Ecology / Ecología

Environmental filters determine the distribution of tree species in a threatened biodiversity hotspot in western Mexico

Los filtros ambientales determinan la distribución de especies de árboles en una región crítica de biodiversidad amenazada en el occidente de México

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Abstract
Background: Analyzing interactions between vegetation and environmental factors at regional scales provide information for the understanding of species assemblages.
Hypotheses: Environmental restrictions at higher elevations produce a decreasing species richness pattern along an elevational gradient and the climatic variables related to temperature and precipitation are the main filters of species distribution.
Objectives: (1) To identify the different assemblages of tree species occurring in a biodiversity hotspot; (2) to analyze the pattern of tree species richness along an elevational gradient; and (3) to analyze the environmental filters that determine the species distribution.
Study site: Serranías Meridionales of Jalisco in western Mexico.
Period of study: 2016-2018.
Methods: Thirty-three rectangular 0.1 ha plots were established for vegetation and environmental characterization. Cluster and canonical correspondence analyses were conducted to analyze tree species composition. We defined three groups of variables (climatic, relief and soil) to evaluate the influence of environmental filters. We used generalized linear models to assess the contribution of each group to the spatial variation in species richness.
Results: A total of 63 tree species were recorded. The cluster analysis defined eight groups within three forest types. The species richness showed a hump-shaped pattern along the elevational gradient and the climatic and soil variables explained a considerable amount of variation in the species richness.
Conclusions: The tree species richness in the Serranías Meridionales of Jalisco is dominated by a striking number of *Pinus* and *Quercus* species. This biodiversity hotspot is an important site for the understanding of tree ecological diversification in Mexico.
Keywords: Biodiversity hotspot, environmental variables, *Pinus*, *Quercus*, species richness.

Resumen
Antecedentes: El análisis de las interacciones entre la vegetación y el ambiente a escalas regionales permite entender el ensamblaje de especies.
Hipótesis: Restricciones ambientales en sitios elevados generan un patrón decreciente de riqueza de especies en gradientes altitudinales y la temperatura y la precipitación son los principales filtros de la distribución de especies.
Objetivos: (1) Identificar los diferentes ensamblajes de especies de árboles en una región crítica de biodiversidad; (2) analizar la riqueza de especies arbóreas en un gradiente altitudinal; (3) analizar los filtros ambientales que determinan la distribución de especies.
Sitio de estudio: Serranías Meridionales of Jalisco, México.
Período de estudio: 2016-2018.
Métodos: Se establecieron 33 parcelas de 0.1 ha para la caracterización de la vegetación y las variables ambientales. Se realizaron análisis de clasificación y canónicos de correspondencia. Utilizamos tres grupos de variables (climáticas, relieve y suelo) y modelos lineales generalizados para estimar las contribuciones de estas variables a la variación espacial en la riqueza de especies.
Resultados: Se registraron 63 especies de árboles. El análisis de agrupación definió ocho grupos dentro de tres tipos de bosques. La riqueza de especies presenta un patrón de joroba en el gradiente altitudinal y las variables climáticas y de suelo explicaron la variación de la riqueza de especies.
Conclusiones: La riqueza de árboles en las Serranías Meridionales of Jalisco es dominado por un número notable de especies de *Pinus* y *Quercus*. Este *hotspot* de biodiversidad es un sitio importante para el entendimiento de la diversificación de árboles en México.
Palabras clave: *Hotspot* de biodiversidad, *Pinus*, *Quercus*, riqueza de especies, variables ambientales.

The assembly of plant communities is influenced by several processes, such as historical diversification, environmental filtering, long-term dispersal and ecological interactions, among others (Götzenberger *et al.* 2011, Zobel 2016, Cavender-Bares *et al.* 2018). Environmental factors impose filters on species survival, so that only those species that possess the proper attributes to face them can become part of the community (Webb *et al.* 2002, Götzenberger *et al.* 2011, de Bello *et al.* 2012). Environmental filters act at different spatial scales; at the local scale, plant species respond to soil pH, moisture and nutrients (Grime 1979, Pausas & Austin 2001), while at the regional scale climatic variables are more relevant (Currie 1991, Götzenberger *et al.* 2011, de Bello *et al.* 2012).

Plant species richness increases with ecosystem productivity, which in turn is related to high temperature, water availability and resources such as soil nutrients (Currie 1991, Pausas & Austin 2001, Tuomisto *et al.* 2014). At the large scale, the water-related variables usually represent the strongest richness predictors in the tropical and subtropical regions for plants (Hawkins *et al.* 2003, Zhang *et al.* 2015). At the regional scale, landscape features like mountains play a central role in the regulation of abiotic conditions such as temperature, precipitation, humidity and soil conditions that usually change along an elevational gradient (Beniston *et al.* 1997, Fiedler & Beck, 2008). Plant species along elevational gradients in mountainous regions can be affected by temperature, precipitation, topography (*i.e.*, slope steepness and aspect) or soil traits (*i.e.,* soil water retention and fertility), all of which determines the amplitude of their spatial distribution (McCain & Grytnes 2010, Scherrer & Körner 2011, Jiménez-Alfaro *et al.* 2014), although the predominant factors underlying this variability appear to be specific to each taxonomic group (Vázquez-García & Givnish 1998, Tuomisto *et al.* 2014).

The understanding of the mechanisms responsible for community diversity along elevational gradients remains controversial (Nogués-Bravo *et al.* 2008, McCain & Grytnes 2010). The complex interaction between geographic and environmental variables at varying spatial scales in different mountain systems produces different patterns of plant species richness (Pausas & Austin 2001, Salas-Morales *et al.* 2015, Zhang *et al.* 2015). McCain & Grytnes (2010) described four main patterns of elevational species richness: decreasing, low plateau, low plateau with a mid-elevational peak and mid-elevational peaks. The decreasing and the mid-elevational or "hump-shaped" patterns are the most frequently reported for plants (Colwell *et al.* 2004, Kessler *et al.* 2011, de Bello *et al.* 2012).

In Mexico, the Mexican Transition Zone is the area where the Nearctic and Neotropical regions overlap (Morrone 2014) and is considered an important biodiversity hotspot for temperate taxa (Challenger & Caballero 1998, Myers *et al.* 2000). Temperate forests in Mexico are dominated by plant species with Nearctic affinities that underwent an extraordinary diversification in mountain chains that served as corridors during cool periods (Nixon 1993, Styles 1993, Hipp *et al.* 2018). Mexican temperate forests are distributed mainly in mountain chains, where the climatic conditions range from subhumid to humid, with freezing temperatures in winter at high elevations (Challenger & Caballero 1998).

The floristic province of Sierras Meridionales of Jalisco (Torres-Miranda *et al.* 2011) is an important biodiversity hotspot due to its high species richness and endemism (González-Villarreal 1986, 2018, Gernandt & Pérez de la Rosa 2014). In the Sierras Meridionales of Jalisco the climate along the elevational gradient shows a linear decrease of temperature and a more pronounced precipitation seasonality in lowlands (SMN 2017).

Vázquez-García & Givnish (1998) identified a decreasing pattern of species richness along the elevational gradient in the Manantlán Biosphere Reserve, where oaks were the dominant species at high elevations. Elsewhere, studies have reported that elevation is an important factor for determining oak species assemblages (Morales-Saldaña 2017, Torres-Miranda *et al.* 2011, 2013). Therefore, studies on the interaction between plants and environmental factors are relevant for the understanding of how plants respond to changes in climate that in turn determine the assemblages of plant communities.

