AFDP), a permanent plot for the study of the dynamics of the dry forest of Alamos, the northernmost distribution of this biome in the Americas. In this plot, at the beginning of 2017, 16 subplots of 20 x 40 m were established and all trees and shrubs ≥1 cm in DBH were marked and identified with a total of 1.28 ha area sampled. These subplots were originally established to identify the role of slope orientation (SO) and topographic position (TP) on the taxonomic and phylogenetic structure of the woody plants community and results have been published elsewhere (Quisejuatl et al 2023). As a result of the combination of these factors, we have the following four conditions: I) North-Low, sites with north slope orientation and in the lower position of the slope; II) North-High, sites with north slope orientation and on the top of the slope; III) South-Low, sites with south slope orientation and in the low position; IV) South-High, sites facing south slope and at the top of the slope. Four replicates were considered for each of these conditions, resulting in the 16 subplots.

Community structure

Fieldwork was conducted by early 2020 and it consisted of the re-census of the individuals marked at the beginning of 2017. Additionally, we censused seedlings (<50 cm height) and saplings (50 > 130 cm height) in four 5x5 m quadrants established in the corners of each plot resulting in 100 m^2 sampled area per subplot. For all size classes the following measurements were obtained to analyze the attributes of the community: i) number of individuals, iii) number of stem, iii) diversity of species (q0, q1, and q2) and iv) basal area.

Community dynamics

The evaluation of the community dynamics consisted in registering survival and growth of the individuals marked in 2017. We also registered recruitment of ≥ 1cm DBH individuals in the 16 subplots. We calculated mortality (equation 1) and recruitment (equation 2) using the following equations (Quinto et al., 2009):

$$M = \{1-[N_0-m/N_0]\,1/\Delta t\} \times 100 \qquad \text{equation 1}$$

$$R = \{[(N_0+r)/N_0]\ 1/\Delta t-1\} \times 100 \qquad \text{equation 2}$$

where N_0 is the number of individuals registered in the first census, m is the number of death individuals in the 2017-2020 period, while r is the number of recruited individuals and Δt the time between census (3 years). Growth rates for all 1≥ cm DBH individuals was estimated based on equation 3:

$$RGR= (lnDBH_2-lnDBH_1/t_2-t_1) \qquad \text{equation 3}$$

Where RGR is the relative growth rate, DBH_2 and DBH_1 are final and initial diameter at breast height and t_1 and t_2 are initial and final time (Hoffmann & Poorter, 2002; Appolinário & Bot, 2005; Santos et al., 2017). To analyze the number of species lost and recruited among censuses, species turnover rate was obtained over time. We used the equation 4:

$$STR = l + g / S * ci \qquad \text{equation 4}$$

where STR is species turnover, *l* is the number of species lost, *g* is the number of species recruited (gained), *S* is the total number of registered species and *ci* is the census interval (Magurran, 2004). Similarly, to assess the changes in the properties of the communities between census we used a relative rate (as in equation 3) for individuals, stems and basal area.

Structure and phylogenetic diversity measures

For phylogenetic reconstruction we considered a species pool with all species registered in the sampled plots as well as species registered in previous studies at the same sampling site (Martin et al. 1998; Van Devender et al. 2000). A total of 106 tree species and arborescent cacti were integrated comprising 105 angiosperms, and using *Cycas revoluta* as an outgroup. Two methods were used to define phylogenetic relationships among species:

1) We first estimated phylogenetic relationships between species using a mega tree available in Phylomatic (Web et al., 2005) This estimation was carried out using the super tree R20120829 (available at http://phylodiversity.net/phylomatic). The super tree topology is based on the phylogenetic relationship of orders and families of APG. The BLADJ algorithm of the Phylocom software was used time calibrate the phylogenetic tree, the age of the nodes was obtained using TIMETREE (http://timetree.org/).

2) We reconstructed phylogenetic relationships among the species pool using Bayesian inference in MRBAYES 3.2.1 (Ronquist et al., 2012). For this end, we used 3 nuclear regions (*ITS-ITS1, 5.8s* and *ITS2*) obtained from GenBank. Sequences were aligned and edited using MEGA X (Kumar et al., 2018). jModelTest (Posada 2008) was used to the choose the model of molecular evolution that best fit our sequence data. The best model for the concatenate

matrix under the Akaike information criterion (AIC) was GTR + I + Γ. We ran the analysis for 30 million generations using four chains (twice), sampling every 1000th generation. We discarded the 25% of the trees prior to stationarity as burning, and the remaining were used to generate a consensus tree. Once the phylogenetic tree was obtained, the Phylocom 4.2 (Webb et al., 2008) software was again used to assign age to the nodes and homogenize the length of the branches, the age of the nodes was estimated using the same database described in the first method.

The topology of the time calibrated tree obtained through the phylogenetic reconstruction method with Bayesian inference was better resolved and supported than the super tree obtained from phylomatic. Therefore, the Bayesian inference tree was used to calculate the phylogenetic diversity and phylogenetic structure indices of the sampled communities.

