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Diversidad de plantas vasculares en la Sierra Madre de Chiapas: patrones para una regionalización fitogeográfica

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Por

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para obtener el grado de **Maestro en Ciencias en Recursos Naturales y Desarrollo Rural**

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No hay nada más maravilloso que ser un científico, en ninguna parte preferiría estar más que en mi laboratorio, manchando mi ropa y cobrando por jugar… Marie Curie

RESUMEN GENERAL

Comprender los patrones de distribución de diferentes grupos de plantas vasculares es fundamental en ecología, conservación y biogeografía. En este estudio se evaluaron los patrones de distribución y partición de diferentes grupos de plantas vasculares y su relación con una serie de variables climáticas (rango térmico, heterogeneidad topográfica, dinámica agua-energía) y de disturbio humano en la Sierra Madre de Chiapas (SMC), sureste de México. Se dividió el sistema montañoso en 123 celdas de cuadricula (10 × 10 km^2) y compilamos 78,132 registros de cinco grupos de plantas vasculares: trepadoras, epífitas, hierbas, arbustos y árboles; recopilados entre 1839 y 2015. Se emplearon modelos lineales para evaluar el patrón altitudinal de la riqueza general y de cada grupo de plantas y se mapeo la distribución de la riqueza de cada grupo. Se usaron modelos aditivos generalizados (GAM, por sus siglas en inglés) para analizar la influencia de las variables explicativas sobre la variación de la riqueza general y de cada grupo de plantas y un análisis de ordenación con escalamiento multidimensional no métrico (NMDS, por sus siglas en inglés) para determinar la variación de la composición de especies de los grupos de plantas a lo largo del gradiente altitudinal en la SMC. La contribución de los diferentes grupos a la riqueza total a lo largo del gradiente se evaluó empleando modelos lineales generalizados (GLM, por sus siglas en inglés). Finalmente, se presentó en el espacio geográfico de la SMC las 10 celdas más ricas y más pobres en riqueza para evaluar la representación proporcional de los grupos de plantas vasculares. Posteriormente, se realizó un análisis permutacional multivariante de la varianza (PERMANOVA, por sus siglas en inglés), esta técnica no paramétrica permite la no verificación del supuesto de normalidad multivariada. La finalidad de la utilización radica en medir si existen diferencias significativas en la composición de especies entre las celdas más ricas al comparar la igualdad de los grupos mediante la utilización matrices de presencia-ausencia y de un *p*-valor obtenido a través de técnicas de permutación para evaluar si son estadísticamente similares, después se realizó el mismo análisis de varianza para las celdas más pobres, para este análisis se tomó a la elevación media de cada celda como el efecto de condiciones distintas. Se encontraron 5,196 especies de plantas vasculares, en 235 familias y 1,439 géneros. Las familias con mayor número de especies fueron Asteraceae (449), seguidas de Fabaceae (435) y Orchidaceae (399); las 10 familias con mayor número de especies aportaron más del 44 % del total de especies. Mientras los géneros con mayor número de especies fueron *Tillandsia* (56), *Solanum* (52) e *Ipomoea* (51). Los 10 géneros con mayor número de especies aportaron en total 32.2 % de todas las especies. La riqueza total y los cinco grupos alcanzan su mayor riqueza alrededor de los 1,900 m y disminuyen hacía los 2,500 m. Los modelos GAM explicaron 35.2 % de la variación de la riqueza total, 32.6 % de trepadoras, 64.9 % de epífitas, 9.6 % de hierbas, 28.1 % de arbustos y 13.2 % de árboles. El análisis NMDS mostró ligeras diferencias en la composición de especies entre elevaciones bajas y altas, y el rango térmico fue relevante sólo en altitudes altas. Una alta riqueza de plantas en general, así como de los grupos se ubica en las partes altas del sistema montañoso y dentro o contiguo a áreas protegidas. Los grupos que contribuyen más con la riqueza total son las hierbas, seguido de árboles y arbustos. La mayoría de las 10 celdas con mayor riqueza de especies se ubican dentro o alrededor de áreas protegidas y las hierbas tienen una mayor proporción. Por el contrario, las celdas con menor riqueza están ubicadas en las partes bajas y fuera de áreas protegidas, siendo los árboles los que proporcionan mayor riqueza. La riqueza general y de los cinco grupos no responde linealmente con el gradiente altitudinal y los grupos de plantas contribuyen de modo distinto a la riqueza regional. En conjunto, nuestros resultados sugieren una alta relevancia de los mecanismos impulsados por factores climáticos en el mantenimiento y variación de la riqueza de distintos grupos de plantas en el sistema montañoso, pero el disturbio humano modifica los patrones de distribución disminuyendo la riqueza para algunos grupos como las epífitas y la riqueza total, y al mismo tiempo puede dar pie a aumentar la riqueza de trepadoras. La alta riqueza de especies en las partes altas del sistema montañoso está asociada a áreas protegidas, lo que podría favorecer su conservación. Sin embargo, las partes bajas tienen niveles altos de disturbio que ponen en riesgo a un considerable número de especies.

Palabras clave: Agua-energía, gradiente altitudinal, riqueza de especies, Sierra Madre de Chiapas, variación topográfica.

CAPÍTULO 1

Introducción general

La disponibilidad de grandes cantidades de datos digitalizados (macrodatos) accesibles para algunos sistemas montañosos pueden servir para analizar los patrones de distribución de distintos grupos taxonómicos y brindan la oportunidad de estudiar los efectos de factores climáticos, evolutivos, geológicos y antropogénicos sobre la variación de estos patrones (Antonelli et al. 2018; Rahbek et al. 2019). El acceso a macrodatos de ocurrencia de especies ha contribuido a mejorar el conocimiento sobre patrones de distribución de especies, bajo distintas escalas espaciales, ya sea a un nivel local, regional o global (Buckley y Jetz 2008; Maldonado et al. 2015). Específicamente los estudios a escala local y regional han contribuido a identificar áreas de alta diversidad, que ayudan a diseñar e implementar programas de conservación, a la par de comprender cómo el clima, el relieve topográfico y el disturbio humano (tala selectiva, expansión de la agricultura, urbanización, etc.), pueden influir en los patrones de diversidad (Ramírez-Marcial et al. 2001; Kessler et al. 2009; Karp et al. 2012; Socolar et al. 2016; Moura et al. 2016).

Los patrones de diversidad en sistemas montañosos están altamente correlacionados con el clima (temperatura y precipitación), que varía a lo largo del gradiente de elevación. De este modo, la temperatura cambia más rápido en entornos de alta montaña que en elevaciones más bajas, amplificando así una gran variedad de nichos, y por lo tanto una alta tasa de especiación en sistemas montañosos (Silveira et al. 2019; Perrigo et al. 2020). Específicamente para plantas vasculares, se ha considerado a la heterogeneidad ambiental como uno de los factores más importantes que rigen los gradientes de riqueza de especies a escala global y regional (González-Espinosa et al. 2004; Ricklefs 2004; Kreft and Jetz 2007; Stein et al. 2014). En sentido amplio la heterogeneidad ambiental incluye la variación de los gradientes ambientales, que aumentan la cantidad de tipos de hábitat y la complejidad estructural, permitiendo la coexistencia de más especies (Currie 1991; Stein et al. 2014). En teoría, los ambientes más heterogéneos tienen más probabilidades de proporcionar refugio con varios nichos ecológicos, lo que a su vez debería promover la persistencia de las especies (Ricklefs 2004; Kreft y Jetz 2007). Se han planteado distintas hipótesis para explicar la variación en la distribución de la riqueza de especies en el espacio y tiempo en sistemas montañosos: (1) la energía; se cree que los cambios o variación en temperatura, disponibilidad de agua y evapotranspiración (subrogado de energía) son impulsores de la variación espacial en la diversidad de especies de plantas (Gentry y Dodson 1987; Chen et al. 2006; Vetaas et al. 2019).Sin embargo, es importante distinguir los efectos climáticos en la distribución y abundancia de especies de los procesos que vinculan el suministro de energía con la diversidad de plantas y animales (Clarke y Gaston 2006). Por lo tanto, (2) los gradientes climáticos crean condiciones distintas a lo largo de un gradiente altitudinal, lo cual promueve posibles eventos de especiación como resultado del aislamiento o la adaptación a diversas condiciones ambientales (Antonelli y Sanmartín 2011). Por otra parte, (3) la heterogeneidad topográfica influye sobre las interacciones bióticas y los rangos de distribución, promoviendo la diferenciación de nicho entre las especies, es decir el cambio en la riqueza de especies está fuertemente influenciado por la rugosidad topográfica, más que la propia altitud o el rango altitudinal (Steinbauer et al. 2016; Badgley et al. 2017). Por último, (4) el disturbio humano ha modificado los patrones de diversidad en los sistemas montañosos tropicales (Ramírez-Marcial et al. 2001; Nogués-Bravo et al. 2007; Peters et al. 2019). Sin embargo, generalmente el impacto es mayor en las partes bajas de los sistemas montañosos (Carvajal-Hernández et al. 2017; Caviedes e Ibarra 2017; Alzate-Q et al. 2019). Esto se ha observado en la Sierra Madre de Chiapas (Martínez-Camilo et al. 2018; Jiménez-López et al. 2020), donde los bosques se han reducido principalmente por el cambio en el uso de suelo de vocación forestal hacia campos de cultivo, potreros y asentamientos humanos (Schroth et al. 2009).

Un grupo importante para analizar patrones de distribución en sistemas montañosos son las plantas, siendo vitales para la estructuración de comunidades biológicas y el funcionamiento de los ecosistemas (Moura et al. 2016). Particularmente en el sur de México, existen estudios sobre patrones de distribución de plantas, incluyendo el efecto de variables climáticas y de disturbio antrópico en gradientes de elevación (Salas-Morales y Meave 2012; Krömer et al. 2013; Gómez-Díaz et al. 2017; Carvajal-Hernández et al. 2017; Martínez-Camilo et al. 2018; Jiménez-López et al.

2020), que han ayudado a una mejor comprensión de la estructuración de comunidades con la elevación. Esta situación es importante debido a que los efectos del disturbio humano han reducido las coberturas boscosas en general y particularmente en las montañas (Nogués-Bravo et al. 2007). Sin embargo, con el incremento en la disponibilidad de grandes bases públicas de datos es factible indagar los patrones de distribución espaciales a escala regional y local para tratar de vincular los posibles efectos de los factores asociados al clima, el relieve y el disturbio humano con el fin de tomar decisiones para su conservación. Por lo tanto, en esta tesis se trata de responder las siguientes preguntas: (1) ¿Cuáles son los patrones de riqueza y la distribución espacial de plantas vasculares en general y de cinco grupos (trepadoras, epífitas, hierbas, arbustos y árboles) en la Sierra Madre de Chiapas, sureste de México?, (2) ¿la variación en la riqueza de cada forma de vida puede ser explicada por variables climáticas (rango térmico, variación en la topografía, la dinámica del agua y la energía) y la perturbación humana? y (3) ¿Cuál es la contribución de cada forma de vida a la riqueza total a lo largo del gradiente altitudinal de la Sierra Madre de Chiapas? Abordando los siguientes objetivos:

Objetivos e hipótesis

1. Analizar los patrones de riqueza y distribución espacial de plantas vasculares en general y por forma biológica (trepadoras, epífitas, hierbas, arbustos y árboles) en un sistema montañoso en el sureste de México.

Hipótesis 1: Debido a las diferentes condiciones ambientales y de disturbio humano a lo largo del gradiente altitudinal de la Sierra Madre de Chiapas, se espera que la distribución de las especies no sea uniforme por formas de vida a lo largo del gradiente altitudinal y el espacio geográfico de la Sierra Madre de Chiapas. Además, se espera una mayor riqueza vegetal en general a mayores elevaciones, con una disminución gradual hacia las tierras bajas

2. Evaluar si el rango térmico, la variación en la topografía, la dinámica agua-energía y perturbación humana explican la variación en la riqueza de cada forma de vida.

Hipótesis 2: El rango térmico, variación en la topografía y dinámica agua-energía explican mejor los patrones de riqueza de cada forma de vida, ya que los mecanismos subyacentes están relacionados con el clima. Además, debido a un alto nivel de perturbación a bajas altitudes del sistema montañoso, se espera que la perturbación humana modifique los patrones de distribución de todas las formas de vida.

3. Determinar la contribución de cada forma de vida a la riqueza total a lo largo del gradiente altitudinal.

Hipótesis 3: La contribución de cada forma de vida a la riqueza total variará según el gradiente de elevación y la zona geográfica particular del sistema montañoso. Además, se espera que las hierbas y los árboles sean las formas de vida más diversas, seguidas por epífitas, debido a que son grupos muy diversos en sistemas montañosos.