The aim of this study was to analyze the effects of environmental filters on the occurrence of different species assemblages in a biodiversity hotspot in western Mexico. The objectives of this study were: (1) to identify the different assemblages of tree species that occur in the Sierras Meridionales of Jalisco, (2) to examine the pattern of tree species richness along an elevation gradient, and (3) to analyze the environmental filters that determine the distribution of the dominant genera. In this study, we tested the following hypotheses: (1) the resource and temperature restrictions at upper elevations cause a decreasing species richness pattern; (2) the climatic variables related to temperature and precipitation are the main filters of the tree species distributions.

Materials and methods

Study site. The study site was located in the Serranías Meridionales of Jalisco floristic province (Torres-Miranda *et al.* 2011), which comprises the "El Tuito-El Cuale-Talpa de Allende" Sierras (20° 20.885'- 20° 9.008' N, and 105° 19.162'- 104° 40.106' W). These mountain complexes are located within Cabo Corrientes and Talpa de Allende counties in Jalisco state, Mexico (Figure 1), at the boundary

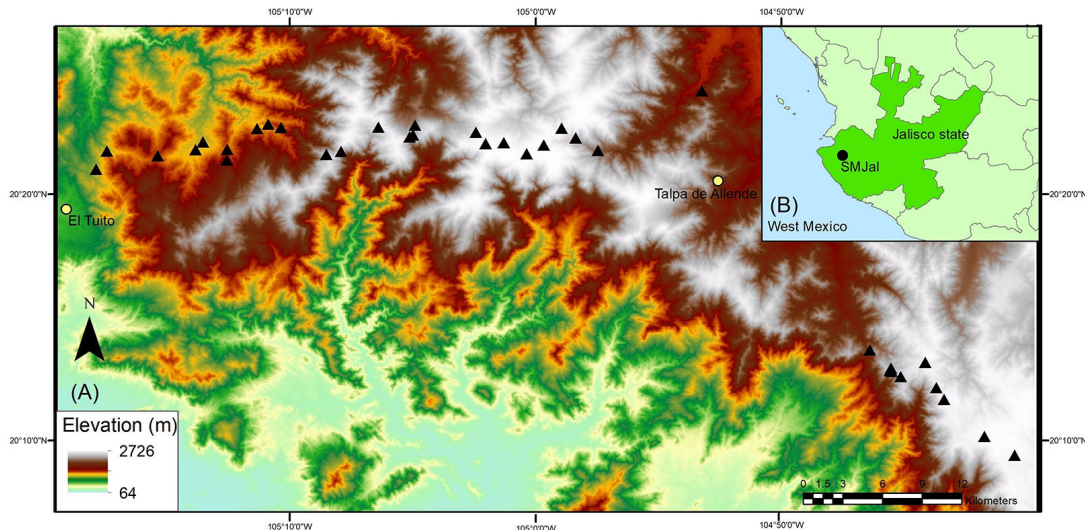**Figure 1.** Study region. (A) Location of the Serranías Meridionales of Jalisco (Jalisco Southern Sierras) in Mexico, (B) Jalisco state and the Serranías Meridionales of Jalisco (SMJal). The black triangles represent the location of the vegetation sampling plots relative to the elevational gradient.

of the Sierra Madre del Sur and the Trans-Mexican Volcanic Belt biogeographic provinces, and they encompass an elevational gradient from 650 to 2,738 m. The dominant soil groups are Cambisol and Regosol (INEGI 2007). The mean annual temperature ranges from 28.5 to 30.6 °C and the annual precipitation ranges from 1,500 to 1,800 mm, with 80 % of the rainfall concentrated between June and October (SMN 2017). In this region, the most common forest types are deciduous forest, oak forest, pine-oak forest, cloud forest, fir forest and its different transition zones (Cuevas-Guzmán *et al.* 2010, Velázquez-Ruiz *et al.* 2012). This floristic region is considered one of the most important centers of floristic endemism (Hernández-López 1995, González-Gallegos & Castro-Castro 2012, Vargas-Rodríguez *et al.* 2010, de la Riva *et al.* 2019), and according to the Mexican Biodiversity Commission (CONABIO) belongs to a priority hydrological basin and a priority land region due to its high biological value in Mexico (Arriaga-Cabrera *et al.* 2000, Arriaga-Cabrera *et al.* 2002).

Data collection. A total of 33 rectangular 0.1 ha plots (50 × 20 m) were established to conduct vegetation sampling and soil characterization. In each plot, all trees with DBH > 15 cm were recorded. Specialists provided taxonomic identifications and vouchers were deposited at the National (MEXU) and Facultad de Ciencias (FCME) herbaria, both at Universidad Nacional Autónoma de México (UNAM).

Climatic and relief variables. The climatic variables for the study region were obtained using the climatic surfaces reported by Cuervo-Robayo *et al.* (2014) and interpolated

using the algorithm of thin plate smoothing splines implemented in ANUSPLIN 4.36 (Hutchinson 2006), using a digital elevation model with 60 m² resolution. Nineteen climatic variables were extracted for each plot and then potential evapotranspiration and the aridity index proposed by the United Nations Environment Programme (UNEP) were calculated (Middleton & Thomas 1997) (see Appendix 1 for the calculations). Additionally, three relief variables (slope steepness, aspect and elevation) were estimated from the digital elevation model, which was processed with the Spatial Analyst tool (ESRI 2013) of Geographical Information System ArcGIS ver. 10.2.

Edaphic characterization by plot. Composite soil samples were collected in the rainy season (August and November 2016) in each plot. The samples were stored in hermetically sealed plastic bags and placed in darkness at 4 °C until laboratory analysis. A subsample of all the soil samples by plot was oven-dried at 70 °C to constant weight, for gravimetric moisture determination and water content adjustment to express nutrient concentration on the basis of dry soil mass. For fresh soil samples, pH was measured in deionized water (soil/solution ratio, 1:2 w/v and litter/solution ratio 1:5 w/v) with a pH meter equipped with a glass electrode (Corning). To obtain the total nutrients for the soil samples, total carbon (TC) was determined with a total carbon analyzer UIC model CM5012 (Chicago, USA), by combustion and coulometric detection (Huffman 1977). Total nitrogen (TN) and total phosphorus (TP) were analyzed by colorimetry and were determined following acid digestion in a mixture of concentrated H_2SO_4 and K_2SO_4 plus $CuSO_4$, the latter as a catalyst; N was

determined by a micro-Kjeldahl method ([Bremmer 1996](#)) and P by the molybdate colorimetric method following ascorbic acid reduction ([Murphy & Riley 1962](#)). Finally, to assess available nutrients the available inorganic N (NH_4^+ and NO_3^-) was extracted from 10 g fresh soil subsamples with 2 M KCl, followed by filtration through a Whatman No. 1 paper filter and then determined colorimetrically by the phenol-hypochlorite method ([Robertson *et al.* 1999](#)). The soil sample weight was corrected by moisture content.