To obtain the phylogenetic structure of species within different size classes, two abundance-based community phylogenetic structure indices were calculated for each of the 16 communities sampled (subplots) with the help of the picante package in R (Kembel et al. 2010). The net relatedness index (NRI) is a standardized measure of the mean pairwise phylogenetic distance (MPD) between all species in the community, while the nearest taxon index (NTI) is a standardized measure of the phylogenetic distance to the nearest taxon (MNTD), which is the mean distance separating each species in the community from its closest relative. NRI measures deeper divergences while NTI divergences near the tips of the phylogeny. NRI was calculated with the picante function *ses.mpd*, and NTI, with the function *ses.mntd* (Webb et al., 2002). Positive NRI or NTI indicates phylogenetic clustering, and negative values indicates phylogenetic evenness, according to Kembel et al., (2010). To statistically determine if communities show phylogenetic clustering or overdispersion, we compared the observed values of NRI and NTI to the patterns expected under null community assembly, using *independent swap* as a model to generate 9999 null communities (Kembel et al., 2010). This maintains the abundance and richness of the species, while randomizing the patterns of species coexistence in the community. Thus, it generates null communities considering all the species of the phylogeny and producing scenarios where the ability of the species to colonize is proportional to its frequency in the local community.

We obtained the alpha phylogenetic diversity of the different size classes (seedlings, saplings, juveniles and adults) through the phylogenetic diversity index (PD; Faith, 1992), using the species presence/absence matrix. PD quantifies the total branch length spanned by the phylogenetic tree including all the species of a community (Faith, 1992). For the beta phylogenetic diversity (PBD), two dissimilarity indices were calculated (COMDIST and COMDISTNT). These indices are a measure of dissimilarity that computes the mean hylogenetic distance between species that co-occur in two different sites and were based on the abundance of the species registered in the 16 subplots for each size class and between conditions (Pearse et al., 2014).

Statistical analysis

From the data obtained in the field, abundance matrices were developed to analyze the effect of the topography on the community structure community dynamics and phylogenetic structure and diversity of the woody plants in four size classes (seedling, saplings, juveniles and adults). Specifically, we used generalized linear models (GLM) with different error distribution depending on the nature of the response variables. For count variables we used a Poisson distribution (number of stems, q0, number of individuals), while for continuous variables we used Normal Gaussian distribution (basal area, NTI, NRI).

For the categorization of juvenile and adult individuals, we used the empirical cumulative distribution function (ECDE) to obtain the empirical measure of the DBH of each species, from this mean, the smallest half were considered juvenile, while the largest half were considered adults. On the other hand, for the categorization of seedlings and saplings, their height was considered, these individuals that presented a height <50 cm were considered seedlings, and the individuals that showed a height of 50 > 130 cm were considered saplings. Therefore, 4 plant subcommunities were generated based on the categorization of sizes classes. Multivariate analyzes were performed to determine the taxonomic differentiation between the communities due to SO and TP and their interaction, for which a nonmetric multidimensional scaling analysis (NMDS) was carried out based in abundance data and Bray-Curtis distance. To assess the habitat association of species we used a Monte Carlo randomization test, this method shuffled the habitats on which each of the species occurred, and calculated a deviation statistic based on the abundance indices of species in each habitat type: ∑[(Randomized – Expected)2 / Expected]. We repeated this 1000 times for each species and compared the observed deviation value with this randomized distribution of deviation values. We consider significant habitat association as observed values greater than 95% of the randomized values (Webb, 2000).

We conducted a principal component analysis (PCA) to explore the variation among the rates of change of attributes and the dynamic variables. Finally, a PERMANOVA was carried out to analyze whether the patterns observed by the multivariate analyzes are significant. All multivariate analyzes were carried out on the vegan package (Oksanen et al. 2017) using the R statistical program (R Development Core Team, 2014).

Results

Community structure

A total of 6559 individuals corresponding to 54 species were recorded, the number of individuals and species was distributed in the size classes as follows: seedlings (223 individuals, 25 spp.), saplings (212 individuals, 33 spp.), juveniles (3090 individuals, 42 spp.), adults (3034 individuals, 53 spp.). In general, Fabaceae was the better represented family (13 spp.), followed by Burseraceae (4 spp.), Cactaceae (5 spp.) and Euphorbiaceae (5 spp.). Euphorbiaceae was the most abundant family. However, this pattern was not maintained throughout size classes. In the case of seedlings, Fabaceae was the richest family in species and most abundant. On the other hand, in the case of saplings, Burseraceae had the highest species richness and Bignoniaceae the highest number of individuals, being *Handroanthus impetiginosus* the dominant species. In the case of juveniles and adults, the general pattern was maintained, where Fabaceae had the higher species richness and Euphorbiaceae was the most abundant family and dominated by *Croton fantzianus*.