Materiales y métodos

Área de estudio. Se delimitó el área de la Sierra Madre de Chiapas con base en: (1) el origen geológico del territorio, (2) el área de influencia del bosque mesófilo de montaña (BMM), utilizando la capa de las regiones y subregiones del BMM en México que proporciona CONABIO (http://www.conabio.gob.mx/informacion/gis/), y (3) el modelo digital de terreno de la base de datos SRTM (http://srtm.csi.cgiar.org/srtmdata/; Farr et al. 2007). Con ayuda del programa QGIS 3.2.3 (QGIS Development Team 2020) se utilizó la herramienta TIN (triangulated irregular network) para proyectar la capa ráster de elevación a una capa de relieve y visualizar los territorios geológicos de la falla de Polochic (entre México y Guatemala) y del macizo de Chiapas (cadena montañosa que se extiende unos 20,000 km^2 paralelo a la costa del Pacífico). Dentro de su origen geológico limita al noroeste con el istmo de Tehuantepec en Oaxaca, al oeste está delimitado por la zona de corte de Tonalá, que se conecta al sur con la Falla Polochic, al este por la Depresión Central de Chiapas (Weber et al. 2005). Sobre esta capa se empalmó la capa de las regiones y subregiones del BMM para delimitar la SMC, que fue el área de superposición entre la capa de relieve y del BMM, teniendo como límite toda aquella porción de terreno que se eleva por encima de 100 m y algún grado de pendiente (Körner 2007). Esta delimitación corresponde en gran medida con los límites de la regionalización fisiográfica de la SMC propuesta por Müllerried (1957). Por lo tanto, la SMC es un sistema montañoso localizado en Chiapas (15° 20’ a 16° 9’ de latitud norte, 92° 29’ a 93° 42’ de longitud oeste) que se extiende por aproximadamente 250 km paralela a la costa del Pacífico (Martínez-Camilo et al. 2018), está situada entre la depresión central al norte y la llanura costera del Pacífico al sur, limita al noreste con la frontera del estado de Oaxaca y que alcanza su límite en su extremo suroeste, en el volcán Tacaná a unos 4,092 m, en la frontera con Guatemala (Müllerried 1957). Se ubica en una de las regiones con mayor biodiversidad y endemismo, pero a la vez una de las más amenazadas en el planeta (Mesoamerican hotspot; Myers et al. 2000), y forma parte de lo que fue el Corredor Biológico Mesoamericano, que alberga cerca del 7 % de la biodiversidad del mundo (Mittermeier et al. 1999).

El sistema montañoso de la SMC incluye las mayores elevaciones del estado de Chiapas. Se eleva a unos 800 m cerca de la frontera con Oaxaca, seguido abruptamente hacia el sureste por elevaciones de unos 2,250 m en la Reserva de la Biosfera La Sepultura (La Sepultura), 2,750 m en La Reserva de la Biosfera El Triunfo (El Triunfo), hasta su pico más alto, con 4,092 m en La Reserva de la Biosfera volcán Tacaná (volcán Tacaná) en la frontera con Guatemala. Estas elevaciones, sumadas a la precipitación promedio anual (entre 1,223 y 2,573 mm) y temperatura promedio anual (entre 16.8° C y 26.2° C), generan condiciones físicas que determinan los patrones climáticos locales y microrregionales que influyen sobre los patrones de distribución de especies de plantas (Martínez-Camilo et al. 2018). En las partes medias de la SMC existen extensas plantaciones de café bajo sombra, las cuales son abundantes en la parte central, en El Triunfo y hacia el noroeste, en la región del Soconusco, donde también se extraen individuos del género *Chamaedorea* Willd. (Arecaceae) para su uso como palmas ornamentales (Martínez-Camilo et al. 2011). Estas actividades, sumadas a la ganadería extensiva en elevaciones más bajas y en la región de la Reserva de La Sepultura contribuyen a la pérdida de cobertura forestal (Schroth et al. 2009), aunque las áreas protegidas en las partes altas de la sierra han favorecido la conservación de la cubierta forestal (Toledo-Aceves et al. 2011). En el siguiente capítulo, se presentan más detalles metodológicos.

CAPÍTULO 2

Plant life-form distribution patterns in a tropical mountain region: effects of climate and human disturbance

Short running title: Life-forms distribution in tropical mountains

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Abstract

Objective: We analyzed the effects of climatic variables and human disturbance on the distribution and partitioning patterns of different vascular plant life-forms (climbers, epiphytes, herbs, shrubs, and trees) in a tropical mountainous system.

Location: Sierra Madre of Chiapas, southeastern Mexico.

Taxon: Vascular plants.

Methods: We divided the mountainous system into 123 grid cells (10 × 10 km) and compiled a total of 78,132 records. We used linear models to evaluate the altitudinal pattern of richness; generalized additive models (GAM) to analyze the effects of climate and human disturbance on variation in total species richness as well as among plant life-forms; and non-metric multidimensional analysis (NMDS) to determine variation in species composition along the elevation gradient. The contribution of each plant life-form to total richness was evaluated using generalized linear models (GLM).

Results: Total richness and that of each plant life-form were highest at approximately 1,900 m and decreased toward 2,500 m. GAM models explained a high proportion of the variation in richness of each plant life-form (35 % for the total richness, 32 % for the climbers, 64 % for epiphytes, 9 % for herbaceous plants, 28 % for shrubs, and 13 % for trees). Human disturbance was associated with a decrease in total species richness and that of epiphytes, but not that of climbers, and thermal range best explained the distribution of floristic composition. The group that most contributed to total richness was herbs, followed by trees and shrubs.

Conclusions: Species richness of each plant life-form is not linearly correlated with the elevation gradient, and each life-form contributed to a different extent to regional species richness. Our results suggest that mechanisms driven by climatic variables contribute to maintenance and variation of the richness of each life-form. However, human disturbance modifies distribution patterns and leads to the differential increase in species richness of some distinctive groups.

Key words: Elevational patterns energy, potential evapotranspiration, Sierra Madre of Chiapas, species richness, topographic variation.

Introduction

Mountainous systems occupy about 25 % of all land area of the Earth´s terrestrial surface area (Rahbek et al., 2019). Nevertheless, they contain approximately to more than 85 % of the world's species of amphibians, birds, and mammals, and are centers of endemism due to a combination of evolutionary and ecological factors (Perrigo et al., 2020; Rahbek et al., 2019). These biodiversity reservoirs continue to be a central topic in biogeography and conservation studies due to the fact that mountainous ecosystems – particularly in tropical regions – are especially vulnerable to the effects of climate change, human disturbance, and the introduction of invasive species (Nogués-Bravo et al., 2007; Peters et al., 2019; Silveira et al., 2019). Studies generally conclude that local stochastic processes (e.g., dispersal limitations and colonization/extinction dynamics) as well as regional deterministic processes (e.g., climatic factors) create a variety of niches that favor distinctive groups of species. These processes may operate simultaneously on different spatial scales to establish patterns of diversity (Chase, 2010). Evidence in favor of deterministic processes is robust, supporting the effect of environmental conditions that select those species capable of surviving and persisting in particular areas in mountainous systems (Buckley & Jetz, 2008). These environmental conditions may be evaluated using proxy variables, such as temperature, precipitation, topographic relief, and water-energy dynamics (Bhatta et al., 2021; Clarke & Gaston, 2006; Vetaas et al., 2019).

Generally, mechanisms linked to distribution patterns, for example topographic relief, have a dual effect on species diversity. First, topographic heterogeneity (TOPO from here on) generates local geographic isolation that promotes speciation (Ruggiero & Hawkins, 2008; Stein et al., 2014; Steinbauer et al., 2016), influencing distribution ranges and promoting niche differentiation among species (Janzen, 1967; Moura et al., 2016; Ruggiero & Hawkins, 2008). Secondly, an elevation range creates varying thermal conditions, which may also contribute to explaining the structure and distribution patterns of species richness (Buckley & Jetz, 2008; Janzen, 1967). Meanwhile, the water-energy dynamics (WED) is a model that explains the relationship between kinetic energy (temperature as a proxy for heat/light-radiation) and control of available water in liquid form. This relationship helps to explain diversity (O'Brien, 2006). In general, high kinetic energy provokes a high rate of potential evapotranspiration (PET), which reduces biological activity due to water limitation. By contrast, a low PET may cause water to freeze, thereby reducing biological activity, while the optimal PET increases availability of liquid water and biological activity, which may promote diversity in mountainous systems (Clarke & Gaston, 2006; O'Brien, 2006; Vetaas et al., 2019).

Human disturbance due to expansion of agriculture, urbanization, and unrestrained natural resource exploitation has led to irreversible changes in plant and animal diversity in tropical mountainous regions, reconfiguring their distribution patterns (Newbold et al., 2015; Peters et al., 2019). Natural and human disturbance induces changes in species composition, favoring establishment of early successional species as a result of greater light incidence; furthermore, interaction between human disturbance and climate change narrows vegetation belts along the elevation gradient and reduces the distribution range of many species (Nogués-Bravo et al., 2007; Peters et al., 2019).

Most studies with vascular plants in mountainous systems include only a single plant group (e.g., trees: Martínez-Camilo et al., 2018; terrestrial herbs: Gómez-Díaz et al., 2017; epiphytes: Krömer et al., 2005, or selected taxonomic groups Kessler, 2001). Yet there is a need for studies that involve multiple plant groups to gain a more comprehensive understanding of richness patterns that may lead to more informed decisions on conservation issues. Integrating several plant life-forms may allow for a better understanding on: (1) how ecological processes influence distribution patterns of communities; (2) how different life-forms respond to environmental factors and human disturbance; and (3) to what extent each plant group contributes to total diversity in a mountainous system.

The distribution patterns of plant life-forms may vary among regions according to other type of vegetation, elevation, conservation/disturbance levels, and climate. For example, in Panama climbers appear to thrive in disturbed habitats as well as in the early successional stages following disturbance (Dewalt et al., 2000). But, unlike in the southern Chile show high climbers species diversity in primary forests (Gianoli et al., 2010). Trees increase in diversity as precipitation and elevation increase along an altitudinal gradient of 100–2200 m in the Mexican state of Chiapas (Martínez-Camilo et al., 2018). While, in the Mexican state of Veracruz, tree composition varied among natural forests and forests with different levels of intensity of use along an altitudinal gradient (Monge-González et al., 2020). In the Mexican state of Veracruz, herbs were found to be more diverse in disturbed environments than in mature forests along an altitudinal gradient up to 2,500 m (Gómez-Díaz et al., 2017). However, terrestrial ferns appear to be constant from sea level to 2,500 m (Hernández-Rojas et al., 2020; Krömer et al., 2013), slightly diminishing at higher elevations (Hernández-Rojas et al., 2020). Generally speaking, vascular epiphytes show a unimodal (hump-shaped) pattern, linked to high precipitation and average temperatures at mid-elevations (Gentry & Dodson, 1987; Krömer et al., 2005). Finally, in the Mexican state of Veracruz the richness of shrubs decreases slightly with elevation and also with anthropogenic influence (Bautista-Bello et al., 2019). Similar pattern has been observed in northern China, at low elevation anthropogenic disturbances contributed to the increase of shrubs diversity (Zhang et al., 2016).

This study aims: (1) to analyze richness patterns and geographic spatial distribution of vascular plants in general and of each of five plant life-forms in a mountainous system in southeastern Mexico; (2) to evaluate whether thermal range, variation in topography, water-energy dynamics, and human disturbance explain variation in richness of each life-form; and (3) to determine the contribution of each life-form to total richness along the altitudinal gradient. We hypothesize that: (1) the species distribution is non-uniform by life-forms along altitudinal gradient and geographic space of the Sierra Madre of Chiapas. Furthermore, higher plant richness is expected in general at higher elevations, with a gradual decrease toward the lowlands; (2) thermal range, variation in topography, and water-energy dynamics best explain patterns of richness of each life-form, as the underlying mechanisms are related to climate. In addition, due to a high level of disturbance at lower altitudes of the mountain system, human disturbance is expected to modify the distribution patterns of all life forms; and (3) the contribution of each life-form to total diversity will vary according to the elevation gradient. Furthermore, we expect herbs and trees to be the most diverse life-forms, followed by epiphytes, shrubs, and climbers.

Materials and methods

Study area. The Sierra Madre of Chiapas (SMC) is a mountainous system located in southeastern Mexico, in the state of Chiapas (15° 20’ to 16° 09’ N latitude, 92° 29’ to 93° 42’ W longitude) that extends for approximately 250 km parallel to the Pacific coast (Figure 1; Martínez-Camilo et al., 2018), between the Central Depression of Chiapas in the north and the Pacific coastal plain in the south. It borders in the northeast with the state of Oaxaca, and in its extreme southeast with the Tacaná volcano on the Guatemalan border (Müllerried, 1957). It is located within the Mesoamerican hotspot, one of the regions of the world with the highest biodiversity and endemism (Myers et al., 2000), but also one of the most threatened (by human disturbance (transformation of forests into agricultural systems), as well as climate change (Escobar Flores & Castillo Santiago, 2021; Schroth et al., 2009). Finally, it forms part of the former Mesoamerican Biological Corridor, which hosts close to 7 % of the world´s biodiversity (Mittermeier et al., 1999).