Environmental filters. To analyze the influence of environment in the species composition, we defined three groups of environmental variables. The first group included climatic variables, the second group contained relief variables and the third group comprised soil traits. To minimize redundancy among environmental variables, a principal component analysis (PCA) was conducted to recognize the variables with the highest factor loading for each group of variables. Thereafter, Pearson's correlation coefficients were calculated for each group of variables and one variable of highly correlated pairs of variables was eliminated to avoid collinearity in subsequent analysis.

Following this criterion, we selected 15 variables divided into three groups. Group one (G1) six climatic variables were selected: maximum temperature of warmest month (mtwm), minimum temperature of coldest month (mtcm), temperature annual range (tar), precipitation of wettest quarter of the year (pwq), precipitation of coldest quarter (pcq) and UNEP aridity index. Group two (G2) corresponds to the relief variables and comprised elevation, slope steepness and aspect. Group three (G3) was composed by the following soil traits: TC, TN, TP, NO_3^-, soil pH, and soil moisture (Sm). The variable TP was transformed with $log_{10}(x+1)$ due to close to zero values.

Statistical analyses. Cluster analysis.- The importance value index (IVI) for each species was estimated in each plot ([Curtis & Mcintosh 1951](#)). This index is estimated based on the sum of the relative density (*RDi*) with respect to the total density of trees, relative dominance (*RDOi*) (based on basal area) relative to total tree dominance, and relative frequency (*RFi*) relative to total frequency of trees. IVI was calculated as: IVI= (*RDi* + *RFi* + *RDOi*) /3. The cluster analysis based on the IVIs of all the species was used to establish the species assemblages; with the Bray-Curtis index the interspecific dissimilarity was calculated with an average linkage (unweighted pair-groups method using arithmetic averages; UPGMA) as clustering algorithm ([Shen *et al.* 2015](#)). This was done in the PATN program ver. 3.01 ([Belbin 1995](#), [2003](#)).

A canonical correspondence analysis (CCA) was conducted to relate community composition with the environmental variables ([de Bello *et al.* 2012](#), [Shen *et al.*](#)

[2015](#)). We performed 999 permutations to evaluate the significance of the CCA model. The CCA was conducted with "vegan" package v.2.4-0 ([Oksanen *et al.* 2016](#)) in the R software v. 3.5 ([R Core Team 2017](#)).

Diversity analysis. We calculated species richness as the number of species per plot as the response variable and we called this variable "all species". To analyze the role of the different environmental filters by species group, we also calculated species richness per plot for the most dominant genera separately (*Quercus* and *Pinus*). In addition, the genus *Quercus* was divided by sections, *Quercus* s.s (white oaks) and *Lobatae* (red oaks).

To analyze the importance of the environmental filters of the target species groups, we used generalized linear models (GLMs) with a Poisson distribution and a log-link function ([Zuur *et al.* 2009](#)). First, we included all explanatory variables by each group of variables (called "Full model") and then the model selection was based on maximum likelihood by using the sample-corrected Akaike Information Criterion (AICc). The best model was selected when variables were removed in a stepwise procedure from the full model, and the difference between the full model and the best model was more than 2 (ΔAICc > 2) ([Burnham & Anderson 2002](#)). By each response variable, we created at least two models by the environmental group (G1, G2 and G3), the full model and the best model, obtaining a total of 30 models.

Residuals of GLMs were graphically explored to check model assumptions (*i.e.,* distribution of residuals, independence, and homoscedasticity). We assessed spatial autocorrelation in model residuals by using Moran's I, which varies between 1 (positive autocorrelation) and -1 (negative autocorrelation). The expected Moran's I value when spatial autocorrelation is lacking is close to 0 ([Borcard *et al.* 2011](#), [Legendre & Legendre 2012](#)). Lastly, to determine the predictive power for each best model, we calculated a Pseudo R^2 with the following formula ([Dobson 2002](#), [Zuur *et al.* 2009](#)):

$$(null\ deviance - residual\ deviance)\ /\ null\ deviance.$$

The GLM was calculated with the "stats" package v. 3.4.3 ([R Core Team 2017](#)), the AICc was calculated with the "'AICcmodavg' package v. 2.2-2 ([Mazerolle 2019](#)) and spatial statistics were performed with the "spdep" package ver. 0.7-7 ([Bivand & Wong 2018](#)) in the R software v. 3.5 ([R Core Team 2017](#)).

Results

Cluster analysis and IVI. A total of 63 tree species corresponding to 31 genera and 21 families were recorded, of which Fagaceae and Pinaceae together represented 50 % of all species, with 22 (*Quercus*) and 10 species,

respectively (nine species of *Pinus* and one of *Abies*). IVIs indicated that these two families represent 74.7 % of the tree community, with the genus *Pinus* being the most important, accounting for 40.7 %, while the genus *Quercus* represented 34 %. The remaining 25.3 % was contributed by trees belonging to the Ericaceae, Clethraceae, Fabaceae, Betulaceae and Theaceae families.

Cluster analysis allowed us to define eight groups, which we defined as species assemblages and later we classified according to their IVI and floristic composition into three forest types (*i.e.,* oak, pine-oak and montane-cloud forests) at a Bray-Curtis similarity of 0.85 (Figure 2). The oak forest corresponded to two groups (Groups 1 and 2), while the pine-oak forest corresponded to four groups (Groups 3, 4, 5 and 6), and the cloud forest was represented by two groups (Groups 7 and 8) (Table 1).

In the oak forest, we found nine oak species that had IVIs values ranging between 7 and 51 % and three species of *Pinus*. The dominant species were *Quercus elliptica, Q. iltisii, Q. liebmannii, and Q. magnoliifolia*. The other species that contributed substantially were *Pinus oocarpa* (8-21 %) and *P. jaliscana* (20 %). In the pine-oak forest, we found seven species of *Pinus* sharing their habitat with 14 species of *Quercus*. The most important *Pinus* species were *Pinus douglasiana*, *P. jaliscana* and *P. oocarpa*, with IVIs values ranging between 6 and 49 %, while the highest

IVIs among oak species were *Quercus cualensis*, *Q. mexiae*, *Q. crassifolia*, *Q. scytophylla*, *Q. jonesii* and *Q. magnoliifolia*, ranging between 8 and 34 %. In the montane cloud forest, we found four species of *Pinus* that presented IVIs values ranging between 6 and 21 % sharing their habitat with *Abies jaliscana*, a species that contributed significantly to forest structure according to its IVI values (12-47 %). The oak species had IVI values ranging between 6 and 17 % with *Quercus nixoniana* (17%) as the most important species, and species of the genera *Cornus*, *Carpinus*, *Magnolia*, *Myrsine* and *Nectandra* contributed with the remaining IVI values ranging between 5 and 16 % (Table 1).

Species richness and elevation. The highest species richness was found in the1,800 to 2,200 m range, where we recorded 38 species (60 % of the total recorded species; Figure 3).