The univariate analyzes to evaluate the effect of the topography on the structural attributes of the community showed significant differences in the following attributes: species richness (q0), being the saplings the only stage that presented significant values exclusively for the topographic position were the high position presented the highest values ($x^2 = 0.22_{(1,14)}$, p=

<0.05) (Table S1), for the case of the number of individuals, number of stems and basal area only adults showed significant differences just for slope orientation, being the south orientation were presented the highest number of individuals, polystem individuals and basal area (x^2 $=5.63_{(1,13)}$, p= <0.05); $X^2=29.12_{(1,14),}$ p=<0.01; X^2=8.88(1,13), p= <0.05) respectively (Figure 1). The interaction between topographic factors did not show significant differences for the attributes of the community, therefore, his term was eliminated from the statistical model.

The results obtained by the nonmetric multidimensional scaling analysis (NMDS) showed a clear separation throughout the size classes influenced by topographic factors (Figure 2). Existing a clear differentiation in the communities presented in each topographic condition Results from PERMANOVA allowed us confirm this, owing to, obtaining significant values in the slope orientation for seedling and saplings ($R^2=0.19_{(1,14)}$, p= <0.01 and $R^2=0.15_{(1,15)}$ p= <0.01) respectively and for position only in seedlings ($R^2=0.12_{(1,14)}$ p= <0.05).

Monte Carlo randomization test showed (Table 2) for seedlings that only three species of 21 (14%) presented a habitat association, and only two species maintained this association in juveniles and adults (*Coursetia glandulosa* and *Handroanthus impetiginosus*). In saplings, eight species of 32 (25%) showed habitat association, of which four maintain this association in the highest size categories (*Brongniartia alamosana*, *Cordia sonorae*, *Lysiloma tergeminum*, *Pachycereus pecten*), only three maintained the association in juveniles and one change the habitat association in adults. In the case of juveniles and adults, twenty-two (53%) out of 41 species were significantly associated with a habitat type, however only fifteen species were similarly associated with the same habitat both as juveniles and as adults, therefore, only seven species were habitat-associated as adults, but not as juveniles.

Community dynamics

Regarding mortality, the GLM showed significant differences in the interaction of condition, slope orientation x topographic position (x^2 $=20.15_{(1,12)}$, p= <0.01), having juveniles the highest mortality rates in the south orientation and high position (Table S4). Recruitment rates did not show significant differences for the topographic factors at any size class stage.

The relative growth rate showed significant differences for juveniles and adults in the slope orientation (x^2 =5.66$_{(1,13)}$, p= <0.05 and x^2 =12.77$_{(1,12)}$, p=<0.01) respectively, where the south low show the highest values. Species turnover (t) showed that only juveniles had significant differences for the topography position (X^2= 6.42$_{(1,12)}$, p=<0.05), being the low positions the sites where the highest values were registered (Figure 3).

Structure and phylogenetic diversity α and β

The phylogenetic structure of the community was not influenced by topographic factors in the saplings, juvenile or adult stages. Seedlings were the only stage that presented significant differences in all factors only for NRI (SO, X^2= 8.59$_{(1,11)}$, P=<0.05; TP, X^2=12.85$_{(1,11)}$, P=<0.01; SO*TP, X^2=10.73$_{(1,11)}$, P=<0.01). The patterns observed with NRI ranged from overdispersion (-0.36 where only one plot showed a significant phylogenetic pattern) in early size classes, to clustering (0.30 resulting two plots whit a significant phylogentic pattern) in higher stages at north facing slopes. On the contrary, the south condition presented clustering patterns in seedlings (0.61 two plots showed a significant phylogenetic pattern) and overdispersion in the subsequent sizes classes (-0.21 two plots showed a significant phylogenetic pattern) (Figure 4).

NTI did not show significant differences for the topographic factors at any size class, and the phylogenetic structure patters were opposite respect to NRI: northern slopes in early stages showed clustering patterns, seedlings and juveniles showed overdispersion and the adults again clustering. In the case of slopes facing south, a clustering pattern was observed with NTI along all size classes.

For phylogenetic diversity (PD), only saplings showed significant differences for TP (x^2=6.23$_{(1,12)}$, P=<0.05). Being the north facing where presented the highest phylogenetic diversity. Conversely, the beta phylogenetic diversity (PBD) using the COMDIST indices showed a pattern of non-random grouping between topographic conditions, presented a clear differentiation throughout the stages, as the size classes progress, the communities differentiate themselves, the communities with values close to zero are evolutionarily similar, therefore suggest being the slope orientation, the main factor causing this differentiation

(Figure 5). The PERMANOVA applied to the distance matrices allowed us to determine this discrepancy, since all stages presented a significant difference for SO in both indices (Table 1).

Discussion

Community structure

In general, we found an influence of topographic factors on the species richness, basal area, number of individual and stem. These results were consistent with those reported by Méndez-Toribio et al., (2016) from the TDF of Tziritzícuaro Michoacán who reported an effect of the topographic condition on the diversity of species. However, other studies have not found an effect of the topography on the attributes of the community (Segura et al., 2003; Gallardo-Cruz et al., 2009; Maass & Burgos, 2011). These contrasting results may be mainly due to two factors: i) the latitudinal effect, since the variation of environmental factors generated by the topography north and south slopes at high latitudes are highly contrasting compared to lower latitudes. Particularly, at our study site, which is the northernmost distribution of the TDF in America, previous studies have found large environmental differences. ii) The effect of grazing by livestock. In other studies, an effect on the community traits and attributes of plant communities has been reported principally on the forest understory on which livestock feed (shrubs, herbs and tree seedlings and saplings) causing a loss of biomass and individuals, mainly in early stages (Maza-Villalobos et al. 2022). Our subplots are exempt of cattle breeding since 2008 (Álvarez-Yépiz et al., 2008; Méndez-Toribio et al., 2014).