This mountainous system contains the highest elevations within the state of Chiapas; it rises from sea level to approximately 800 m close to the border of Oaxaca, up to approximately 2,250 m in the La Sepultura Biosphere Reserve (La Sepultura), up to 2,750 m in the El Triunfo Biosphere Reserve (El Triunfo), to its highest peak, and up to 4,092 m in the Tacaná Volcano Biosphere Reserve (Tacaná). Average annual temperature of our study area is 21.8° C (min. = 6.1, max. = 27.5), and average annual rainfall is 1,862 mm (min. = 827, max. = 3,716: Figure 1).

Database and selection of plant groups. Occurrences of native vascular plants in the SMC were compiled from several sources that include collections from 1839 to 2015. Our final database consisted of 78,132 records from five native plant life-forms: climbers, epiphytes, herbs, shrubs, and trees. See Appendix S1 for details regarding the compilation of the database, updating nomenclature, correcting spatial errors, analysis to determine grid cell size, and selection of plant groups.

Explanatory variables

(1) *Energy-water relationship*: From the CHELSA database Version 1.2 (Karger et al., 2017) we downloaded the raster layer of annual precipitation with a 30-second span resolution (1 km), and from the ENVIREM database we downloaded the raster layer of potential annual evapotranspiration (PET; Title & Bemmels, 2016). These two variables were used as a proxy for the water-energy dynamics (WED). The WED model proposes that species richness will increase as thermal energy increases; yet beyond a certain threshold water deficits due to high rates of evapotranspiration will reduce the ecophysiological activity of species at low elevations, and therefore, their richness; on the other hand, freezing of water due to low temperatures in the higher areas of the elevational gradient also limits species activity (O'Brien, 2006; Vetaas et al., 2019).

(2) *Topographic heterogeneity (TOPO)*. Topographic heterogeneity was obtained with the standard deviation of variation in elevation based on all pixels within each grid cell (Ruggiero & Hawkins, 2008). We used a digital elevation model of the state of Chiapas downloaded from the INEGI database (INEGI, 2013) with a spatial resolution of 90 m to obtain the values for standard deviation for each cell, using the zonal statistics tool in QGIS 3.2.3 (QGIS Development Team, 2020).

(3) *Thermal range*. Given that topographic relief also defines complex thermal ranges in mountainous systems, this also may contribute to explaining species richness and distribution patterns (Ghalambor, 2006; Janzen, 1967). In order to represent thermal range, we used mean annual temperature (the difference between the highest and lowest average temperature within a cell) using the mean annual temperature layer downloaded from the CHELSA database, version 1.2 (Karger et al., 2017), and obtained the range using the zonal statistical tool in QGIS 3.2.3 (QGIS Development Team, 2020).

(4) *Human disturbance*. As a proxy for human disturbance, we used the Human Influence Index (HII) (Peters et al., 2019), which is a measurement composed of eight

layers of global data regarding urban extension, population density, highways, navigable rivers, and agricultural land (accessed at: http://sedac.ciesin.columbia.edu/data/set/wildareas-v2-human-footprint-geographic; spatial resolution: 1 km^2). HII values range from 0 (low disturbance) to 64 (high disturbance) (Wildlife Conservation Society, 2005); for our study area the HII varied from 11.52 to 46.81. We obtained average data for each grid cell using the zonal statistical tool in QGIS 3.2.3 (QGIS Development Team, 2020)(QGIS Development Team, 2020). For temperature, rainfall, and PET we obtained data for each record and later calculated the mean value for each cell using the zonal statistical tool in QGIS 3.2.3 (QGIS Development Team, 2020); before extracting the values, all raster layers were changed to pixel resolution to 10 × 10 km to match and be comparable to the resolution of grid cells of Sierra Madre of Chiapas.

Data analysis

Diversity and distribution patterns. First, we evaluated the distribution patterns for the whole vascular flora and for each plant life-form along the elevational gradient (mean elevation of each grid cell), using a third order polynomial that represented the best fit in the variation in species richness of each group. These analyses were carried out with the *lm* function in the R program. Afterwards, we evaluated the effect of thermal range, human disturbance, TOPO, and WED on variation in total richness and richness of each life-form through generalized additive models (GAM), including null models to determine whether variation in richness is related to stochastic or deterministic processes. We selected GAM models as the best option as plants do not necessarily respond in a linear manner to environmental changes (Bhatta et al., 2021; Peters et al., 2019; Vetaas et al., 2019). We followed a backward selection approach with Akaike´s information criterion (AIC), reviewing the results of the ANOVA model to identify the optimal models. These models were created using the *mgcv* package (Wood, 2020). Before conducting the analysis, Pearson correlation coefficient tests were carried out to observe whether collinearity exists among the explanatory variables, using those variables with the least collinearity among each other ($r^2 \leq 0.70$). To visually observe the structure among groups of data (species richness of each life-form and mean elevation of each grid cell as sampling units) and their relation to the explanatory variables, a non-metric multidimensional scaling analysis (NMDS) was carried out using the *metaMDS* function of the *vegan* package, version 2.5-7 (Oksanen et al., 2020). Finally, to observe their tendencies in the mountainous system we mapped the patterns of total richness, as well as that of each life-form, using QGIS 3.2.3 (QGIS Development Team, 2020).

Partitioning and proportion of plant life-form groups to total diversity. Quasi-Poisson and binomial generalized linear models (GLM; for proportional data) were used to evaluate the proportion of each life-form to total diversity in each cell, using their mean elevation. For all GLM models, we used the *lm* function, discarding those cells with fewer than three plant species, in order to reduce distortion of global patterns. Finally, we represented the 10 cells within the SMC with the highest and lowest richness and graphed the contribution of each plant life-form to the total diversity within each cell. Afterwards, we carried out an analysis of variance for presence-absence matrices and a permutation test with pseudo-F ratios (PERMANOVA) using the *Adonis* function of the *vegan* package (Oksanen et al., 2020) to evaluate whether species composition in the cells was statistically similar, taking mean elevation of each cell to establish the different conditions. All analyses were carried out with the R program (R Development Core Team, 2020). To visualize the results, we used the *ggplot2* package (Wickham, 2009), and when necessary, spatial visualization was carried out with QGIS 3.2.3 (QGIS Development Team, 2020).

Results

Species richness and composition. A total of 5,196 vascular plant species were recorded, belonging to 235 families and 1,439 genera. Families with the highest number of species were Asteraceae (449), followed by Fabaceae (435) and Orchidaceae (399); the 10 families with the highest species numbers provided more than 44 % of the total floristic richness (Figure S1-a). The genera with the highest number of species were *Tillandsia* L. (56), *Solanum* L. (52), and *Ipomoea* L. (51). The 10 genera with the highest numbers of species contributed a total of 32.24 % of all species (Figure S1-b). The most species-rich plant life-form was herbs (1,961 species; 37.74 %), followed by trees (997; 19.19 %), shrubs (911; 17.53 %), epiphytes (645; 12.41 %), and climbers (555; 10.68 %); together, these groups almost accounted for the total species richness of the SMC (97.56 %; Figure S2). Aquatic plants, arborescent plants which includes arborescent ferns and families Asparagaceae (genera: Furcraea Vent. and Yucca L.) and Zamiaceae (genus Dioon Lindl.), mycoheterotrophic herbaceous plants, palms, and parasitic plants were not considered in this study as they together only represented 2.44 % of all plants in the study region (Figure S2).

Diversity and distribution patterns. Linear models showed similar patterns of total richness and of the five plant life-forms ($0.06 < r < 0.23$; all $p \leq 0.0089$; Figure 2). All groups reached their highest richness around 1,900 m elevation and decreased toward 2,500 m. Climbers showed another peak in lowlands (100–300 m). Epiphytes presented a unimodal pattern with sharper declines at both extremes of the elevation gradient. Herbs maintained a relatively constant richness along the gradient, decreasing slightly toward 700 m. Shrubs, trees, and total richness showed a common pattern, with considerable richness at lower elevations (100-300 m; Figure 2).

We generated a total of 19 GAM models (Table S1). None of the null models explained variation in species richness in the study region, and although the best models explained variation in richness, a high level of deviance was observed for most of the plant life-forms. The best models explained 35.2 % of total richness, 32.6 % of that of climbers, 64.9 % for epiphytes, 9.6 % for herbs, 28.1 % for shrubs, and 13.2 % for trees (Table S1). The model that best explained variation in total richness took into account thermal range, human disturbance, and topographical heterogeneity (TOPO). Variation in climbers was explained by all predictor variables. Variation in epiphytes responded to the model which incorporated thermal range, human disturbance, and TOPO. Herbs and trees were better explained by thermal range than by the other two factors. Finally, variation in shrub richness was best explained by thermal range and water-energy dynamics (Table S1). Upon graphing the GAM models, the species richness of all groups increased when the thermal range increased (Figure 3a). Climbers did not respond to human disturbance, but total richness and that of epiphytes markedly decreased with an increase in human disturbance (Figure 3b). A hump-shaped pattern was observed for total richness, epiphytes, and climbers with TOPO (Figure 3c). Finally, shrubs and climbers showed curvilinear responses with water-energy dynamics (Figure 3d).

The NMDS analysis showed slight differences in species composition between low and high elevations, and thermal range was relevant only at high altitudes. The vector adjustment for all variables was significant (Figure 4, Table S2). A considerable quantity of the species composition was related to negative values of the evapotranspiration gradient (PET; R^2 = -0.35, p = 0.001) and to human disturbance (R^2 = -0.20, p = 0.001), both at elevations from approximately 500 to 1,500 m (Figure 4; Table S2). Similarly, a lower proportion of species was related to TOPO and precipitation at higher elevations (approximately 1,000 to 2,000 m, TOPO: R^2 = 0.35, p = 0.001; precipitation: R^2 = 0.64, p = 0.001). Finally, species composition was also related to thermal range at high elevations (>1,500 m; R^2 = 0.27, p = 0.001; Figure 4; Table S2).

Within the SMC, a higher species richness of vascular plants in general, and of each plant life-form, was found at higher elevations of the mountainous system and within or adjacent to protected areas (Figure 5a-f). For total richness, cell 121 – located within Tacaná – had the highest richness, with 1,397 species (average elevation 1,270 m; Table S3), followed by cell 86 – located between the protected areas El Triunfo and Pico del Loro – with 1,005 species (average elevation 895 m; Table S3). The highest richness of climbers was found in cell 12 –located within La Sepultura – with 23 species (average elevation 517 m; Table S3). Epiphytes, herbs, and shrubs had their highest richness in cell 121 within Tacaná (239, 512, and 287 species respectively; Figure 5c-d and f; Table S3). The highest richness of trees was found in cell 86 – located between the protected areas El Triunfo and Pico del Loro – with 239 species (Figure 5e; Table S3).

Contribution of plant life-form to total diversity. The contribution of species richness of the plant groups to total richness varies along the elevation gradient. The following patterns may be observed: the proportion of richness of herbs and trees decreases slightly with elevation; that of shrubs remains constant with a minimal increase; and that of epiphytes and climbers clearly increase. The groups that most contribute to total richness are herbs and trees, followed by shrubs, epiphytes, and climbers. This is a constant pattern along the gradient, except at 2,500 m where epiphytes contribute slightly more than trees and shrubs (Figure 6).

Upon exploring the 10 grid cells with the highest species richness, we observed that the majority are located within or adjacent to protected areas (Figure 7a) and have moderate human disturbance values (average = 20.23, min. = 14.83, max. = 31.59). In general, a greater proportion of herbs was observed, followed by trees, shrubs, epiphytes, and climbers, with some exceptions; for example, in cell 1 of figure 7a, herbs represent over 35 % of total richness, and trees (220 species) are the fourth most diverse group, exceeded by epiphytes and shrubs (239 and 287 species, respectively). In cells 3 and 4, epiphytes are the third richest group (198 and 156 species, respectively), and in cell 6 they are second (148 species). Furthermore, statistically significant differences were found in species composition among these cells (PERMANOVA: R^2=0.19, p = 0.013). Upon examining the 10 cells with the lowest richness (Figure 7b), we observed that trees provide the greatest richness, followed by herbs, shrubs, and epiphytes, and that – similar to the 10 cells with the highest richness – human disturbance values were moderate (average = 20.06, min. = 14.83, max. = 24.21). However, those cells with the lowest richness are located at low elevations, the majority of which are outside of the protected areas. Trees represented over 50 % in cell 10 and over 75 % in cell 2. Nevertheless, no statistically significant differences were found in species composition among these cells (PERMANOVA: R^2=0.11, p = 0.329).

