SPECIES DISTRIBUTION OF *QUERCUS* (FAGACEAE) ALONG AN ALTITUDE GRADIENT, REVEALS ZONATION IN A HOTSPOT

DISTRIBUCIÓN DE ESPECIES DE *QUERCUS* (FAGACEAE) A LO LARGO DE UN GRADIENTE ALTITUDINAL, REVELA UNA ZONIFICACIÓN EN UN HOTSPOT

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Abstract

Background: The genus *Quercus* has a keystone role in the temperate forests in the northern hemisphere; thus this offers an interesting opportunity to use it as a model to know altitudinal species richness patterns which could be used in further studies and projects in biodiversity conservation.

Questions: It is possible to detect an altitudinal gradient based on the genus *Quercus* distribution? What climatic variables are most important in the altitudinal distribution of the genus *Quercus*?

Study site: The physiographic province of Sierra Madre del Sur (SMS) located southwest of Mexico.

Methods: Based on 3,267 herbarium registers of 61 species, a data matrix was created with the presence/absence of each species in altitudinal intervals of 100 m. Then a similarity matrix was obtained using the Sorensen-Dice index in the R software. Through a discriminant analysis, we evaluated for environmental differences among the altitudinal zones previously obtained through a cluster analysis.

Results: We found three altitudinal zones, each one defined by exclusive species, and two important species turnover points. The species richness distribution showed a hump-shaped pattern along the altitudinal gradient. The overall model was highly significant, evidencing the existence of different temperature and precipitation regimes throughout the altitudinal distribution of oak species in SMS.

Conclusions: The altitudinal distribution of oak species in the SMS is not homogeneous and is restricted mainly due to differences in the precipitation and temperature regimes. The altitudinal distribution pattern found in this study could be explained considering ecological and historical factors.

Keywords: Biogeography, climatic variables, Neotropic, oaks, Sierra Madre del Sur.

Resumen

Antecedentes: El género *Quercus* tiene un papel clave en los bosques templados del hemisferio norte, ofreciendo una interesante oportunidad al considerarlo como modelo para conocer patrones de riqueza altitudinal que podrían ser utilizados en futuros estudios y proyectos de conservación de la biodiversidad.

Preguntas: ¿Es posible detectar una zonificación altitudinal con base en la distribución del género *Quercus*? ¿Qué variables climáticas tienen mayor importancia en la distribución altitudinal del género *Quercus*?

Sitio de estudio: Provincia fisiográfica de la Sierra Madre del Sur localizada al suroeste de México

Métodos: Con base en 3,267 registros de herbario de 61 especies, se creó una matriz de presencia/ausencia de cada especie en intervalos altitudinales de 100 m. Luego se obtuvo una matriz de similitud usando el índice de Sorensen-Dice en el software R. Mediante un análisis discriminante evaluamos las diferencias ambientales entre las zonas altitudinales obtenidas previamente mediante un análisis de conglomerados.

Resultados: Encontramos tres niveles altitudinales definidos por especies exclusivas, y dos importantes puntos de reemplazo. La riqueza de especies mostró un patrón en forma de joroba. El modelo general fue altamente significativo, evidenciando la existencia de diferentes regímenes de temperatura y precipitación a lo largo de la distribución altitudinal de las especies de encino en la SMS.

Conclusiones: La distribución altitudinal de las especies de encinos en la SMS no es homogénea y está restringida principalmente por diferencias en el régimen de temperatura y precipitación. El patrón de distribución altitudinal encontrado en este estudio, podría explicarse considerando factores ecológicos e históricos.

Palabras clave: Biogeografía, encinos, Neotrópico, Sierra Madre del Sur, variables climáticas.

Altitude is recognized as one of the factors of major influence in patterns of species richness in montane regions (Olvera-Vargas *et al.* 2010, Acebey *et al.* 2017). The study of the distribution of species along an altitudinal gradient provides information on the possible factors or processes that generate or limit such distributions (Grytnes 2003, Hemp 2006). Stevens (1992) stated that the variation patterns in the number of species along an altitudinal gradient could be considered as an extension of the Rapoport's rule, which recognizes a decrease of species richness as altitude increases. However, several studies report an additional pattern where the richest zone of species can be found in regions of intermediate altitudes (Grytnes & McCain 2007, Grytnes *et al.* 2008, Grytnes & Romdal 2008, Guo 2013, Gao *et al.* 2018). These richness patterns are commonly determined by climate, habitat heterogeneity, edaphic conditions and evolutionary history (Grytnes & Vetaas 2002, Hemp 2006, Löbel *et al.* 2006, McCain & Grytnes 2010, Jiménez-López *et al.* 2020).