We detected a differential effect of topography throughout size classes. Therefore, it could be suggested that the composition and structure of the community is affected in different ways throughout the ontogeny of the plant communities of the northernmost dry forest in the Americas. At mesoscale, topographic heterogeneity is associated with a change in the availability and quantity of resources like water availability, humidity and light, which in turn causes a change in the composition of the tree community. The patterns obtained through the NMDS allowed us to observe these changes throughout the size classes of the dry forest. This result can be supported based on the environmental filter hypothesis, where the early stages are the most vulnerable to the forces underlying the habitat filtering process (see below).

Community dynamics

The mortality rate reported in this study is low compared to other results obtained in dry forests of Brazil and Bolivia (de Souza Werneck & Villaron Franceschinelli, 2004; Uslar et al., 2004; Reis et al., 2017; Santos et al., 2017). It is likely that the short time elapsed between both censuses (three years) affected our mortality estimations, however, our results support the assumption of dry forest, where the water it is de driving factor of the mortality and establishment (Reis et al., 2018). Due to the mortality rate was highest un the south facing, where presented the hardest conditions. The species turnover was highest in north orientations, where the microclimatic conditions are more favorable and allows a better establishment and survival of the species. This is consistent with the low mortality observed on these slopes that in turn, contrasted with the south orientations, where only those species able to tolerate drought and harsh microclimatic conditions were able to establish themselves. In the same way, the relative growth rate hold this result, given the greatest values were presented in the south slope, due to the species that establish and grow in each conditions present a trade-off between growth and produce leaves (Poorter, 1989; Poorter & Kitajima, 2007; Chaturvedi et al., 2011; Tripathi et al., 2020) illustrated by the two major axis of species differentiation in the dry forest, tolerant and avoiding dry (see below).

Structure and phylogenetic diversity α and β

Based on the observed phylogenetic patterns, the overdispersion found in the facing south and the clustering in the north facing plot, it is suggested that the plant community assemblage is being influenced by the microclimatic conditions of each topographic factor, being the abiotic conditions and the ecological differences of the species what allows the coexistence species Coinciding with results reported in tropical forest in brazil, were reported that the vegetal community is assembled by climatic conditions and process related with the niche (Letcher, 2010; Letcher et al., 2012; Swenson et al., 2012; Baldeck et al., 2013; Duarte et al., 2014; Moro et al., 2015). However, our hypothesis were not confirmed, the overdispersion patter found in the south is result of convergent evolution in traits that allow plants tolerate drought.

Plant species of the dry forest have physiological, morphological and even phenological features that allow them to face the harsh climatic conditions that characterize this ecosystem, such as severe dry season and high levels of solar radiation. As a result, two major strategies have been widely reported in plant communities to cope with drought conditions and make efficient use of water when this resource is available, such strategies are drought tolerant and avoided species (Poorter & Kitajima, 2007; Méndez-Alonzo et al., 2013). Tolerant species generally have dense tissue on leaves, stems and roots and with long lasting leaf. They are species with resource conservation traits to face the low availability of water in unfavorable periods. On the other hand, species that avoid drought have soft stems with a high growth capacity and water efficiency when this resource is available, having large, short-lived leaves (Swenson & Enquist, 2009; Pineda-García et al., 2015; Méndez-Toribio et al., 2017).

Therefore, under this scenario and based on the overdispersion found in the facing south and the clustering in the north facing plot observed in this study, it can be inferred that the species assembly of the dry forest of northwestern Mexico is being influenced by the presence of environmental filters generated by topographic conditions. This ecological force generated an evolutionary convergence in the attributes that allow species to be drought tolerant. In this way, an overdispersion pattern was obtained on the southern slopes in the higher size categories, allowing the coexistence of tolerant species under these conditions. In the same way, the clustering patter observed in the seedlings could be an effect of the harsh condition to the germination of seeds. In contrast, we found a phylogenetic clustering pattern in advanced stages at the northern slopes. This is probably due to niche conservatism in the attributes that allow species to avoid drought. As a result, there is a niche differentiation between the species that inhabit the northern and southern slopes. This premise was supported with the results of beta phylogenetic diversity, suggesting that southern slopes are less phylogenetically related to northern slopes. The Monte Carlo randomization test, confirm this result due to we can observed a species association to a particular topographic condition from de seedlings to adults in some species.

Evaluating the structure and phylogenetic diversity throughout different plant biological stages allowed us to more easily detect the vulnerability of the species to the environmental filter. Since in both orientations, there is a change in the phylogenetic pattern from seedlings to sapling and from this stage the pattern is maintained throughout the rest of the subsequent size classes, in both slope orientations. As a result, it is suggested that the transition from seedling to sapling is key to determining the establishment of individuals.