Discussion

Although studies have recently been carried out regarding distribution patterns of different plant life-forms along elevation gradients, for example in the island of Crete and in other regions of Greece (Lazarina et al., 2019) and the Himalayas in Asia (Bhatta et al., 2021; Vetaas et al., 2019), to our knowledge, our study in the Sierra Madre of Chiapas is one of the few within the Neotropics (Vázquez & Givnish, 1998) that has evaluated diversity and distribution patterns of different plant life-forms as well the contribution of each plant life-form to total richness. Our results indicate that species richness in the SMC is governed by deterministic processes as well as by climatic variables and human disturbance. These factors have a combined effect on the distribution patterns of the plant groups evaluated.

Composition and general patterns of species richness. The extraordinary richness of vascular plants of the SMC corresponds to approximately 60 % of the vascular plants present in Chiapas, and 22.2 % of the all flora of Mexico (Villaseñor, 2016). The families (Asteraceae, Fabaceae and Orchidaceae) and genera (*Tillandsia*, *Solanum* and *Ipomoea*) with the greatest species richness in this study are frequently reported among the best represented taxa for flora in other regions of the continent (e.g. Ulloa Ulloa et al., 2017; Villaseñor, 2016), and it has been suggested that their high levels of species richness in mountainous systems is a consequence of their evolutionary radiation triggered by varying combinations of geographic, environmental, and historical factors (Givnish et al., 2015). Epiphytes, trees, shrubs, and total richness have a hump-shaped pattern of altitudinal richness and are the most represented in tropical and subtropical areas (Rahbek, 1995). In lowlands, it has been documented that plant richness is influenced by high temperatures, rates of PET, and levels of human disturbance that modify distribution patterns and provoke a reduction in diversity of vascular plants (Gómez-Díaz et al., 2017; González-Espinosa et al., 2004; Guzmán-Jacob et al., 2020; Peters et al., 2019). Nevertheless, disturbance also may act in an opposite manner by increasing richness of certain groups, such as climbers, due to the fact that they broaden their niches following disturbance events (Dewalt et al., 2000), which could explain their peak of richness in the lower part of our study. The reduction in species richness of all groups at higher elevations of the gradient is due to stress factors such as low temperatures, high levels of evapotranspiration, and strong winds that provoke desiccation of plant tissue and reduce photosynthetic activity of the species (Rahbek, 1995; Vetaas et al., 2019).

In general, the GAM models that best explained variation in total richness and that of the five plant life-forms was thermal range, which is consistent with that documented by Ruggiero & Hawkins (2008) for birds, and Buckley & Jetz (2008) for amphibians and birds on a large scale. According to initial hypotheses by Janzen (1967), and that has been confirmed by Ghalambor (2006). Therefore, the association among range of elevation, climatic diversity, and isolation of populations may promote an increase in species richness in regions with high topographic relief, such as the SMC. Topographical heterogeneity (TOPO) was also a significant predictor of total richness, as well as richness of epiphytes and climbers, confirming that thermal range and TOPO are good predictors of the variation in diversity patterns in our study area, because they act on climate variation along the altitudinal gradient (Ghalambor, 2006; Janzen, 1967; Ruggiero & Hawkins, 2008). In the region of the Tacaná volcano, in the extreme southern part of our study area, elevation, orientation, and slope of the ravines influenced the high local richness of epiphyte species (Damon et al., 2015). The degree and orientation of the slopes are also important factors for trees in these areas (R. Martínez-Camilo pers. comm.), evidencing environmental determination of the composition of communities in relation to the climatic and topographic gradients on a local and regional scale (Janzen, 1967; Jones et al., 2011; Steinbauer et al., 2016).

Previous studies suggest that patterns of species richness may be explained by energy-related factors or WED (Bhatta et al., 2021; Hawkins et al., 2003; Kreft & Jetz, 2007; Vetaas et al., 2019), pointing out that WED predicts a low level of biodiversity in extreme cold as well as warm regions of an energy gradient (Currie, 1991; Hawkins et al., 2003; O'Brien, 2006). In our study, the models that incorporated WED explained variation in climbers and shrubs, suggesting that the patterns of species richness tend to have a non-linear response to energy (Vetaas et al., 2019). This pattern was previously corroborated for trees in the state of Chiapas; González-Espinosa et al. (2004) found a positive relationship between tree diversity and increase in actual evapotranspiration, as an indirect indicator of biologically available energy. In the Himalayas, Vetaas et al. (2019) found that PET (considered as an indicator of available energy) largely explained the distribution patterns of plants and other taxonomic groups. The responses with non-linear tendencies of WED to distribution patterns of climbers and shrubs are explained by a reduction in richness of these groups at low elevations related to low values of PET, and at high elevations due to occasional frost. Therefore, water in its liquid form is less available due to increases in PET, while with optimal values of PET (1,600-1,850 mm/yr) richness of climbers and shrubs is maximized, which was corroborated by our NMDS analysis. These predictions are consistent with several studies (Bhatta et al., 2021; González-Espinosa et al., 2004; Vetaas et al., 2019).

Finally, but no less important, was human disturbance. Total richness decreased with an increase in human disturbance. In the low areas of the mountainous system, the level of human disturbance is high, due to an increase in population density as well as expansion of agriculture and deforestation (Escobar Flores & Castillo Santiago, 2021; Schroth et al., 2009). In the GAM models, human disturbance determined the reduction in richness of trees and epiphytes. In the SMC and other mountainous systems in Mexico, reduction in both groups with an increase in human disturbance has previously been documented (Guzmán-Jacob et al., 2020; Jiménez-López et al., 2020; Martínez-Camilo et al., 2018; Monge-González et al., 2020). Therefore, although we have evidence that climatic variables highly explain general richness as well as that of each of the plant life-form, the influence of human disturbance has more predictive power in the low areas of the SMC, reconfiguring their distribution patterns. This latter factor, along with climate change, could lead to massive species loss and changing patterns of species richness and distribution (Nogués-Bravo et al., 2007).

Partitioning of richness. Our results reveal that different plant life-forms vary in their contribution to total richness along the elevation gradient and the geographic space of the mountainous system. Prior studies indicate a high diversity of trees, epiphytes, and terrestrial ferns in high altitudes of the SMC (Campos-Sánchez et al., 2017; Hernández-Rojas et al., 2020; Jiménez-López et al., 2020; Martínez-Camilo et al., 2018). However, the contribution of other diverse groups such as climbers, herbs, and shrubs are still unknown. Our analyses show that climbers have a significant peak of richness in the lower areas of the elevation gradient, where they are related to higher levels of human disturbance, which confirms that climbers prosper in disturbed habitats and in early successional stages following disturbance (Dewalt et al., 2000). Nevertheless, we recorded some cells with high climber richness at higher elevations (1,900 m); thus, they have another peak in primary forests of the SMC. Epiphytes and climbers increase their contribution to total species richness in the highest areas of the altitudinal gradient, where they provide almost 25 % and 20 %, respectively, of total diversity; the occurrence of these groups is correlated with high values of precipitation and moderate temperatures, which are key drivers of their distribution (Gentry & Dodson, 1987; Kreft & Jetz, 2007; Krömer et al., 2005). At higher elevations in the SMC, cloud forests are found, in which a large amount of horizontal precipitation occurs in the form of clouds or fog, allowing for a high interception of water that promotes diversity of epiphytes (Jiménez-López et al., 2020; Karger et al., 2021).

On the contrary, at low altitudes, herbs were found in a greater proportion than the other plant groups, providing almost 30 % of total diversity, given that they include weeds, which are specialized to support high levels of disturbance and insolation resulting from changes in structure of primary forests (Vázquez & Givnish, 1998), which are highly fragmented or have been converted into secondary vegetation in the low areas of the SMC (Escobar-Flores & Castillo-Santiago, 2021). Although the contribution of herbs to total richness decreased slightly with elevation, they still provided a high level of richness, partly due to terrestrial ferns, which increase in diversity at high elevations (1,500-2,000 m). Ferns usually present the highest number of species in humid montane forests (Hernández-Rojas et al., 2020; Kessler, 2001; Krömer et al., 2013), but can occasionally have even higher richness in natural lowland rainforests (Hernández-Rojas et al., 2018). Shrubs were the third richest group; their proportion remains almost stable throughout the elevation gradient, although their greatest contribution to species richness was recorded from 700 to 1,800 m, similar to that reported for an altitudinal gradient in Veracruz, Mexico (Bautista-Bello et al., 2019) and northern China (Zhang et al., 2016). Meanwhile, the contribution of trees decreases with elevation, due to the effect of a higher contribution of other life-forms in the SCM. A high richness of herbs, trees and epiphytes has already been documented in the higher areas of the SCM (González-Espinosa et al., 2004; Hernández-Rojas et al., 2020; Jiménez-López et al., 2020; Martínez-Camilo et al., 2018)

Limitations, biases, and warnings. We recognize some inherent difficulties in using a large amount of data from multiple sources. In our study, we were cautious regarding acquisition of information, taxonomic revision, the minimum number of records in each cell, cell size, and spatial corrections, and therefore consider that we obtained a robust methodological route to improve the quality of our taxonomic and geographic information database (Ball-Damerow et al., 2019; Cruz-Cárdenas et al., 2014; Zizka et al., 2019). Nevertheless, we are conscious that some data might present biases due to non-systematic sampling throughout the study region, the pattern of collection of botanical explorers, heterogeneous seasons of sampling, and errors of omission or commission in database construction that could influence our results (Hughes et al., 2021). For this reason, the interpretations resulting from our study should be taken with caution. Our study provides a reasonable interpretation of some of the principal patterns. With our analysis of the relationship of species richness to variables on a regional scale, we aim to contribute to knowledge of possible factors involved in structuring the vegetation of tropical mountains of southern Mexico. Furthermore, we believe that the conceptual frameworks developed in the present study will help to reduce these biases (Hughes et al., 2021; Zizka et al., 2019). Finally, the considerable differences in richness of the 10 cells with the lowest and highest richness may be the result of varying intensity of collection, rather than human disturbance or another underlying factor. Intensity of collection is substantially highest in the 10 richest cells (total = 28,291 records, average = 2,829.1, min- = 1,520, max = 5,412) as compared to the 10 cells with the least richness (total = 527 records, average = 57.2, min. = 46, max = 80).

Conclusions

Total richness and that of the five plant life-forms evaluated in this study do not respond in a linear manner to the elevation gradient, and each of the plant life-forms contributes in a different proportion to regional richness. Our results suggest a high relevance of mechanisms promoted by climatic variables to maintenance and variation of richness of different plant groups in the mountainous system; however, human disturbance modifies the distribution patterns, and may cause some groups to increase their richness. The high species richness of vascular plants at higher elevations of the SMC may be attributed to their proximity to the borders of protected areas, which favors their conservation. Nevertheless, lower areas have high levels of disturbance, which may pose risks for a considerable number of species. Finally, the contribution of the different plant groups to total richness varies with elevation, as well as throughout the SMC, which presents a great challenge for designing conservation strategies for plant groups.

Declaration of competing interest

The authors declare they have no conflict of interest.