Mexico presents one the steepest orography in the world, with more than half of the territory above 1,000 m asl and complex montane systems such as the *Sierra Madre del Sur* (SMS), which is considered as one of the regions of greatest biological diversity and endemism (Vargas *et al.* 1991, 1994, García-Mendoza *et al.* 2004). The SMS has a major role in the diversification of animals (Martínez-Ramírez *et al.* 2016, Navarro-Sigüenza *et al.* 2016), fungi (Villegas *et al.* 2016) and plants (Contreras-Medina 2016, Solano *et al.* 2016, Tejero-Díez *et al.* 2016, Valencia-A. & Morales-Saldaña 2016). The SMS belongs to the Mesoamerican hotspot (Espinosa *et al.* 2016) and constitutes a primary center of species richness for the genus *Quercus* at a global level (Govaerts & Frodin 1998, Nixon 1993, 2006, Valencia-A. 2004). However, it is also one of the most threatened regions due to the habitat loss by anthropogenic activities (Myers *et al.* 2000), which makes the study of its species diversity and distribution most important. The wide environments in which the genus *Quercus* thrives (Nixon 2006, Hipp 2010), their high abundance, diversity and the keystone role it plays in the communities it is found (Aldrich & Cavender-Bares 2011, Valencia-A. & Gual-Díaz 2014), offer an interesting opportunity to use the species richness of this genus as a model in order to identify zonation along altitudinal gradients (Fattorini *et al.* 2019), which could be used with another temperate taxa in the south-southwest region of Mexico.

The aims of this study were, i) to determine the altitudinal distribution patterns of the species richness of the

genus *Quercus* in the SMS, which is one of the primary centers of diversity at a global level and ii) to estimate the climatic differentiation between the altitudinal zones in the SMS. Finally, we discuss the possible factors that determine the pattern of distribution of oaks in the SMS.

Materials and methods

Study area. The physiographic province of SMS is located southwest of Mexico, between 15° 40' - 19° 40' N, and 94° 45' - 104° 40' W. It has an extension of 195,700 km². It comprises the southeast of Jalisco, over 80 % of Colima, the southern region of the State of Mexico, Michoacán, Puebla and almost the complete extension of Guerrero, with the Istmo de Tehuantepec as the geographic limit in Oaxaca. The altitudinal gradient ranges from 0 to 3,710 m asl (Figure 1), (INEGI 2001).

Species richness and altitudinal zoning. Specimens of *Quercus* at National Herbarium (MEXU), the herbaria from Facultad de Ciencias (FCME), Universidad de Guadalajara (IBUG) and Instituto de Ecología A.C. (IEB) were revised and curated to create a database of 3,267 non-duplicated records, which was used to determine the species richness in the SMS and obtain information about the altitudinal distribution of the species diversity. Based on altitudinal data, a series of boxplots were calculated to identify the altitudinal variation patterns of each species and each section. We also evaluated the altitudinal distribution of species richness both by section and jointly. Analyses were conducted in R Core Team (2013).

Using the $Q_1 - Q_3$ interval of the boxplot, a data matrix was created based on the presence/absence of each species in intervals of 100 m. The rows of the matrix represent altitudinal zones and the columns represent species. Zero equals absence and one equals presence of the species in the different altitudinal intervals. Based on this matrix, a similarity matrix was obtained using the Sorensen-Dice index applying the "ade4" package (Dray & Dufour 2007). Afterwards, a cluster analysis was carried out using the Ward method. The resulting dendrogram allowed to recognize the altitudinal zones of the SMS based on the distribution of the oak species diversity. Using these altitudinal zones, we generated a heatmap that reflects the distribution of each species in the different altitudinal zones based on the percentage of records of each species for a given altitudinal zone. To eliminate the potential effects of outliers, we considered that a species belongs to a certain altitudinal zone only if their records in a given

Figure 1. Location map of the study area the Sierra Madre del Sur, Mexico According with [INEGI \(2001\)](#).

altitudinal zone were greater than 25 %, this percentage corresponds to the value obtained from the boxplot analysis. Finally, the altitudinal zoning was mapped using QGIS 3.8.3 ([QGIS Development Team 2019](#)).

Climate differentiation of the altitudinal zones. A total of 19 bioclimatic variables were downloaded for the 3,267 records from the WorldClim database v1.4 ([Fick & Hijmans, 2017](#)) (www.worldclim.org). From these records, a correlation analysis was conducted to eliminate those highly correlated variables. A total of nine bioclimatic variables (Bio2, Bio3, Bio4, Bio5, Bio6, Bio14, Bio15, Bio16 and Bio18) were used to evaluate which climatic variables have greater discriminating power among different altitudinal zones detected through cluster analysis. However, since not all variables discriminate in the same way, a stepwise variable selection was conducted. As a general criterion to select a variable, F value associated with each variable was used, in such a way that if the F value was small, the variable would discriminate little,

while large values of F suggest greater discriminating power. Initially, we selected the variable with the highest F value, subsequently the F value was evaluated for the unselected variables and a new variable with the highest F value was selected. This procedure was repeated until a variable with the highest F value was statistically non-significant. The discriminant analysis was conducted with the software [SAS \(2012\)](#) using a linear discriminant method.