Conclusion

This study was designed to analyze the role of environmental filters, understood as the microclimatic conditions generated by topographic factors on the establishment and assembly of the plant communities of the dry forest in northwestern Mexico. Our results showed evidence of the role of environmental filtering process on the woody plant community in early stages to determine the establishment and survival of individuals. The incorporation of phylogenetic tools made it possible to determine and clarify the processes that are taking place in the community. However, analyzing the phylogenetic structure throughout different stages helped to better understand the community assembly.

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TABLES

Table 1. Results of the multivariate analysis using PERMANOVA, evaluating the effect of the slope orientation and topographic position on the patterns observed on the phylogenetic beta diversity (PBD) indices of the plant community of four biological stages of the dry forest of Alamos, Sonora, Mexico. Values in parentheses represent degrees of freedom.

PERMANOVA	**Slope orientation**		**Topographic position**		**SO*TP**	
COMDIST						
Seedlings	$0.08_{(1,14)}$	**<0.05**	$0.08_{(1,14)}$	**<0.05**	$0.07_{(1,14)}$	0.09
Saplings	$0.77_{(1,15)}$	**<0.05**	$0.06_{(1,15)}$	0.51	$0.06_{(1,15)}$	0.72
Juveniles	$0.07_{(1,15)}$	**<0.05**	$0.06_{(1,15)}$	0.46	$0.06_{(1,15)}$	0.14
Adults	$0.072_{(1,15)}$	**<0.01**	$0.06_{(1,15)}$	0.32	$0.06_{(1,15)}$	0.56
COMDISTNT						
Seedlings	$0.20_{(1,14)}$	**<0.01**	$0.17_{(1,14)}$	**<0.05**	$0.13_{(1,14)}$	**<0.05**
Saplings	$0.17_{(1,15)}$	**<0.01**	$0.06_{(1,15)}$	0.42	$0.05_{(1,15)}$	0.53
Juveniles	$0.23_{(1,15)}$	**<0.01**	$0.04_{(1,15)}$	0.51	$0.08_{(1,15)}$	0.18
Adults	$0.24_{(1,15)}$	**<0.01**	$0.08_{(1,15)}$	0.15	$0.06_{(1,15)}$	0.32

Table 2. Species association of woody community of the norhernmost dry forest in the Americas to a particular slope orientation using a Monte Carlo randomization test (NA= not associated, - = not registered).

	Associated			
Especie	Plantulas	Brinzales	Juveniles	Adultos
Acacia cochliacantha	NA	NA	South	South
Brongniartia alamosana	-	South	South	South
Bursera grandifolia	NA	NA	North	North
Bursera penicillata	NA	South	South	NA
Bursera sp	-	NA	North	North
Ceiba acuminata	-	NA	North	NA
Cordia sonorae	NA	South	South	South
Coursetia glandulosa	South	NA	South	South
Croton fantzianus	NA	NA	South	NA
Croton flavescens	NA	NA	South	South
Diphysia occidentalis	-	-	NA	South

Erythrina flabelliformis	-	-	NA	North
Erythroxylum mexicanum	-	NA	North	North
Fouquieria macdougalii	NA	South	NA	NA
Handroanthus impetiginosus	North	NA	North	North
Haematoxylum brasiletto	NA	NA	NA	North
Hintonia latiflora	NA	NA	North	NA
Karwinskia humboldtiana	-	NA	NA	North
Lonchocarpus hermannii	NA	NA	NA	North
Lysiloma divaricatum	South	NA	North	NA
Lysiloma tergeminum	NA	North	North	North
Maclura tinctoria	-	NA	NA	South
Pachycereus pecten	-	South	South	South
Randia echinocarpa	NA	North	NA	South
Randia thurberi	NA	NA	South	South
Sebastiania pavoniana	NA	NA	North	North
Senna palida	-	-	North	NA
Sp3.	-	-	North	North
Stenocereus montanus	-	-	South	South
Zanthoxylum fagara	NA	North	North	NA

FIGURE LEGENDS

Figure 1. Average values (± 1 standard error) of two attributes (species richness and Number of individual of the community of the norhernmost dry forest in the Americas.

Figure 2. Nonmetric multidimensional scaling analysis (NMDS) of four size classes based on Bray Curtis under different slope orientation (North and South) and topographic position (Low and High).

Figure 3. Average values (± 1 standard error) for the community dynamic of juvenile (mortality, turnover species and relative growth rate) and adults (relative growth rate) of the norhernmost dry forest in the Americas.

Figure 4. NRI patterns throughout four size classes of the norhernmost dry forest in the Americas. Evaluated between slope orientation (North and South) The asterisk represent a subplot with significant pattern.

Figure 5. Phylogenetic beta diversity (PBD). Dendogram of dissimilarity of four size classes, using the *Comdist* index. Where NH: North-high, NL: North-low, SH: South-high, SL: South-low

FIGURES

Figure 1.