FIGURES

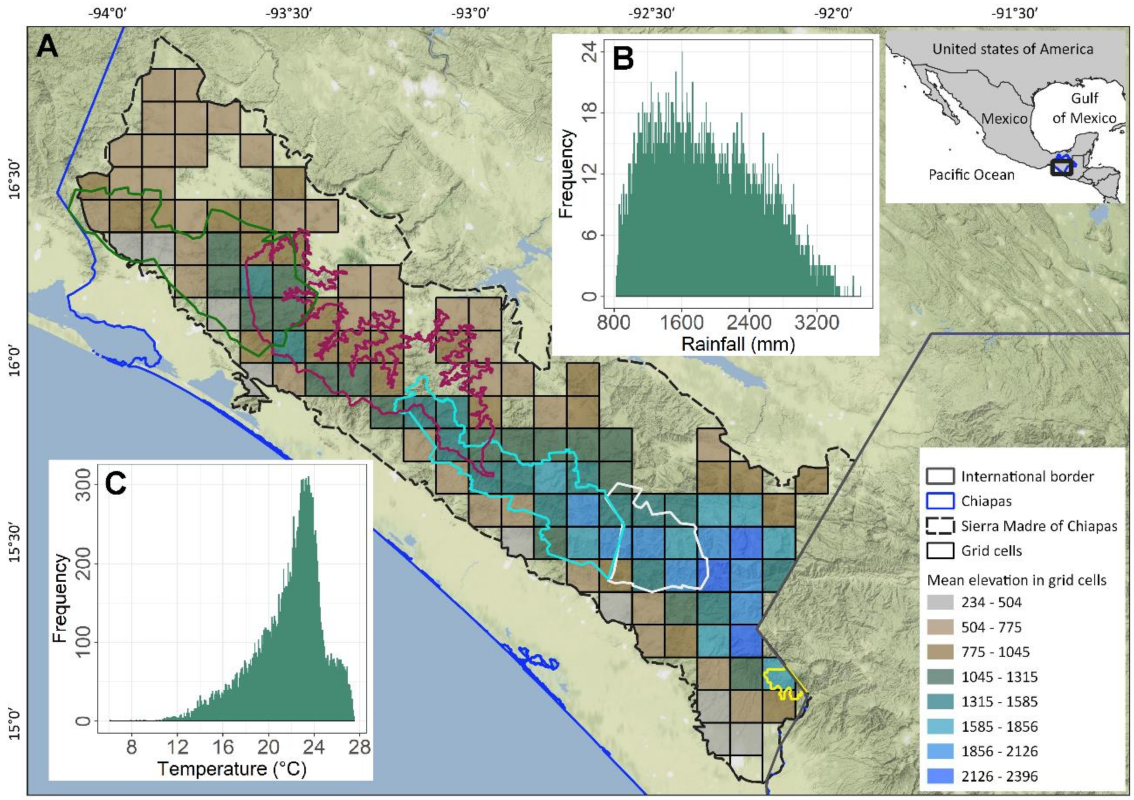

Figure 1. Location of the Sierra Madre of Chiapas (SMC) mountainous system, in southeastern Mexico. a) Sierra Madre of Chiapas and the 123 grid cells (10 × 10 km) used for this study (see supplementary material on analysis of patterns for details). b and c) variation and frequency of total annual precipitation and average annual temperature in the SMC. Data were extracted from the raster layers with a 1 km^2 resolution from the CHELSA database, version 1.2 (Karger et al., 2017). Polygons within

the SMC correspond to natural protected areas. Green: La Sepultura Biosphere Reserve; purple: La Frailescana Flora and Fauna Protection Area; light blue: El Triunfo Biosphere Reserve; white: Pico El Loro-Paxtal Zone Subject to Ecological Conservation; and yellow: Tacaná Volcano Biosphere Reserve.

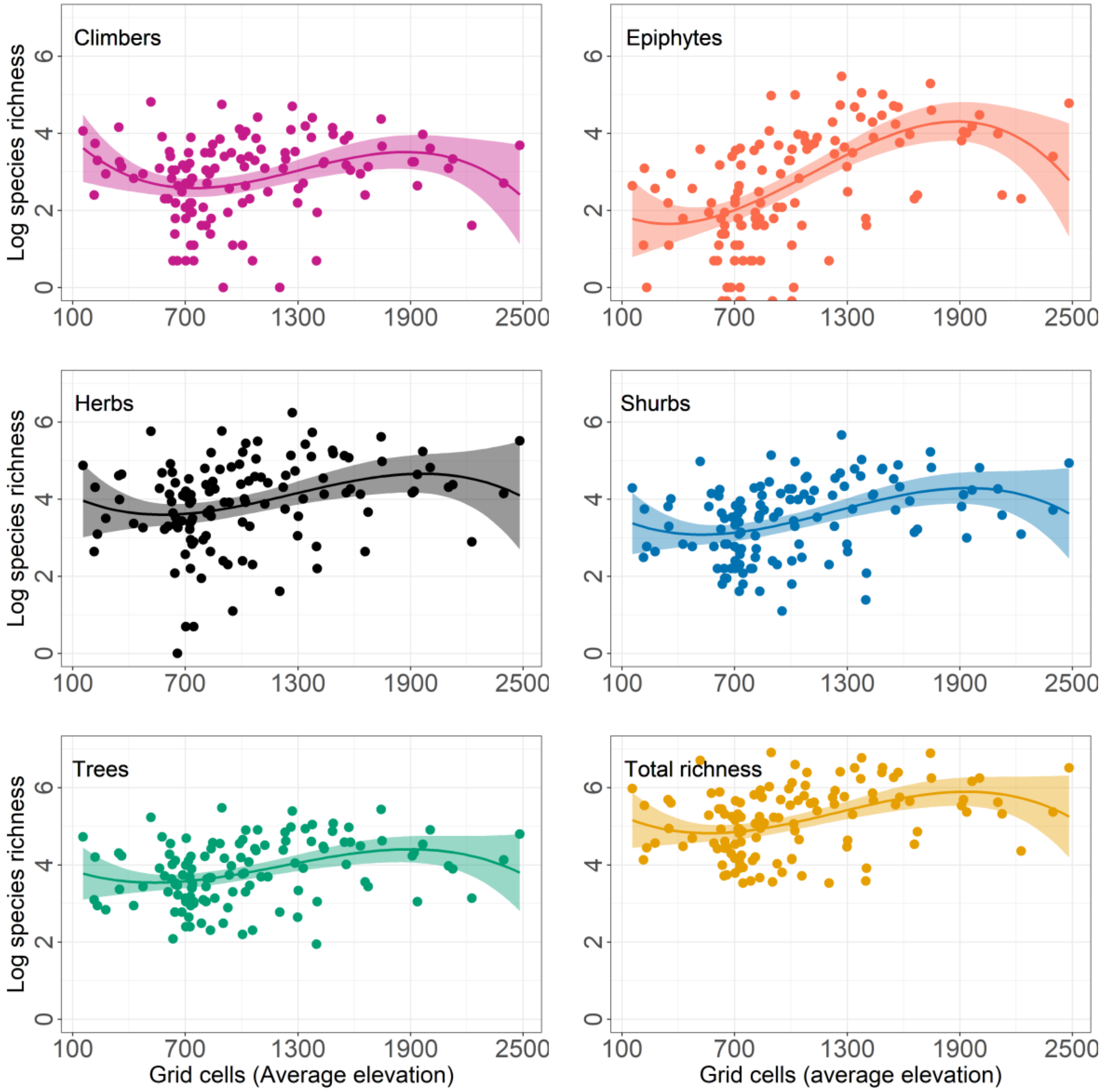

Figure 2. Variation in total species richness and that of five plant life-forms along the elevation gradient (10 × 10 km grid cells) of the Sierra Madre of Chiapas, Mexico. Climbers (*p* = 0.0089, r = 0.15); epiphytes (*p* = 8.24e-09, r = 0.23); herbs (*p* = 0.00328, r = 0.06); shrubs (*p* = 5.42e-05, r = 0.12); trees (*p* = 0.0008665, r = 0.08); and total richness (*p* = 0.000175, r = 0.10). Dots indicate observed richness, and lines expected

richness, based on linear models with third order polynomial adjustment, with a 95 % confidence interval. All response variables were transformed to their natural logarithm.

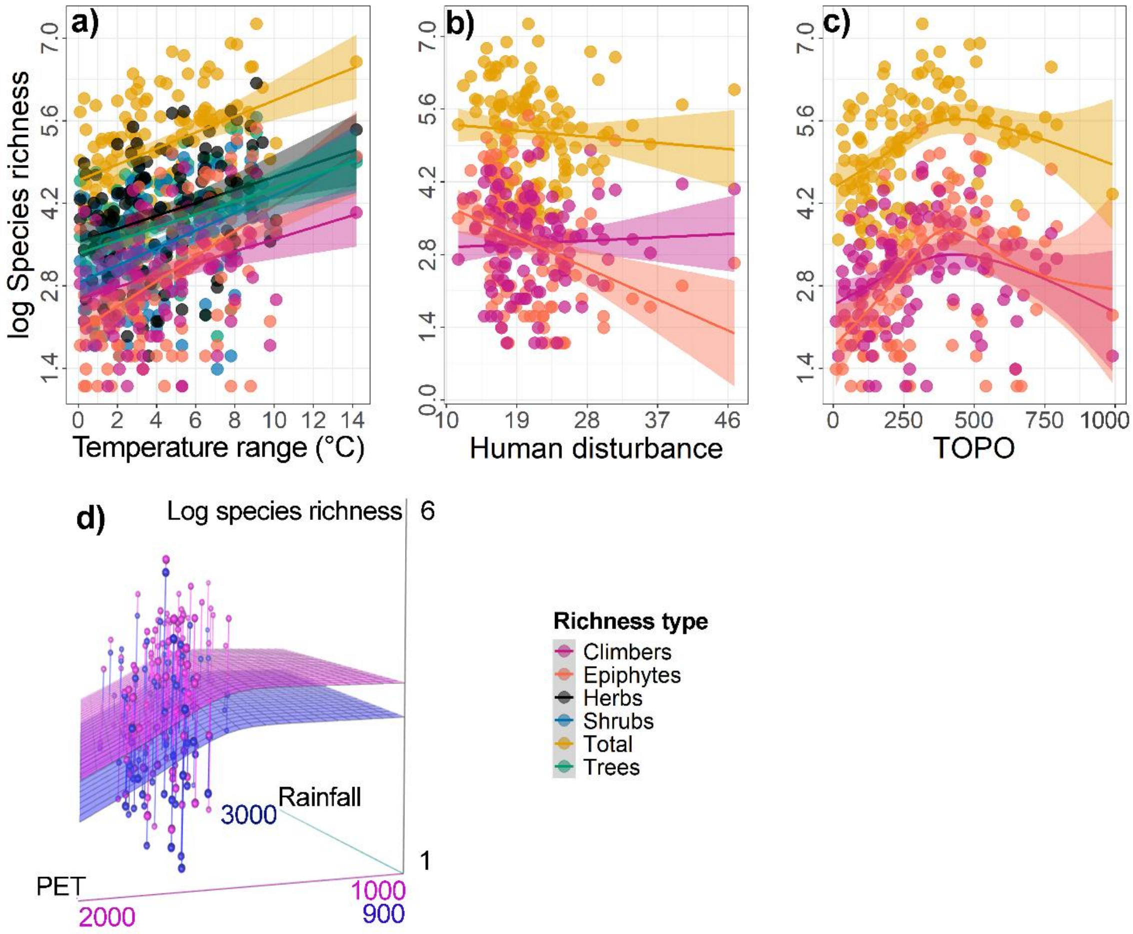

Figure 3. Generalized additive models (GAM) representing the relationship between the predictor variables and richness for each plant life-form recorded in the Sierra Madre of Chiapas. In each panel, variation in richness of each group is shown only if the predictor variable explained its variation in the best models selected. The percentage of deviance explained for each plant group is indicated in Table S1. Dots indicate observed richness and lines expected richness based on GAM models with first order polynomial adjustment, with a 95 % confidence interval.

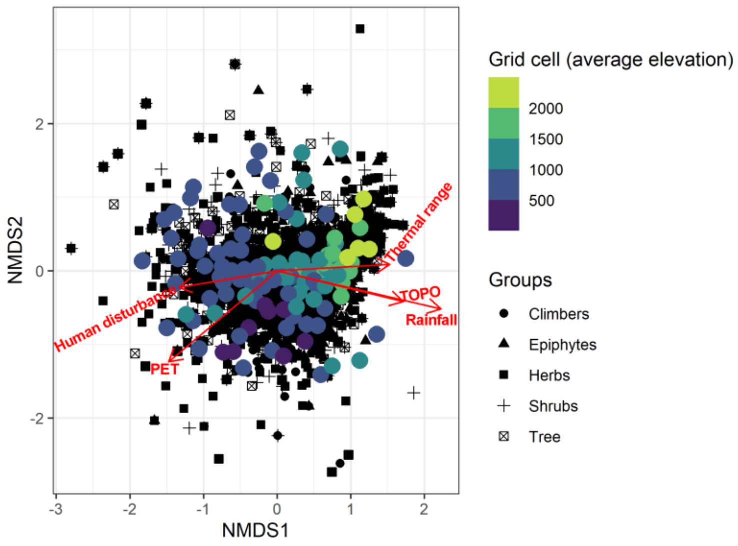

Figure 4. NMDS ordination of partitioned species composition for each plant life-form evaluated in relation to the environmental variables selected. Colors define the range of elevation of the cells in the Sierra Madre of Chiapas.