The elevational pattern for tree species richness showed a hump-shaped pattern, with a reduction at 1,600 m, and a drastic increase up to 2,200 m, at which point it decreases again until reaching the highest elevation. Elevational patterns for *Pinus* and *Quercus* also showed hump-shaped patterns. We recorded nine pine species, most of them in the 2,000 to 2,400 m range; the pines showed a gradual increase of species until reach 2,400 m; however, at the plot level the
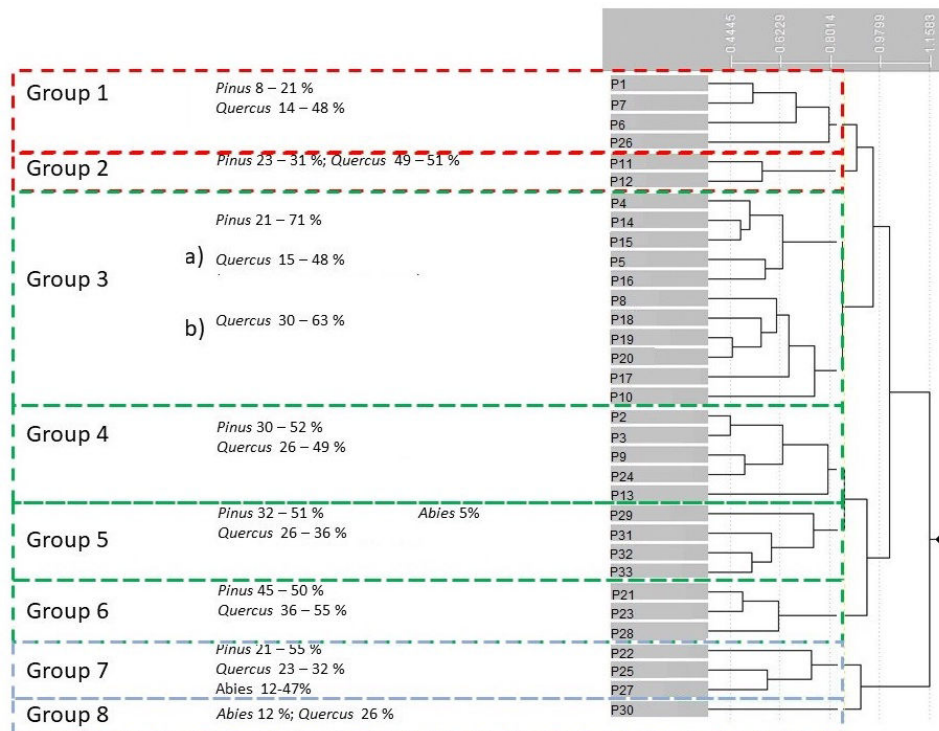

Figure 2. Dendrogram produced by the classification of vegetation samples based on the Bray-Curtis index. The genera along with the ranges of their importance value are shown. Groups 1 and 2 comprise the oak forests (red). Groups 3, 4, 5 and 6 comprise the pine-oak forests (green). Groups 7 and 8 comprise the cloud forests (blue).

Table 1. Species assemblages classified into three forest types according to their importance value index (IVI) (%) and floristic composition after a cluster analysis. Endemic species indicated by an asterisk (*).

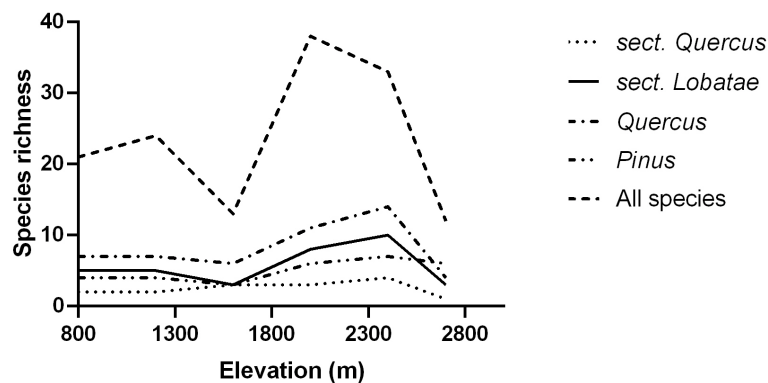| Forest type	Elevation range (m)	Group	*Pinus* species (IVI %)	*Quercus* species (IVI %)	Other species (IVI %)
Oak forest	850 - 1208	1	*P. devoniana* (10) *P. oocarpa* (8 - 21)	*Q. aristata* (14) *Q. elliptica* (14-21) *Q. glaucescens* (7) *Q. liebmannii* (32) *Q. magnoliifolia* (16-51)	*Bejaria mexicana* (5-10) *Byrsonima crassifolia* (6-8) *Clethra sp.* (8-9) *Conostegia xalapensis* (5-14) *Lysiloma acapulcense* (13) *Ternstroemia lineata* (10)
		2	*P. jaliscana* * (20) *P. oocarpa* (10-12)	*Q. iltisii* * (15-34) *Q. mexiae* * (8) *Q. resinosa* (14-17)	*Conostegia xalapensis* (10) *Clethra sp.* (8-9) *Ficus petiolaris* (9)
Pine-Oak forest	892 - 2439	3	*P. douglasiana* (6-14) *P. jaliscana* (11-38) *P. oocarpa* (9-29)	*Q. castanea* (11-15) *Q. cualensis* * (5-31) *Q. eduardii* (10-11) *Q. elliptica* (10-21) *Q. jonesii* (12) *Q. laeta* (8-18) *Q. magnoliifolia* (12-34) *Q. mexiae* (11-15) *Q. obtusata* (10) *Q. tuitensis* * (15-20)	*Acacia macracantha* (10) *Arbutus xalapensis* (6-9) *Bejaria mexicana* (5-20) *Clethra rosei* (6-10) *Juniperus jaliscana* * (5-6)
		4	*P. douglasiana* (15-20) *P. oocarpa* (14-32) *P. devoniana* (12-17)	*Q. castanea* (14-16) *Q. jonesii* (12-17) *Q. mexiae* (25-45) *Q. crassifolia* (33) *Q. resinosa* (30) *Q. scytophylla* (10)	*Acacia macracantha* (25) *Arbutus xalapensis* (11) *Baccharis conferta* (8) *Clethra rosei* (8-9) *Conostegia xalapensis* (16-18) *Gaultheria angustifolia* (8)
		5	*P. douglasiana* (9-12) *P. herrerae* (10-12) *P. oocarpa* (14-20) *P. devoniana* (12-15) *P. pseudostrobus* (20)	*Q. calophylla* (5-10) *Q. castanea* (9-10) *Q. mexiae* (5-10) *Q. elliptica* (11) *Q. obtusata* (7-17) *Q. scytophylla* (6-15)	*Abies jaliscana* (5-6) *Arbutus xalapensis* (5-8) *Clethra rosei* (5-9) *Myrsine juergensenii* (5) *Prunus sp.* (5-7) *Ternstroemia dentisepala* (5-6)
		6	*P. douglasiana* (11-49) *P. herrerae* (22-29) *P. lumholtzii* (11-20)	*Q. jonesii* (20-25) *Q. crassifolia* (19) *Q. obtusata* (8-9) *Q. scytophylla* (18-35)	*Arbutus xalapensis* (7-8) *Cleyera integrifolia* (15-16)
Cloud forest	2155 - 2507	7 and 8	*P. ayacahuite* (14-21) *P. maximinoi* (22) *P. pseudostrobus* (11-22) *P. douglasiana* (6-10)	*Q. crassifolia* (6) *Q. laurina* (10-16) *Q. martinezii* (16) *Q. nixoniana* (17) *Q. obtusata* (7) *Q. scytophylla* (7-17) *Q. uxoris* (8)	*Abies jaliscana* (12-47) *Alnus acuminata* (5) *Arbutus xalapensis* (10-11) *Carpinus tropicalis* (9) *Cornus disciflora* (14) *Magnolia pacifica* (5) *Myrsine juergensenii* (15) *Nectandra salicifolia* (16) *Ostrya virginiana* (16)