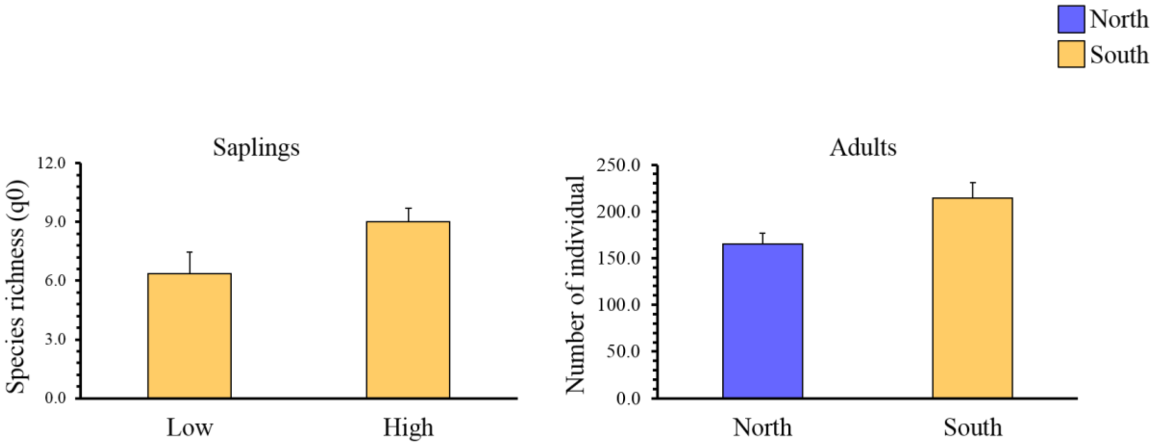
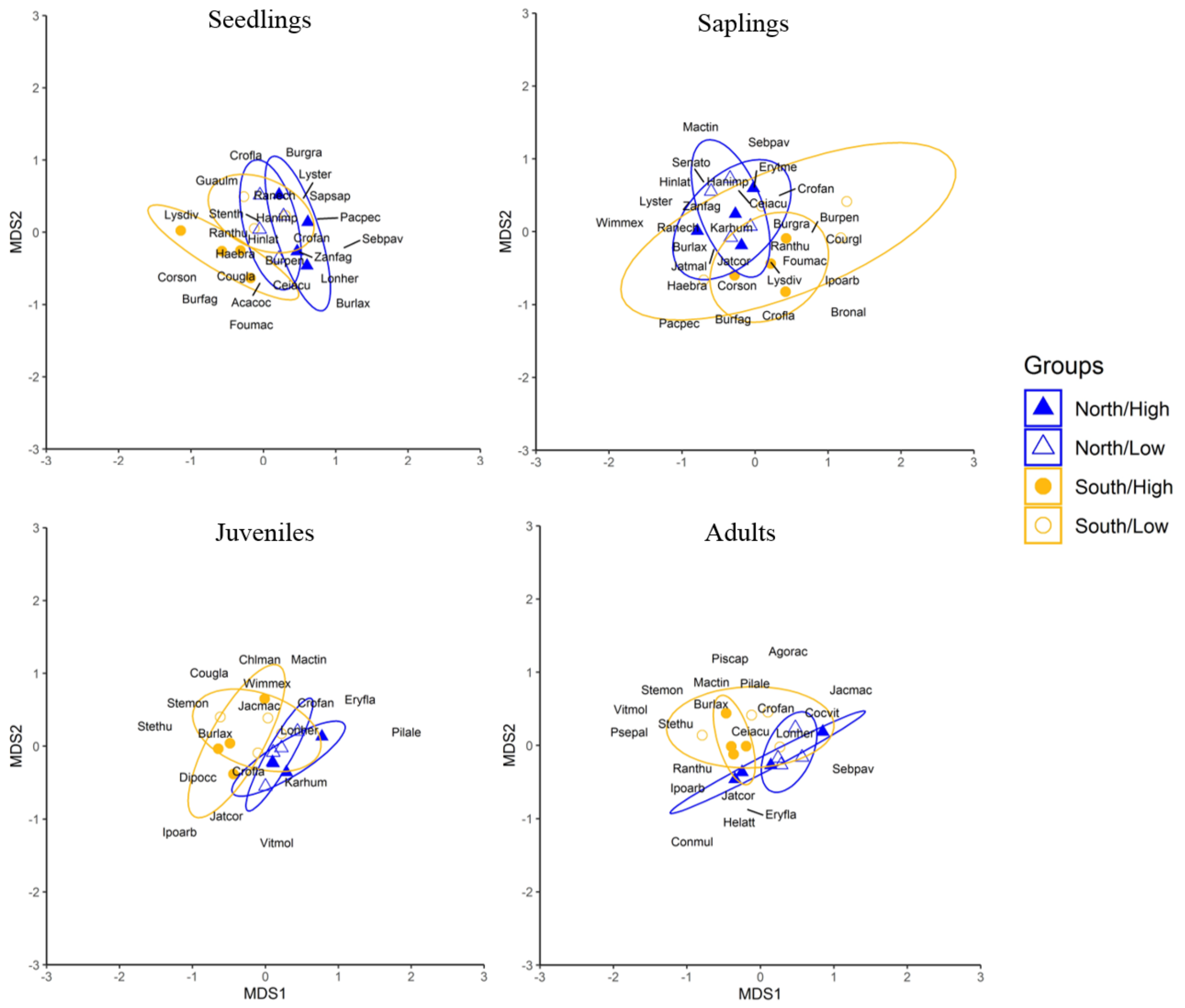


Figure 2.