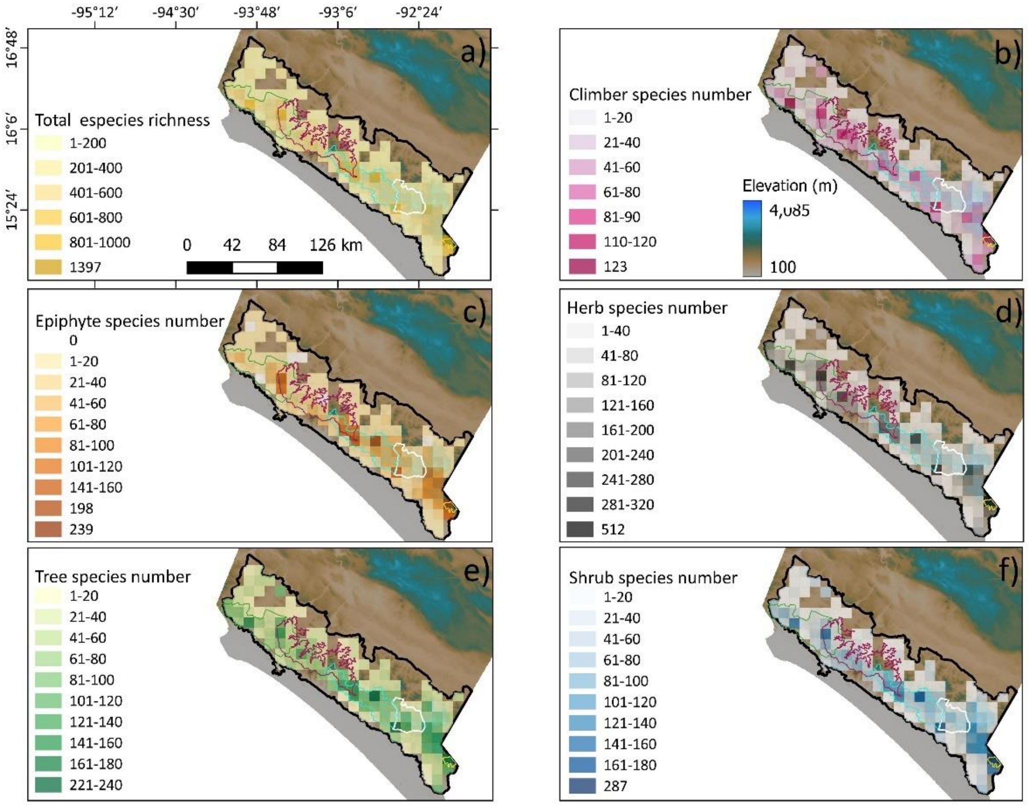

Figure 5. Spatial distribution patterns of species richness of each life-form in 10 × 10 km grid cells representing the Sierra Madre of Chiapas mountainous system. We decided to include layers of protected areas only to visually evaluate their location and overlapping of the spatial patterns of richness of the different groups. Total richness represents the sum of richness of the five life-form groups. Polygons within the SMC correspond to protected areas. Green: La Sepultura Biosphere Reserve; purple: La Frailescana Flora and Fauna Protection Area; light blue: El Triunfo Biosphere Reserve; white: Pico El Loro-Paxtal Zone Subject to Ecological Conservation; and yellow: Tacaná volcano Biosphere Reserve. The layer of protected areas was obtained from Protected Planet: https://www.protectedplanet.net/en.

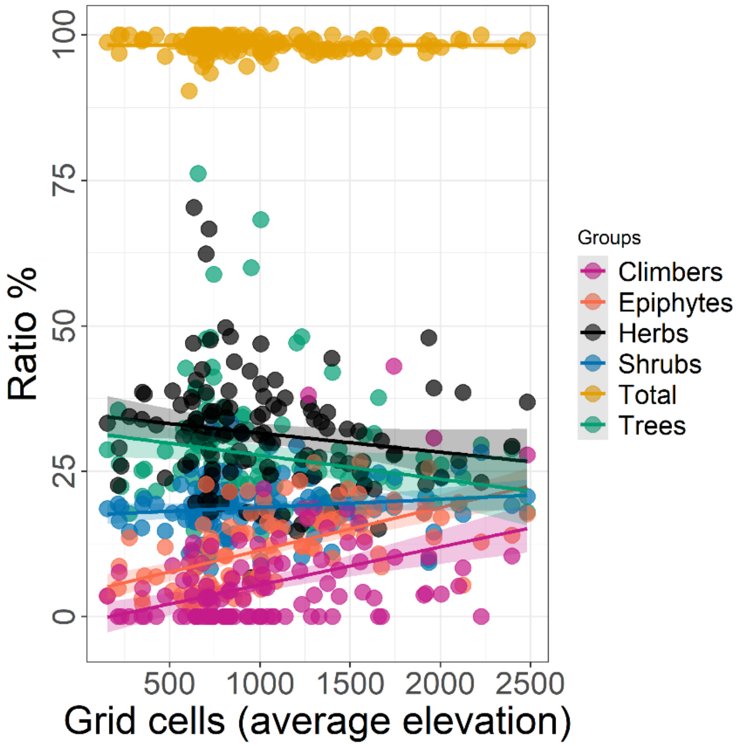

Figure 6. Partitioning of the five plant life-forms along the elevation gradient (average elevation of each grid cell). Dots indicate observed richness and lines indicate the expected proportion based on generalized linear models (GLM) with first order polynomial adjustment. Colored bands indicate a 95 % confidence interval.

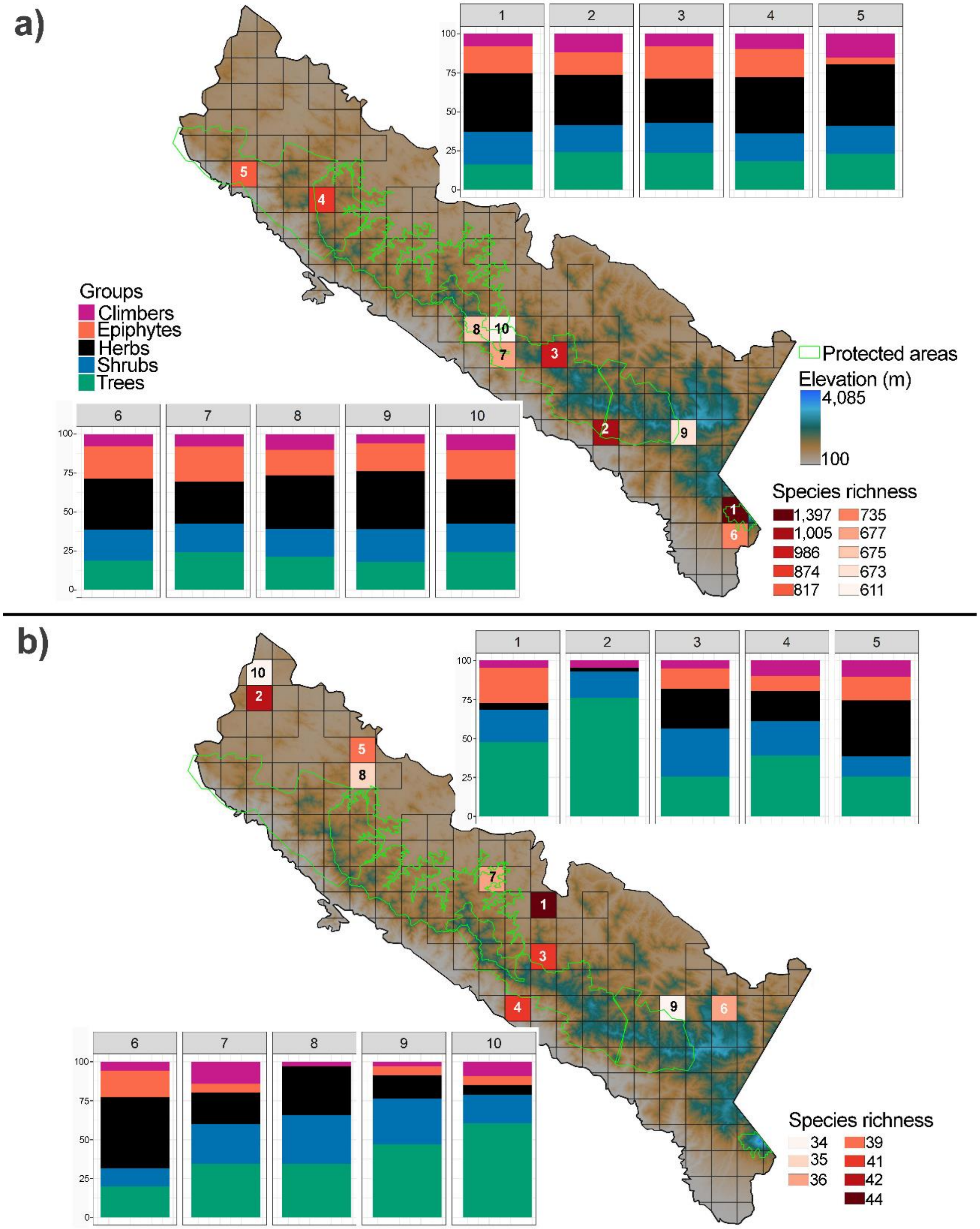

Figure 7. Partitioning of richness of five plant life-forms in the Sierra Madre of Chiapas, Mexico. a) the 10 cells with the highest species richness, b) the 10 cells with the lowest richness. Numbers within cells in the map correspond to numbers within each bar graph, indicating the contribution of each group in these cells.

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BIOSKETCH

Derio Antonio Jiménez-López is an ecologist interested in describing natural history, particularly that related to plants, as well as more thoroughly understanding the processes and mechanisms behind diversity patterns across different scales along the neotropics using vascular plants as a study model. Authors' contributions: All the authors conceived and designed the study; D.A.J.L. gathered the information, D.A.J.L. designed the methodology with assistance from N.R.M., T.K., and M.G.E.; D.A.J.L. and N.R.M. analyzed the data; and D.A.J.L. and N.R.M. wrote the article, which was revised by all the authors.

Supplementary material

S1. *Construction of databases.* Construction of the database of native vascular plants for the SMC followed the recommendations of Chapman (2005) and (Castillo et al., 2014), and included the following stages:

(1) *Gathering of information*. In 2018, from a variety of sources, we requested and downloaded records of vascular plants for the Mexican state of Chiapas. The original database included 273,306 records provided by the SNIB-REMIB (National Information System on Biodiversity of Mexico) of CONABIO (National Commission for Knowledge and Use of Biodiversity), and 35,014 from the online data base of the National

Herbarium of Mexico (MEXU). Furthermore, from curators of the following herbariums, we requested records of vascular plants for the study area: 46,603 records from MO, 4,075 from CH, and 36,245 from HEM. These sources provided a total of 395,243 records. Acronyms of the herbariums mentioned in the text are according to Thiers (2016).

(2) *Geographic filter*. We applied a geographic filter to select those records whose origin was within the borders of the SMC. This was necessary as it was clear that many of the 395,243 records obtained from different sources were not recorded within the SMC. We strictly applied the criteria that any record with geographic coordinates outside the polygon of the SMC should be eliminated, while any record within the polygon was retained, independently of closeness to the border of the SMC. This procedure was carried out using QGIS 3.2.3 (QGIS Development Team, 2020). Application of the geographic filter resulted in a total of 102,046 records remaining in the database.

(3) *Taxonomic and nomenclatural revision*. The final phase of database construction consisted of reviewing taxonomic and nomenclatural information, including standardization, and updating the database. First, we standardized the scientific names and those of the authors according to the database The Plant List v. 1.1 (The Plant List, 2013). This homogenization procedure was carried out automatically in the R software 3.5.2 version (R Development Core Team, 2020), with the *Taxonstand* package (Cayuela et al., 2012). Nevertheless, due to frequent actualization of botanical nomenclature, we decided to follow the botanical nomenclature of the Flora of Mexico (Villaseñor, 2016); thus, the database was reduced to 98,909 records. The taxonomic arrangement of the verification list follows (APG VI, 2016) for angiosperms, (Christenhusz et al., 2011a) for gymnosperms, and (Christenhusz et al., 2011b) for ferns and lycophytes.

(4) *Elimination of duplicates and spatial errors.* The database thus constructed included a certain level of redundancy given that a specimen collected by a single person could have fed the database through different information sources. Therefore, a final step

consisted of eliminating 7,261 redundant records and 1,728 spatial errors detected using *CoordinateCleaner* v. 2.0-9 (Zizka et al., 2019) implemented using the R software (R Development Core Team, 2020). Due to the fact that records in public databases are prone to spatial errors (Maldonado et al., 2015), this step excluded: (a) records that are imprecise due to *post hoc* geo-referencing of vague descriptions of localities; (b) records with a notified uncertainty greater than 100 km; and (c) records marked as potentially problematic, based on country centroids, in the locality where botanical gardens are located, and those without coordinates or with equal latitude and longitude. Through this procedure, the database was reduced to 89,920 records.

Analysis of patterns. Given the auto-correlation inherent in spatial records, a randomness analysis was carried out with the total number of records using the ILWIS 3.8 software (http://52north.org/ilwis). This analysis is similar to estimating the distance between two points; therefore, it allowed for estimating the distance to which the collection points are not correlated (Cruz-Cárdenas et al., 2014). The distance found (0.08 degrees) - approximately 10 km - was used to define the size of each grid cell (10 × 10 km), which was the optimal arrangement among distribution, collection effort, and number of cells. Furthermore, upon delimiting the polygon of the SMC, some cells were not completely within the borders of the polygon. In order to reduce noise due to sample size, we decided to exclude those grid cells which had less than 70 % of their surface area (<700 km) within the SMC. Finally, only 123 grid cells were included. In order to set a minimum number of records for each cell, we considered that small sample sizes could cause considerable distortions in analysis of patterns of diversity (González-Orozco et al., 2014), and decided to use a minimum of 40 total records per cell, providing a good representation of richness in each cell indicated by a high proportion of records, due to variations in sampling effort throughout the length and width of the SMC. Through this step, the database was reduced to 78,132 records.