Figure 3. Elevational pattern of species richness for all species together, for the genera *Quercus* and *Pinus*, and for the sections *Quercus* s.s. and *Lobatae* of the genus *Quercus*.

largest pines species richness (four species) was located at 2,300 m. For oaks we recorded 22 species (seven and 15 species for sections *Quercus s.s.* and *Lobatae*, respectively); this genus showed a gradual increase up to an elevation of 2,400 m and then a decrease to a minimum of four species at the highest elevations. At the plot level, the highest oak species richness (four species) was recorded at 1,900 m (one and three species for sections *Quercus s.s.* and *Lobatae*, respectively). At the section level, the section *Quercus s.s.* showed a slight increase at 1,600 m and remained stable up to 2,400 m, beyond which elevation it showed a decrease in species richness; conversely sect. *Lobatae* showed a gradual increase in species richness with a small reduction at 1,600 m and, with a subsequent drastic increase until reaching 2,400 m and then a subsequent decrease. Tree species belonging to the families Lauraceae, Betulaceae and Theaceae were restricted to the cloud forest, thus displaying a very restricted elevational distribution in the area. However, the tree species that belong to the Ericaceae (five species), Fabaceae, Theaceae (three species each) and Clethraceae (two species) showed low values of species richness, but a wider distribution along the elevational gradient.

Effect of the environment on species distributions. The results of the canonical correspondence analysis (CCA) showed that aridity index, the maximum temperature of the warmest month, the available inorganic nitrogen and total carbon were the most important variables, indicating that the species' distributions were mainly related to a gradient of soil nutrient content and water availability (Figure 4). The first two axes of the CCA explained 0.52 of total variation (CCA1 = 0.29, *P* < 0.001; CCA2 = 0.23, *P* < 0.001). The first axis showed a soil nutrient gradient and the second axis a water availability gradient.

Individual GLMs were constructed for each group of species richness with each group of environmental variables

(G1= climatic variables; G2 = relief factors; G3 = soil characteristics) and we reported the results of the best model obtained (Table 2; Appendix 2). Spatial autocorrelation in model residuals (Moran's I) ranged from -0.11 to 0.11. For total richness (*i.e.*, all species together), the soil variables explained 26 % of the variation, among which pH and soil moisture (Sm) were the most important variables; in contrast, climatic variables only explained 18 % of the variation where precipitation of the wettest quarter and the aridity index were the most important ones (Table 2). For *Pinus* richness, climatic variables explained 50 % of the variation, with minimum temperature of the coldest month being the most important predictors, while soil and relief variables explained 33 % and 33 % of the variation, respectively. For the *Quercus* genus, soil variables explained 18 % of the variation, among which soil moisture was the variable with the most significant contribution, while climatic variables explained 15 %. For the section *Quercus* s.s., the soil variables explained 16 % of the variation of the species richness, where total nitrogen was the most important variable, while both climatic and relief variables explained a minute proportion of total variance (6 % each). In turn, the climatic variables explained 28 % of the variation the species richness of the *Lobatae* section, where precipitation of the wettest quarter was the most important variable (Table 2).

Discussion

The temperate forests in Mexico are distributed along the mountain ranges and are characterized by a high biological diversity under a large environmental heterogeneity expressed at different spatial scales (Challenger & Caballero 1998, Rzedowski 2006). The high species richness in the Serranias Meridionales of Jalisco is mainly represented by the genera *Pinus* and *Quercus*, which together account for 49 % of total species richness and 74 %
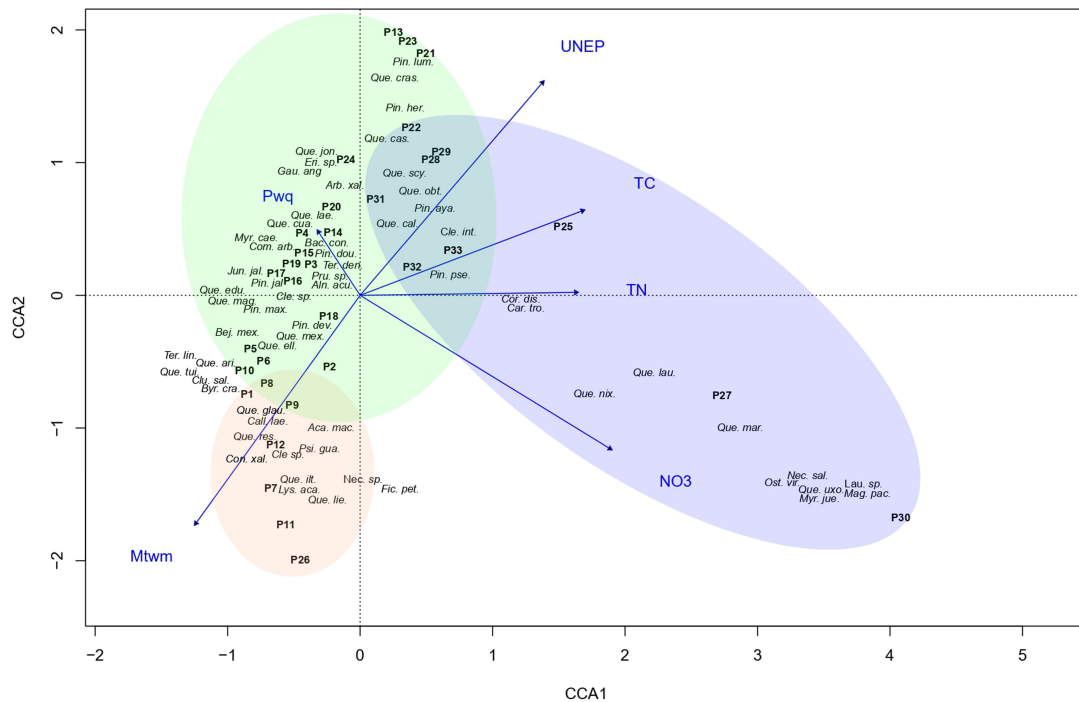
Figure 4. Sample ordination produced by the canonical correspondence analysis. The colored ellipses represent the three main forest groups detected in the cluster analysis encompassing the sampling plots (P1 to P33); red, oak forest; green, pine-oak forest; blue, cloud forest. UNEP, UNEP aridity index; Mtwm, Maximum temperature of warmest month; Pwq, Precipitation of wettest quarter; NO3, Nitrate; TC, Total Carbon and TN, Total Nitrogen. Abbreviations of the species use the first three letters of the genus and the first three letters of the species name. *Abies jaliscana, Abi jal*; *Acacia macracantha, Aca mac*; *Arbutus xalapensis, Arb xal*; *Baccharis conferta, Bac con*; *Bejaria mexicana, Bej mex*; *Alnus acuminata, Aln acu*; *Byrsonima crassifolia, Byr cra*; *Calliandra laevis, Cal lae*; *Carpinus tropicalis, Car tro*; *Ostrya virginiana, Ost vir*; *Clethra rosei, Cle ros*; *C. hartwegii, Cle har*; *Cleyera integrifolia, Cle int*; *Clusia salvinii, Clu sal*; *Comarostaphylis arbutoides, Com arb*; *Conostegia xalapensis, Con xal*; *Cornus disciflora, Cor dis*; *Juniperus jaliscana, Jun jal*; Ericaceae sp., Eri sp.; *Ficus petiolaris, Fic pet*; *Gaultheria angustifolia, Gau ang*; Lauraceae sp., Lau sp.; *Lysiloma acapulcense, Lys aca*; *Magnolia pacifica, Mag pac*; *Myrica cerifera, Myr cer*; *Myrsine juergensenii, Myr jue*; *Nectandra salicifolia, Nec sal*; *Nectandra* sp., *Nec* sp.; *Pinus ayacahuite, Pin aya*; *P. devoniana, Pin dev*; *P. douglasiana, Pin dou*; *P. herrerae, Pin her*; *P. jaliscana, Pin jal*; *P. lumholtzii, Pin lum*; *P. oocarpa, Pin ooc*; *P. pseudostrobus, Pin pse*; *P. maximinoi, Pin max*; *Prunus* sp., *Pru* sp.; *Psidium guajava, Psi gua*; *Quercus aristata, Que ari*; *Q. calophylla, Que cal*; *Q. castanea, Que cas*; *Q. jonesii, Que jon*; *Q. mexiae, Que mex*; *Q. crassifolia, Que cra*; *Q. cualensis, Que cua*; *Q. eduardii, Que edu*; *Q. elliptica, Que ell*; *Q. glaucescens, Que gla*; *Q. iltisii, Que ilt*; *Q. laeta, Que lae*; *Q. laurina, Que lau*; *Q. liebmannii, Que lie*; *Q. magnoliifolia, Que mag*; *Q. martinezii, Que mar*; *Q. nixoniana, Que nix*; *Q. obtusata, Que obt*; *Q. resinosa, Que res*; *Q. scytophylla, Que scy*; *Q. tuitensis, Que tui*; *Q.* aff. *uxoris, Que uxo*; *Ternstroemia lineata, Ter lin*; *T. dentisepala, Ter den*.