Seedlings
Crofla
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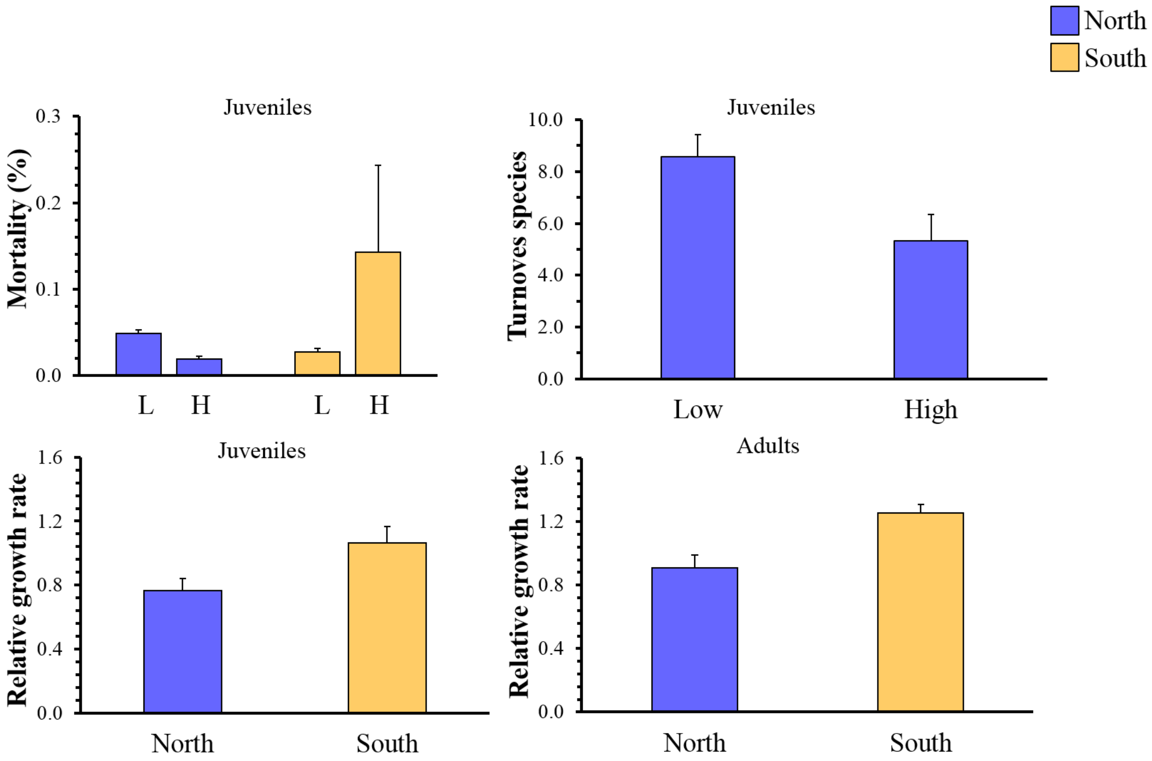
Lyster
Guaulm
Ranech
Sapsap
Lysdiv
Stenth
Hanimp
Pacpec
Ranthu
Hinlat
Crofan
Sebpav
Haebra
Burpen
Zanfag
Corson
Cougla
Ceiacu
Lonher
Burfag
Acacoc
Burlax
Foumac
Saplings
Mactin
Sebpav
Senato
Erytme
Hinlat
Hanimp
Crofan
Lyster
Zanfag
Ceiacu
Wimmex
Ranech
Karhum
Burgra
Burpen
Burlax
Ranthu
Courgl
Jatmal
Jatcor
Foumac
Haebra
Corson
Lysdiv
Ipoarb
Pacpec
Burfag
Crofla
Bronal
Juveniles
Chlman
Mactin
Cougla
Wimmex
Stemon
Jacmac
Crofan
Eryfla
Stethu
Burlax
Lonher
Pilale
Dipocc
Crofla
Karhum
Jatcor
Ipoarb
Vitmol
Adults
Piscap
Agorac
Stemon
Mactin
Pilale
Jacmac
Vitmol
Burlax
Crofan
Cocvit
Psepal
Stethu
Ceiacu
Lonher
Ranthu
Sebpav
Ipoarb
Jatcor
Eryfla
Helatt
Conmul
MDS2
MDS1
3
2
1
0
-1
-2
-3
Groups
▲ North/High
△ North/Low
● South/High
○ South/Low

Figure 3.


North
South
Juveniles
Mortality (%)
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Juveniles
Turnoves species
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4.0
2.0
0.0
Low
High
Juveniles
Relative growth rate
1.6
1.2
0.8
0.4
0.0
North
South
Adults
Relative growth rate
1.6
1.2
0.8
0.4
0.0
North
South

Figure 4.