Taxonomic groups selected according to the resolution of the information. It was noted that the historic information gathered is not proportional among the plant life-forms (e.g., trees, herbs, and palms) and growth habits (e.g., terrestrial, epiphytic, aquatic) of vascular plants according to the different efforts of botanical exploration within the SMC. Therefore, for this study, vascular flora was analyzed by integrating five plant life-forms: (1) climbers (i.e. plants that germinate on the ground (terrestrially) and climb supported by their flexible stem), including hemiepiphytes (i.e. plants that germinate on a host tree but later establish contact with the soil through their roots; Zotz et al., 2021), (2) epiphytes (including holoepiphytes i.e. species that never connect their roots with the soil, excluding accidental and facultative epiphytes), (3) herbs, (4) shrubs, and (5) trees. These five plant life-forms together contain 98.29 % of all records and 97.56 % of the total of richness of our database.

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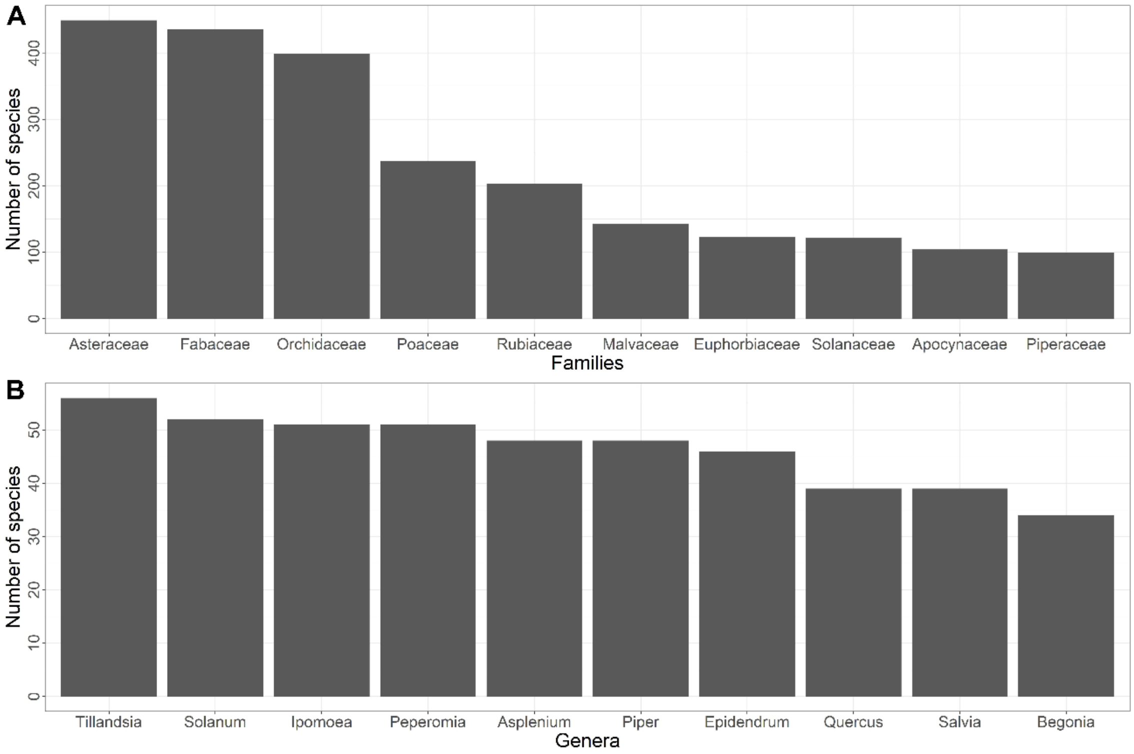

Figure S1. The ten families and genera with the highest species richness in the Sierra Madre of Chiapas. a = families and b = genera.

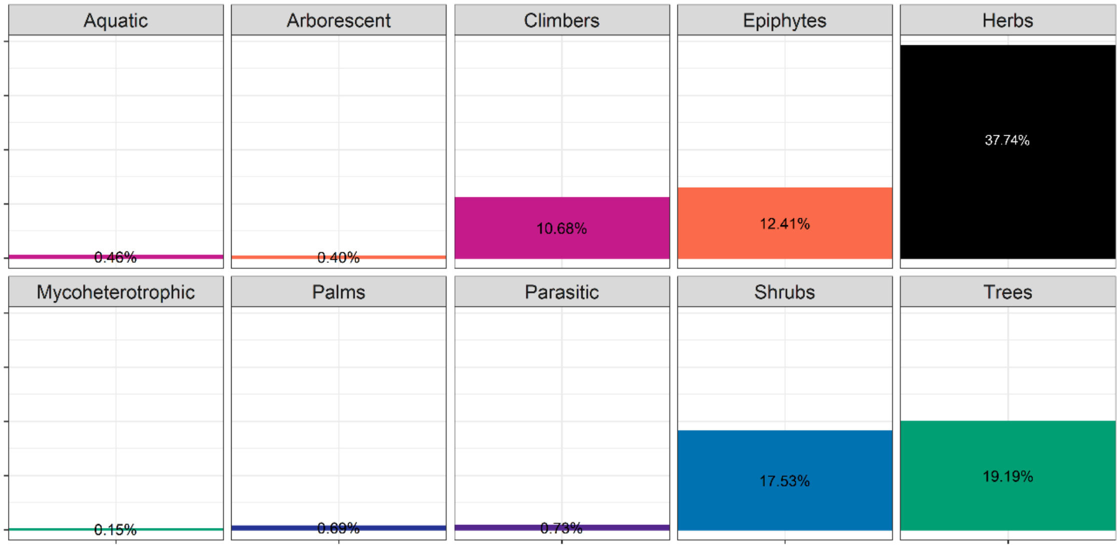

Figure S2. Partition of vascular plant richness in the Sierra Madre of Chiapas. Numbers within bars indicate the proportion of species richness for each plant life-form; 100 % = 5,196 species.

Table S1. Summary of statistics of all GAM models constructed for each plant life-form following a backward selection approach. Number of base dimension (k); effective degrees of freedom (edf). AIC = Akaike´s information criterion. ANOVA = analysis of variance. Elevation was excluded from the model as it had a high correlation value with PET (Pearson´s r = -0.78, *p* <0.001). All response groups were transformed to their logarithms. In the models, WED is the relationship between the variables total annual precipitation and PET. Numbers in red indicate statistically non-significant variables.

GAM MODELS						
TOTAL RICHNESS						
Null model						
AIC	ANOVA (Chis-sq)		k	edf	% Expl. dev.	*p*-value
NA	NA		-	-	-3.39E-16	<2e-16
Saturated model						
Predictors	AIC	ANOVA (Chis-sq)	k	edf	% Expl. dev.	*p*-value
Thermal range	13.48005	0.0123	9	1	37.00	0.0141
TOPO			9	5		0.0479
Human disturbance			9	2.48		0.0167
WED			24	3		0.2191
Best model						
Predictors	AIC	ANOVA (Chis-sq)	k	edf	% Expl. dev.	*p*-value
Thermal range	10.77876	0.02687	9	1	35.20	0.00432
TOPO			9	5.28		0.00783
Human disturbance			9	2.5		0.02089
CLIMBERS						
Null model						
AIC	ANOVA (Chis-sq)		k	edf	% Expl. dev.	*p*-value
NA	NA		NA	NA	0.00E+00	<2e-16

Best model

Predictors	AIC	ANOVA (Chis-sq)	k	edf	% Expl. dev.	*p*-value
Thermal range	12.04432	1.79E-06	9	1.291	32.60	0.0451
TOPO			9	2.324		0.0549
Human disturbance			9	1		0.0579
WED			24	5.429		0.0588

EPIPHYTES

Null model

AIC	ANOVA (Chis-sq)	k	edf	% Expl. dev.	*p*-value
NA	NA	NA	NA	1.90E-14	<2e-16

Saturated model

Predictors	AIC	ANOVA (Chis-sq)	k	edf	% Expl. dev.	*p*-value
Thermal range	18.41077	9.08E-04	9	1	58.60	0.000908
TOPO			9	5.729		0.012048
Human disturbance			9	1.96		0.063626
WED			24	4.036		0.134919

Best model

Predictors	AIC	ANOVA (Chis-sq)	k	edf	% Expl. dev.	*p*-value
Thermal range	14.28050	4.81E-05	9	1	64.9	< 2e-16
TOPO			9	5.59		8.77e-06

Human disturbance			9	6.4		7.18e-05

HERBS

Null model

AIC	ANOVA (Chis-sq)	k	edf	% Expl. dev.	*p*-value
NA	NA	NA	NA	-3.03E-14	<2e-16

Saturated model

Predictors	AIC	ANOVA (Chis-sq)	k	edf	% Expl. dev.	*p*-value
Thermal range	10.305506	0.02154	9	1	21.80	0.0486
TOPO			9	2.059		0.3436
Human disturbance			9	2.247		0.0829
WED			24	3		0.1313

Model reduction

Predictors	AIC	ANOVA (Chis-sq)	k	edf	% Expl. dev.	*p*-value
Thermal range	5.073212	5.07E-02	9	1	13.50	2.71E-04
TOPO			9	2.614		0.218735

Best model

Predictors	AIC	ANOVA (Chis-sq)	k	edf	% Expl. dev.	*p*-value
Thermal range	3.000036	3.98E-04	9	1	9.62	3.98E-04

SHRUBS

Null model

AIC	ANOVA (Chis-sq)	k	edf	% Expl. dev.	*p*-value
NA	NA	NA	NA	0.00E+00	<2e-16

Saturated model

Predictors	AIC	ANOVA (Chis-sq)	k	edf	% Expl. dev.	*p*-value
Thermal range	10.740053	0.002	9	1	33.10	0.0244
TOPO			9	2.297		0.1199
Human disturbance			9	2.442		0.0187
WED			24	3		0.0324

Model reduction

Predictors	AIC	ANOVA (Chis-sq)	k	edf	% Expl. dev.	*p*-value
Thermal range	8.845281	3.59E-02	9	1	29.40	2.12E-03
Human disturbance			9	2.121		0.10102
WED			24	3.724		0.01279

Best model

Predictors	AIC	ANOVA (Chis-sq)	k	edf	% Expl. dev.	*p*-value
Thermal range	8.211004	5.49E-02	9	1	28.10	3.84E-03
WED			9	5.211		0.00857

TREES

Null model

AIC	ANOVA (Chis-sq)	k	edf	% Expl. dev.	*p*-value
NA	NA	-	-	0.00E+00	<2e-16

Saturated model

Predictors	AIC	ANOVA (Chis-sq)	k	edf	% Expl. dev.	*p*-value
Thermal range	10.417	1.49E-06	9	1	27.60	0.0349
TOPO			9	2.33		0.2004

Human disturbance			9	2.09		0.0403
WED			24	3		0.0839
Model reduction						
Predictors	AIC	ANOVA (Chis-sq)	k	edf	% Expl. dev.	*p*-value
Thermal range	8.2748	0.009898	9	1	21.70	1.10E-05
Human disturbance			9	5.27		0.167
Best model						
Predictors	AIC	ANOVA (Chis-sq)	k	edf	% Expl. dev.	*p*-value
Thermal range	3.000035	1.63E-05	9	1.12	13.70	1.10E-05

Table S2. Results of NMDS ordination of the data set of environmental and disturbance variables related to species richness by plant life-form in the Sierra Madre of Chiapas

Variable	NMDS1	NMDS2	*P*	R^2
Climatic gradient	1.00000	-0.00175	0.001	0.27
Topographic heterogeneity	0.93201	-0.36243	0.001	0.35
Rainfall	0.93632	-0.35115	0.001	0.64
PET	-0.85037	-0.52618	0.001	0.35
Human disturbance	-0.98578	-0.16807	0.001	0.20

Table S3. Summary of the quantity of records and species richness of the different plant life-forms in each 10 × 10 km grid cell. T = trees, S = shrubs, H = herbs, E = epiphytes, C = climbers

Grid cells	Average elevation	Records	T	S	H	E	C	Proportion of the five groups	Total richness
1	837.67	1,025	83	76	182	2	33	376	378
2	621.91	1,020	95	70	136	24	30	355	361
3	700.62	99	23	16	13	2	8	62	65