of the IVI in the study region. The remaining species richness is distributed among the families Ericaceae, Clethraceae, Fabaceae, Betulaceae, Theaceae and Magnoliaceae, showing that the Serranías Meridionales of Jalisco hosts a high phylogenetic richness.

The cluster analysis identified eight groups, with a clear dominance of several *Pinus* and *Quercus* species, that we classify according to their IVI and floristic composition into three forest types (*i.e.,* oak, pine-oak and montane-cloud forests) occurring along two main environmental gradients (nutrient soil conditions [NO$_3^-$], and water availability, as

measured by the UNEP aridity index). The oak forest showed a floristic composition dominated by deciduous oaks, with the presence of drought tolerant species or xeric affinity registered in other oak forest (Aguilar-Romero *et al.* 2016, de la Riva *et al.* 2019). The pine-oak forest showed a floristic composition dominated by a high diversity of red oaks and pines, with the presence of several temperate species typical of Mexican temperate forest (Challenger & Caballero 1998, Rzedowski 2006). The montane-cloud forest hosts several tropical and temperate tree species, which has been suggested that the area could be a Tertiary

Table 2. Results of the individual GLM for each group of variables. Model selection (best model) was based on the best-supported models according to maximum likelihood (smallest AICc) and (ΔAICc > 2). Variables in bold font are those that show statistical significance ($P < 0.05$). Mtwm, Maximum temperature of warmest month; Mtcm, Minimum temperature of coldest month; Pwq, Precipitation of wettest quarter of the year; Tar, Temperature annual range; Pcq, Precipitation of coldest quarter; UNEP, aridity index; Elev, Elevation; Slp, slope steepness; Asp, aspect; TC, Total Carbon; TN, Total Nitrogen; TP, Total Phosphorus; NO_3^-, Nitrate; pHs, soil pH and Sm, soil moisture.

Group of variables		Full model	Best model		
		AICc	AICc	ΔAICc	*Pseudo R²*
Climatic	**Full model** (Mtwm, Mtcm, Pwq, Tar, Pcq, UNEP)				
	Best model				
	All species	**Pwq, UNEP**	175.1	173	2.1	0.18
	Pinus	**Mtcm**	110.5	97.89	12.61	0.50
	Quercus	Pwq, Pcq, UNEP	116.4	112.3	4.1	0.15
	Lobatae	**Pwq**, Pcq, UNEP	95.97	91.06	4.91	0.28
	Quercus s.s.	Mtcm, Tar, Pcq	76.93	66.71	10.22	0.06
Relief	**Full model** (Asp, Elev, Slp)				
	Best model				
	All species	Asp, Elev, Slp	175.85	-	-	0.06
	Pinus	**Elev**	103.06	98.47	4.59	0.33
	Quercus	Asp, Elev, Slp	112.76	-	-	0.12
	Lobatae	Asp	92.24	88.31	3.93	0.08
	Quercus s.s.	Asp, Slp	66.71	63.97	2.74	0.06
Soil	**Full model** (TC, TN, TP, NO3-, pHs, Sm)				
	Best model				
	All species	**pHs, Sm**	174.95	165.08	9.87	0.26
	Pinus	**TC, NO3-**	112.9	100.86	12.04	0.33
	Quercus	TC, pHs, **Sm**	120.89	112.24	8.65	0.18
	Lobatae	TC, pHs	102.96	90.96	12	0.06
	Quercus s.s.	**TN**	77.01	61.4	15.61	0.16

refuge being the most important forest in terms of richness and floristic composition for western Mexico (Vargas-Rodríguez *et al.* 2010, 2015).

The eight species assemblages included red and white oaks, which could indicate a phylogenetic overdispersion, which has been suggested as an explanation for how high oak diversity is maintained at the community level (Cavender-Bares *et al.* 2004). Oaks and pines have a temperate Nearctic origin and had a subsequent diversification in Mexico in montane regions, with 161 and 49 species, respectively (Valencia-Á. 2004, Gernandt & Pérez de la Rosa 2014, Hipp *et al.* 2018). The high diversity and high IVI values of both genera suggest that they play an important role in the ecosystem function in these temperate forest; however, more studies at the functional level are needed to understand the role of both genera in the ecosystem functioning (de la Riva *et al.* 2019).

The Serranías Meridionales of Jalisco is a biodiversity hotspot with a high number of species including several endemic species of *Quercus* and *Pinus*, among others. This could be one of the regions with the highest oak species richness in the world with 22 species recorded. However, various floristic studies and new descriptions in the region could increase this number to 30 oak species (Morales-Saldaña 2017, González-Villarreal 2018), indicating that this region hosts 14 % of the species richness at country level (161 species), 49 % of state species richness (> 45 species). Comparing with other regional studies in Mexico, Ramírez-Toro *et al.* (2017) found that in the state of Oaxaca (the richest state in oak species with 52 species),

the physiographic provinces of the Sierra Madre de Oaxaca and Montañas y Valles del Occidente could be the richest regions in oak species in the country, with 38 and 29 species, respectively. Furthermore, compared to the species richness with other countries, the Serranías Meridionales of Jalisco has three times as many oak species as there are in Canada (10 species), and nearly the same as Central America (34) (Nixon 2006), India (35) (Negi & Naithani 1995) or Europe (30) (Xu *et al.* 2019).