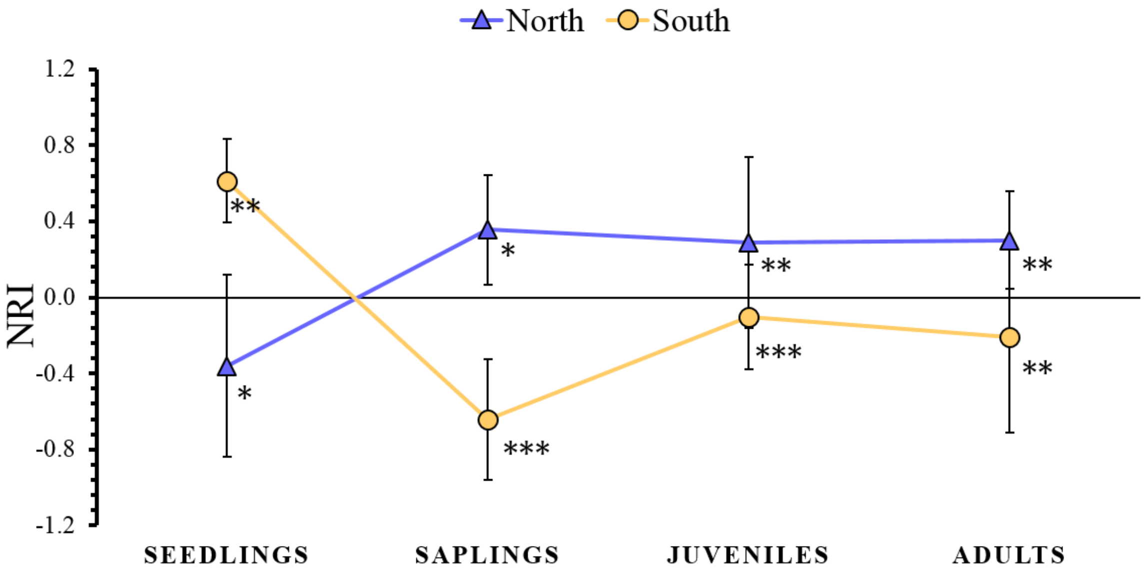
North
South
NRI
1.2
0.8
0.4
0.0
-0.4
-0.8
-1.2
SEEDLINGS
SAPLINGS
JUVENILES
ADULTS
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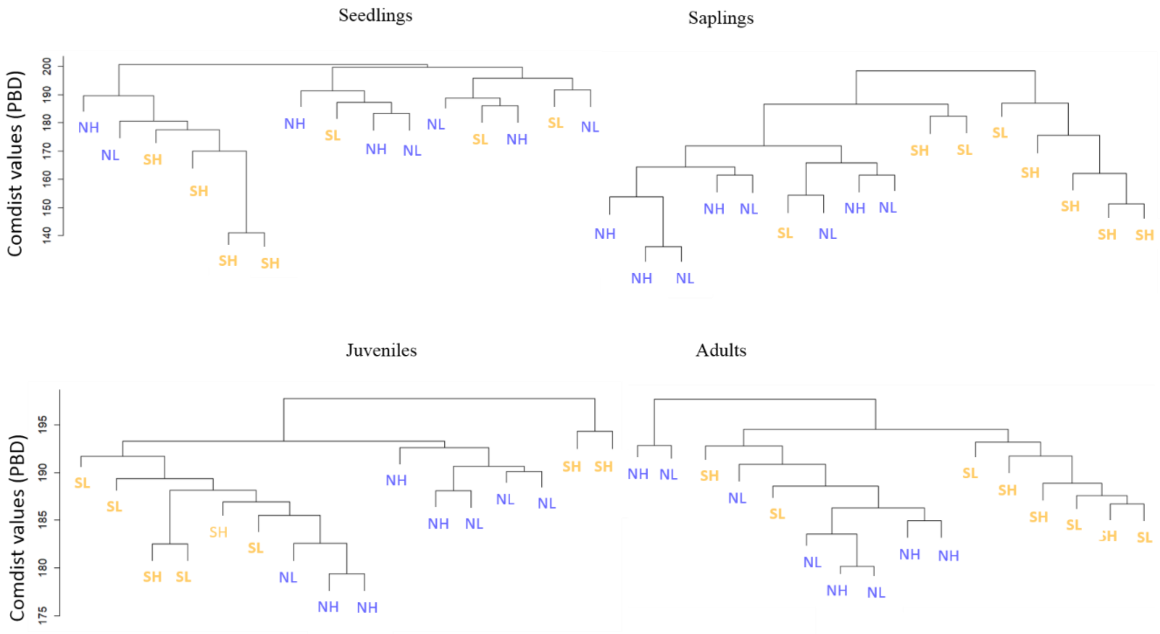
Figure 5.


Seedlings
Saplings
Juveniles
Adults
Comdist values (PBD)
Comdist values (PBD)
140
150
160
170
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NH
NL
SH
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SH
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SL
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