4	795.93	108	22	9	19	2	8	60	61
5	885.68	1,553	95	85	118	58	47	403	414
6	361.17	610	69	55	104	19	23	270	272
7	744.97	65	20	6	2	2	3	33	34
8	658.48	52	32	7	1	0	2	42	42
9	631.65	528	55	38	109	4	21	227	232
10	729.75	96	19	13	19	1	3	55	55
11	858.19	335	23	41	71	5	22	162	162
12	517.09	3,240	187	145	317	36	123	808	817
13	724.62	210	38	30	25	14	15	122	124
14	590.30	159	41	16	25	2	10	94	96
15	744.87	70	21	8	18	2	2	51	51
16	681.92	143	16	9	31	1	12	69	73
17	647.56	521	61	33	83	5	21	203	204
18	736.50	95	30	15	17	0	7	69	70
19	563.70	293	50	45	72	7	22	196	198
20	810.47	260	31	21	79	6	21	158	159
21	1,140.99	482	40	34	83	49	12	218	221
22	1,039.50	560	59	54	87	53	30	283	291
23	616.47	720	72	59	62	3	34	230	233
24	576.34	716	113	63	108	9	50	343	350
25	927.32	99	18	10	10	8	7	53	56
26	1,006.28	1,255	105	71	184	36	51	447	460
27	1,377.00	3,707	155	152	307	156	82	852	874
28	1,548.67	1,632	98	92	168	111	46	515	527
29	838.39	333	39	47	35	9	6	136	141
30	350.43	371	29	27	54	3	26	139	140
31	834.03	46	10	5	14	6	4	39	39
32	902.70	47	12	11	11	0	1	35	35
33	829.41	377	39	33	66	12	19	169	170
34	1,022.00	220	27	27	50	9	14	127	132

35	1,014.80	345	44	31	55	1	23	154	158
36	1,285.07	826	57	76	113	38	34	318	320
37	805.14	845	68	73	121	35	33	330	336
38	635.14	86	8	6	38	0	2	54	54
39	908.44	539	65	34	50	6	30	185	187
40	1,085.39	2,042	135	98	244	36	83	596	600
41	946.05	794	53	63	125	19	33	293	296
42	648.50	138	34	17	34	4	9	98	100
43	717.72	299	61	37	58	12	33	201	203
44	989.46	989	95	71	135	27	61	389	393
45	1,077.39	1,086	79	94	155	44	48	420	426
46	627.00	167	38	25	51	6	17	137	138
47	660.54	100	25	17	26	1	14	83	85
48	728.45	79	24	10	9	0	7	50	50
49	996.74	569	66	54	80	27	28	255	256
50	1,070.92	686	83	62	98	51	27	321	328
51	1,328.63	295	50	42	55	33	15	195	201
52	846.53	583	97	60	86	21	41	305	314
53	703.00	169	11	11	58	3	6	89	93
54	786.00	72	12	9	7	2	5	35	36
55	1,372.50	1,008	100	99	164	83	49	495	507
56	1,340.00	1,854	139	119	226	108	66	658	675
57	726.00	111	11	5	29	3	9	57	61
58	646.83	137	33	7	28	7	6	81	84
59	723.62	198	40	22	49	3	25	139	139
60	719.70	310	14	15	92	6	8	135	138
61	811.17	95	21	12	21	7	5	66	67
62	1,263.30	1,520	145	107	169	113	60	594	611
63	1,488.92	1,882	160	121	178	149	53	661	677
64	644.63	80	16	9	8	4	4	41	41
65	702.85	53	21	9	2	10	2	44	44

66	1,058.75	51	10	12	10	5	2	39	41
67	1,633.65	600	89	52	62	53	19	275	283
68	705.43	437	109	46	66	35	22	278	287
69	214.98	93	22	12	14	3	11	62	62
70	815.66	205	38	15	38	5	15	111	111
71	1,043.90	136	32	17	27	17	10	103	105
72	1,743.31	3,265	229	185	274	198	79	965	986
73	1,435.71	554	88	60	94	73	25	340	350
74	1,005.99	99	9	11	30	3	9	62	64
75	734.23	140	30	23	31	5	9	98	99
76	733.88	253	49	41	52	24	17	183	188
77	953.18	49	27	3	3	8	3	44	45
78	1,440.73	461	83	62	62	49	26	282	289
79	1,919.72	655	75	61	67	57	26	286	295
80	1,909.69	510	69	45	64	45	26	249	253
81	729.96	477	68	52	61	37	49	267	274
82	1,402.96	80	21	8	9	5	7	50	50
83	1,124.89	486	91	68	48	42	22	271	276
84	1,222.61	618	80	60	74	73	22	309	314
85	1,936.82	311	21	20	103	55	14	213	215
86	895.54	2,981	239	170	319	145	115	988	1005
87	220.36	462	67	42	74	22	42	247	255
88	1299.30	164	14	17	21	23	9	84	87
89	1580.57	483	98	75	71	43	21	308	314
90	1232.58	588	127	27	42	32	33	261	264
91	475.68	180	31	16	26	13	19	105	109
92	276.78	142	17	14	33	13	19	96	96
93	1204.19	59	16	10	5	2	1	34	34
94	1658.06	174	35	23	14	10	11	93	93
95	2227.35	124	23	22	18	10	5	78	78
96	1104.87	434	40	53	96	40	36	265	268

97	832.88	370	39	36	41	41	33	190	191
98	609.35	136	27	9	27	2	10	75	83
99	1005.18	113	43	6	11	0	3	63	63
100	1235.44	813	101	94	101	45	28	369	374
101	2102.92	665	53	71	74	54	22	274	276
102	2482.54	2598	121	139	248	119	40	667	673
103	1485.19	1657	130	117	193	87	63	590	599
104	1748.96	1558	102	124	145	99	39	509	518
105	935.06	334	42	39	50	40	13	184	185
106	425.65	126	19	17	29	6	17	88	88
107	231.89	116	19	16	22	1	27	85	85
108	739.05	182	33	42	33	5	17	130	130
109	1399.48	47	7	4	16	6	2	35	36
110	2396.93	363	62	41	63	30	15	211	215
111	1965.43	1056	93	69	187	65	53	467	476
112	1571.14	1594	144	132	159	107	51	593	597
113	2005.74	1317	135	123	124	88	37	507	518
114	1557.69	444	55	41	64	69	24	253	259
115	687.08	360	42	34	60	30	24	190	190
116	346.34	714	74	45	100	9	64	292	295
117	155.64	826	113	73	131	14	58	389	394
118	1302.76	220	28	14	35	12	13	102	103
119	2125.76	344	49	36	79	11	28	203	205
120	1674.12	274	31	25	39	11	23	129	129
121	1270.56	5412	220	287	512	239	110	1368	1397
122	1022.28	1832	134	144	232	148	57	715	735
123	702.71	386	54	28	67	9	15	173	174

CAPÍTULO 3

Consideraciones finales y Conclusiones

Este proyecto de investigación inicialmente tenía el objetivo de determinar la diversidad alfa y beta de plantas vasculares, además de las regiones fitogeográficas en el sistema montañoso de la Sierra Madre de Chiapas (SMC). Estas ideas se justificaban por la gran diversidad de plantas vasculares y extensas áreas protegidas. Es y sigue siendo necesario reconocer cómo son los patrones de distribución de plantas vasculares en una región determinada, para comprender cómo las variables ambientales y su alteración por el disturbio humano contribuyen a explicar esta distribución. Asimismo, es relevante analizar como el recambio de la composición de especies puede estar relacionado con cambios en el ambiente a lo largo de un gradiente altitudinal. Dicho análisis permitiría reconocer las unidades fitogeográficas presentes en la región y ayudaría a ubicar zonas de alta biodiversidad en el espacio geográfico de la SMC. Analizar estas ideas contribuye a desentrañar las consecuencias de las actividades humanas en los ecosistemas de montaña, tales como perder su capacidad para suministrar funciones esenciales del ecosistema.

Transformé las preguntas iniciales en preguntas cuya respuesta pudiera generar un interés internacional dado que los patrones pueden ser observados en otros contextos geográficos. Un primer paso fue indagar sobre los vacíos de información en estudios sobre la distribución de plantas vasculares en sistemas montañosos. Encontré dos vacíos: (1) los patrones de distribución de plantas vasculares en sistemas montañosos o dentro de un gradiente altitudinal casi siempre se estudian incorporando un grupo particular de plantas vasculares (por ejemplo, árboles: Martínez-Camilo et al. 2018; hierbas terrestres: Gómez-Díaz et al. 2017; o epífitas vasculares: Krömer et al. 2005), que han contribuido a esclarecer los procesos y mecanismos vinculados a los patrones de diversidad de plantas vasculares. (2) los estudios que han analizado la riqueza total y de distintos grupos de plantas vasculares en el Neotrópico son escasos (Vázquez y Givnish 1998). Este tipo de estudios son relevantes para la conservación debido a que permiten identificar las áreas con mayor riqueza de especies y determinar qué grupos son más importantes en cuando a la riqueza que proporcionan a lo largo de un gradiente altitudinal en sistemas montañosos. Presento los hallazgos más importantes de este estudio y las implicaciones para la conservación de especies y ecosistemas prioritarios.

Riqueza y composición. La riqueza de plantas vasculares de la SMC corresponde a 60 % de la flora del estado de Chiapas (Villaseñor 2016), encontrándose en solamente 20 % de su territorio (73,311 km^2; Müllerried 1957). Las familias con mayor número de especies fueron Asteraceae (449), Fabaceae (435) y Orchidaceae (399), mientras que los géneros con mayor número de especies fueron *Tillandsia* L. (56), *Solanum* L. (52), e *Ipomoea* L. (51). Esto hace a la SMC un sistema montañoso de gran diversidad que requiere de mayor esfuerzo en el inventario de su biodiversidad, estudios ecológicos, y acciones de conservación dirigidas a investigar las amenazas frente al cambio climático y el aumento del disturbio humano (Ramírez-Marcial et al. 2001; Silveira et al. 2019).

Patrones de distribución. Los patrones de distribución de la riqueza de las distintas formas de vida analizadas no mostraron una tendencia lineal. Los modelos lineales mostraron similitud entre los patrones de riqueza total y las cinco formas de vida. Todos los grupos alcanzaron su mayor riqueza alrededor de los 1900 m de elevación y disminuyeron hasta los 2500 m. Este punto intermedio de alta riqueza en sistemas montañosos ha sido documentado para la región Neotropical (Rahbek 1995). Se emplearon modelos GAM y encontramos una explicación relativamente alta en la variación de la riqueza de cada forma de vida evaluada. Cuando aumentó el rango térmico aumentó la riqueza de todas las formas de vida, mientras que al aumentar el disturbio humano disminuyó la riqueza general y la de epífitas; por último, se observó una relación curvilínea entre la dinámica agua-energía (WED, por sus siglas en inglés) y la riqueza de trepadoras y arbustos. Se sugiere abundar en el empleo de este tipo de variables con otros grupos taxonómicos, pues podrían ser útiles para predecir la variación de la riqueza de especies (Ruggiero y Hawkins 2008). El uso de modelos GAM se basó en que han probado ser útiles para modelar respuestas no lineales de variables biológicas (Peters et al. 2019). Los modelos GAM pueden manejar los efectos lineales y no lineales de las variables predictoras sobre las variables de respuesta mediante funciones de suavizado. Por lo tanto, son análisis apropiados para investigar patrones de distribución, con múltiples grupos taxonómicos (Peters et al. 2019), como plantas (Lazarina et al. 2019; Vetaas et al. 2019) y mamíferos (Magalhães de Oliveira et al. 2018).

Partición y contribución de los diferentes grupos a la diversidad total. La contribución a la riqueza total de cada forma de vida difiere a lo largo del gradiente altitudinal y a lo largo del espacio geográfico de la SMC. Algunos grupos como las epífitas y trepadoras aumentan su contribución al aumentar la elevación, contrario a la contribución de árboles y hierbas que disminuyen ligeramente en las mayores altitudes. En el espacio geográfico se observó un patrón consistente, en el cual todos los grupos mostraron mayor riqueza en las partes altas del sistema montañoso. Esto tiene implicaciones relevantes para definir acciones y políticas de conservación. En las partes altas de la SMC existen áreas considerables incluidas en áreas naturales protegidas, en teoría se estaría conservando una alta riqueza de plantas vasculares (Toledo-Aceves et al. 2011; Karger et al. 2021). Estas partes altas también coinciden con la presencia de bosques de niebla o nubosos, en los que se produce una gran cantidad de precipitación horizontal en forma de nubes o niebla, lo que permite una alta interceptación de agua que promueve una gran diversidad de flora (Karger et al. 2021). La contraparte es el alto disturbio humano en las partes bajas, aunque también en las partes altas las plantaciones aledañas de café de sombra y la extracción de palmas posiblemente ya tienen efectos que no se han evaluado. Este último factor -el disturbio humano- promueve la reconfiguración de los patrones de distribución de las formas de vida aquí estudiadas, con la posible consecuencia de pérdida de numerosas especies. Algunos estudios han alertado sobre las consecuencias del disturbio humano y el cambio climático y sus posibles consecuencias con la pérdida de su biodiversidad en la SMC y otros sistemas montañosos de Chiapas (Ramírez-Marcial et al. 2001; Schroth et al. 2009).

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