Elevational patterns. We expected species richness to decrease towards higher elevations, but we found that the tree species richness presented a hump-shaped pattern in the Serranías Meridionales of Jalisco. Several studies of species richness in plants have revealed 'hump-shaped' patterns along elevational gradients such as ferns (Kluge *et al.* 2006, Kessler *et al.* 2011), epiphytes (Krömer *et al.* 2005), oaks (Morales-Saldaña 2017) and vascular plants (Kessler 2000), which seems to be the most frequent, but not the only one. The potential causes underlying the hump-shaped pattern of species richness have been discussed extensively, and it has been observed that the relationship between species richness and elevation varies greatly with the scale of the extent and if the full elevational gradient was surveyed or when the lower or upper limits were omitted (Nogués-Bravo *et al.* 2008).

It is important to recognize that our study encompassed a partial elevation range from 800 to 2,600 m, which imposes a limit to our interpretations for the full gradient.

The hump-shaped pattern in the Serranías Meridionales of Jalisco may be a consequence of the overlap of species of tropical and temperate affinities, reflecting their ecological characteristics, due to the local adaptation in mountainous areas as tolerance to cold temperatures and functional strategies to avoid water stress (Cavender-Bares & Holbrook 2001, Koehler *et al.* 2012).

The *Quercus* and *Pinus* species as dominant at mid-elevations has been explained by their ability to disperse and had undergone extensive adaptative radiation and the capacity to partitioning resources effectively (Hernández-López 1995, Vázquez-García & Givnish 1998). In addition, an important contribution to the total species richness at mid-elevations was the presence of typical cloud forest elements like *Magnolia pacifica*, *Alnus acuminata* and several Lauraceae species, among others. Conversely, we observed a decrease in the species richness at 1,600 m dominated by white oaks as *Quercus magnoliifolia* and *Q. resinosa*, both of which are characteristic of drier areas.

Other studies on species richness along elevational gradients in Mexico have reported a decreasing pattern of vascular plants (Vázquez-García & Givnish 1998, Salas-Morales & Meave 2012) or a hump-shaped pattern (Sánchez-González & López-Mata, 2005). Some of the

discrepancies in assessing spatial richness patterns between different studies could be sampling effort (*i.e.,* plot size and number), selection of growth forms (*i.e.,* trees, shrubs, herbs and epiphytes) and partial or total analysis across the elevational gradient (Lomolino 2001, Nogués-Bravo *et al.* 2008, McCain & Grytnes 2010). In our study, the collecting effort was homogeneous, but we analyzed a partial elevational gradient, so it would be important to perform the complete elevation gradient and see if the same elevation pattern is maintained.

Ecological filtering in Serranías Meridionales of Jalisco. In plant communities, it has been suggested that species with similar distributions respond similarly to environmental filters across ecological gradients (Ferrer-Castán & Vetaas 2003). In this context, mountain regions are good models to assess whether taxa respond differently to environmental filters (Jiménez-Alfaro *et al.* 2014). Plant species distribution over elevational gradients can be affected in diverse ways by climate, relief (*i.e.,* slope aspect and inclination) or soil characteristics (*i.e.,* soil water retention and heterogeneous distribution of fertility) (Pickering & Green 2009, Scherrer & Körner 2011, Jiménez-Alfaro *et al.* 2014, Estrada-Castillón *et al.* 2015). In our study, the soil and climatic variables explained the most of the variance in the different groups of species analyzed. When we analyzed the species richness for all species together, the soil variables, including pH and soil moisture, contributed with the most variance explained by the model (26 %), followed by the climatic variables (18 %). In general, climatic variables are the main factors that determine large scale patterns of species richness (Francis & Currie 2003, Götzenberger *et al.* 2011, de Bello *et al.* 2012).

In the lowland Neotropics, species richness of woody plants increases with the increment of annual precipitation and the decrease of the dry season length (Gentry 1988, Currie 1991, Clinebell *et al.* 1995, Francis & Currie 2003). However, studies at regional scale in temperate species showed that soil variables were more important than climatic variables (Diekmann *et al.* 2015, Walthert & Meier 2017). At local scales, soil traits like soil pH are key drivers of plant species richness (Pärtel 2002, Dubuis *et al.* 2013, Rao *et al.* 2018). In fact, our results indicate that soil moisture and soil pH could be important factors influencing species richness patterns at regional scale. Several studies at local scales (mostly in tropical forest) have reported that plant species richness and density increase with soil fertility (Grime 1979, Pausas & Austin 2001), although the generality of this conclusion has been questioned (Tuomisto *et al.* 2014).

The high species richness of the genus *Pinus* in Mexico is explained by the existence of two diversification centers, one of them located in the Trans-Mexican Volcanic Belt,

and the second in north-eastern Mexico (Farjon & Styles 1997), along with migration processes that resulted in regions with high endemism and species richness. Therefore, Mexico is considered a secondary center of diversification and richness for this genus, with 49 (40 %) of the approximately 120 species in the world (Gernandt & Pérez de la Rosa 2014).

The variable group that mostly contributed to *Pinus* richness was the climatic (50 %), followed by soil (33 %) and relief (33 %) variables. Also, the importance of temperature and precipitation, and more particularly of its seasonality, were the primary factors determining the vegetation types and functional responses, due to thermal conditions in the growing season (Tang & Fang 2006, Zhou *et al*. 2016). Seasonal patterns in temperature and precipitation influence seed germination, seedling growth, productivity, phenology and litterfall production, all of which has an impact on the survival and establishment of plants in mountainous areas (Tang & Fang, 2006, Salamon-Albert *et al*. 2017).

The genus *Quercus* occurs across gradients of fertility, fire regimen and soil moisture (Cavender-Bares *et al*. 2004). Soil moisture was an important contributor in our analysis (18 %) in relation to species richness in this genus, followed by climatic variables related to precipitation (15 %). In Northern Florida, the soil moisture gradient was shown to explain part of the variation of the hydraulic properties of the species, which in turn are correlated with the distribution of individual species and their success in their respective habitats (Cavender-Bares & Holbrook 2001, Cavender-Bares *et al*. 2004), thus reflecting the great ability of oaks to adapt to different climatic and moisture gradients and promoting their occurrence in diverse habitats and climates that range from dry to temperate and subtropical forests (Valencia-Á. 2004, Hipp *et al*. 2018). The high species richness and high endemism of Mexican oaks have been highlighted by Manos *et al*. (1999), Nixon (1993), Valencia-Á. (2004), Torres-Miranda *et al*. (2011, 2013) and Rodríguez-Correa *et al*. (2015). This extraordinary diversification has been explained as a result of their ability to establish along moisture gradients in mountainous areas as the Mexican Transition Zone (Nixon 1993, Morales-Saldaña 2017, Hipp *et al*. 2018).

When dissecting the genus *Quercus* into its two sections, we found several differences. In the case of section *Lobatae*, the climatic variables contribute with the largest variance explained by the model (28 %), followed by the soil variables (6 %) for species richness. The results showed an increase in richness in those areas with higher precipitation within the warmest quarter of the year, which are not necessarily the areas receiving the highest annual rainfall. Particularly, seasonal water availability through precipitation has an impact on variables such as soil moisture (Concilio *et al*. 2009, Salamon-Albert *et al*. 2017). Several studies on the distribution of oak species conducted at regional scales have suggested that species of section *Quercus s.s*. are more resistant to drought than section *Lobatae* (Abrams 1990, 2003, Nixon 1993, Aranda *et al*. 2014). However, through a study conducted across an aridity gradient in central Mexico, Aguilar-Romero *et al*. (2017) did not support this idea because they found that physiological components of the water-use strategy did not differ between oak sections, although they suggest a higher resistance to water stress in red than in white oaks.

Quercus s.s. species richness was primarily affected by soil traits such as total nitrogen soil content (16 %). This could be due to the ability of some white oaks to improve soil conditions; for example, Chávez-Vergara *et al*. (2015) found that *Q. deserticola* (sect. *Quercus s.s.*) produced more nutrient-rich litter with higher nitrogen concentration, thus enhancing microbial activity in the forest litter and soil fertility to the benefit of other coexisting species like *Q. castanea* (sect. *Lobatae*).

In this study, soil and climatic variables explained most of the variance in tree species richness of the different species groups analyzed. Temperature and precipitation across the elevational gradient affect numerous soil processes and properties; however, plant species also affect soil properties such as nutrient status, mainly by species-specific litter input having a deterministic impact on the survival and establishment of species assemblages (Walthert & Meier 2017, Salamon-Albert *et al*. 2017). In the Serranías Meridionales of Jalisco, seasonal patterns in temperature and precipitation, the length of the nutrient gradient, the influence of pH on nutrient availability, and the correlation with soil moisture may all influence the shape of the response of species richness. The variation was not fully explained by the environmental filters examined, which suggests that other factors, such as interactions among species, might also be influencing their distribution.

Implications for conservation. In Mexico deforestation rates are high; during the last decade, the Food and Agriculture Organization (FAO) classified Mexico in the seventh place in the world with the yearly average surface deforested reaching almost one million hectares (Eguiluz-Piedra 2003, Rosete-Vergés *et al*. 2014). This alarming rate of forest cover loss urgently requires strong efforts to protect areas that feature high species richness and endemism, such as the Serranías Meridionales of Jalisco. Implementing a general protection and conservation program is needed to preserve not only species richness and endemism but all ecological processes that occur at different spatial scales. While conducting fieldwork for this study, we witnessed illegal tree cutting and forest clearing in this important biodiversity hotspot. The corruption of authorities is the main obstacle to preserve and protect the biodiversity in Mexico.

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Appendix 1. Potential evapotranspiration and aridity index calculations

Potential evapotranspiration was calculated with Hargreaves and Samani (1985)'s method, based on the following equation:

$$Evap\ eq = Rs*1/\lambda$$

ETo = potential evapotranspiration by mm/day

C_i = constant 0.0023

T_{med} = average temperature in °C

T_{max} = maximum temperature in °C

T_{min} = minimum temperature in °C

Evap eq = equivalent evaporation in mm/day

R*s* = Solar extraterrestrial radiation based on latitude and longitude in M Jules/m²/day (NASA 2016).

$1/\lambda$ = inverse of the latent heat of vaporization (0.408) (Allen et al. 2006).

The aridity index proposed by the United Nations for the Environment (UNEP) expresses the relationship between average annual precipitation (Pa) and potential evapotranspiration (Evpot) in a given area (Middleton & Thomas 1997), which was calculated as: I = *Pa*/*Evpot*.

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Appendix 2. Estimates of the coefficients of the best models of generalized linear models (GLM).

Climatic variables

Mtcm, Minimum temperature of the coldest month; Pwq, Precipitation of the wettest quarter of the year; Tar, Temperature annual range; Pcq, Precipitation of the coldest quarter; UNEP, aridity index.

Richness		Estimate	Std. Error	Z value	Pr(>|z|)	AICc
All species	Intercept	5.514	7.049	0.782	0.043	173
	Pwq	-0.124	0.450	-0.277	0.041	
	UNEP	-0.494	1.034	-0.478	0.014	
Pinus	Intercept	2.398	0.914	2.624	0.008	97.89
	Mtcm	-0.060	0.033	-1.776	0.043	
Quercus	Intercept	5.581	38.791	0.144	0.886	112.3
	Pcq	0.057	2.937	0.02	0.978	
	Pwq	-0.701	4.013	-0.175	0.899	
	UNEP	0.123	4.897	0.025	0.978	
Lobatae	Intercept	-2.974	49.392	-0.06	0.085	91.06
	Pwq	-0.048	5.088	-1.723	0.013	
	Pcq	0.957	3.766	0.254	0.566	
	UNEP	-1.308	6.300	-0.208	0.103	
Quercus s.s.	Intercept	-12.934	41.165	-0.314	0.753	66.71
	Mtcm	1.223	3.038	0.403	0.786	
	Tar	1.662	6.179	0.269	0.82	
	Pcq	-0.090	1.1280	-0.08	0.982	

Relief variables

Elev, Elevation; Slp, slope steepness; Asp, aspect.

Richness		Estimate	Std. Error	Z value	Pr(>|z|)	AICc
All species	Intercept	2.267	0.23	9.857	2e-16	175.85
	Elev	-9.37e-05	1.16e-04	-0.803	0.442	
	Asp	5.09e-04	5.39e-04	0.943	0.232	
	Slo	-4.77e-08	4.10e-08	-1.163	0.254	
Pinus	Intercept	-4.704	2.820	-1.668	0.095	98.47
	Elev	0.736	0.377	1.952	0.040	
Quercus	Intercept	1.676	3.305	0.507	0.061	112.76
	Elev	-0.050	0.305	-0.165	0.679	
	Asp	0.114	0.095	1.200	0.297	
	Slope	-0.057	0.185	-0.308	0.448	
Lobatae	Intercept	0.293	0.901	1.326	0.074	88.31
	aspect	0.074	0.172	1.430	0.034	
Quercus s.s.	Intercept	1.295	4.065	0.319	0.750	63.97
	aspect	0.034	0.123	0.282	0.911	
	slope	-0.076	0.280	-0.274	0.843	

Soil variables

TC, Total Carbon; TN, Total Nitrogen; TP, Total Phosphorus; NO$_3$ $^-$, Nitrate; pHs, soil pH and Sm, soil moisture.

Richness		Estimate	Std. Error	Z value	Pr(>|z|)	AICc
All species	Intercept	5.9612	1.2768	4.669	3.03e-06	165.08
	pHs	-1.7930	0.7099	-2.526	0.0115	
	Sm	-0.2567	0.1191	-2.155	0.0302	
Pinus	Intercept	1.95394	0.64651	3.022	0.00251	100.86
	TC	0.31876	0.18017	1.769	0.08786	
	NO3-	-0.05410	0.03758	-1.440	0.08497	
Quercus	Intercept	3.59608	1.3537	2.656	0.0079	112.24
	TC	2.35352	4.83049	0.487	0.4611	
	pHs	-0.3875	0.2454	-1.579	0.3734	
	Sm	-0.01878	0.01055	-1.780	0.0160	
Lobatae	Intercept	2.0486	1.6561	1.237	0.216	90.96
	TC	2.3309	5.5546	0.420	0.401	
	pHs	-0.2635	0.3161	-0.834	0.509	
Quercus s.s.	Intercept	0.5524	0.2636	2.096	0.0361	61.4
	TN	-307.5232	186.9178	-1.645	0.0999	