Results

Species richness and altitudinal zoning. A total of 61 species of the genus *Quercus* were registered in the SMS, representing 37.9 % of the total species of the genus reported for Mexico ([Valencia-A. 2004](#)). From these, 36 belong to the section *Lobatae*, 24 to the section *Quercus* and one to the section *Virentes* ([Denk et al. 2017](#)). A total of 45 species are endemic to Mexico and 13 are endemic to the SMS (see [Appendix 1](#)). The altitudinal distribution of total species richness had its highest value (20-28 species) be-

tween 1,500 - 2,000 m with an important second peak of species richness (20 species) at 2,200 m, which coincided with the third peak of species richness detected exclusively for the *Quercus* section (Figure 2). From this altitude, the total species richness decreases constantly until reaching less than five species above to 2,800 m (Figure 2). When species richness was analyzed by section, a similar pattern was observed between section *Lobatae* and section *Quercus*. The section *Lobatae* had the highest species richness values between 2,300 - 2,400 m, while section *Quercus* showed three important peaks of species richness at 1,600, 1,800 and 2,200 m (Figure 2).

We found 18 oak species of the section *Lobatae* with altitudinal ranges > 1,000 m, *Q. acutifolia*, *Q. aristata*, *Q. calophylla*, *Q. castanea*, *Q. konzattii*, *Q. crassifolia*, *Q. elliptica*, *Q. confertifolia*, *Q. grahamii*, *Q. laurina*, *Q. mexiae*, *Q. nixoniana*, *Q. planipocula*, *Q. salicifolia*, *Q. scytophylla*, *Q. trinitatis*, *Q. urbanii* and *Q. uxoris*. In altitudinal ranges < 1,000 m we found *Q. acherdophylla*, *Q. benthamii*, *Q. crassipes*, *Q. crispifolia*, *Q. cualensis*, *Q. depressa*, *Q. eduardi*, *Q. hintonii*, *Q. iltisii*, *Q. jonesii*, *Q. mulleri*, *Q. pinnativenulosa*, *Q. rubramenta*, *Q. sartorii* and *Q. skinneri*. The species of the section *Quercus* with altitudinal range > 1,000 m were *Q. corrugata*, *Q. glabrescens*, *Q. glaucescens*, *Q. glaucoides*, *Q. insignis*, *Q. laeta*, *Q. liebmanii*, *Q. magnoliifolia*, *Q. martinezii*, *Q. microphylla*, *Q. obtusata*, *Q. peduncularis*, *Q. resinosa*, *Q. rugosa*, *Q. segoviensis* and *Q. sororia*. The species of the section *Quercus* with altitudinal ranges < 1,000 m were *Q. centenaria*, *Q. deserticola*, *Q. frutex*, *Q. greggii*, *Q. macdougallii*, *Q. polymorpha*, *Q. sebifera* and *Q. subspathulata*. While *Q. oleoides*, the only species of the section *Virentes* in the SMS, also had an altitudinal range < 1,000 m.

The cluster analysis segregated the SMS in three altitudinal zones (Figure 3A-B). The first altitudinal zone (Altitudinal A zone) corresponds to a level ranging from 500 to the altitudinal band of 1,100 m (orange color). Geographically, this zone comprises the Pacific Coastal Plain and the Balsas river Basin. In this altitudinal zone, we found 14 oak species (Figure 3C), two of them as exclusive to this level, *Q. oleoides* (the only species of the section *Virentes* of the region) and *Q. tuitensis*, and three endemic species to SMS (*Q. iltisii*, *Q. salicifolia* and *Q. tuitensis*). The altitudinal B level (green color) (Figure 3A-B) corresponds to the interval between 1,200 m and the altitudinal band of 2,200 m, the largest species richness of oaks was registered in this level with 47 species, eight of them exclusive for this level (*Q. benthamii*, *Q. eduardi*, *Q. hintonii*, *Q. jonesii*, *Q. mulleri*, *Q. pinnativenulosa*, *Q. sebifera*, *Q.*

skinneri) (Figure 3C) and nine endemic species to SMS (*Q. centenaria*, *Q. cualensis*, *Q. liebmanii*, *Q. martinezii*, *Q. mulleri*, *Q. nixoniana*, *Q. rubramenta*, *Q. salicifolia*, *Q. uxoris*). Likewise, the altitudinal A and B zones showed seven species in common (*Q. acutifolia*, *Q. elliptica*, *Q. confertifolia*, *Q. glabrescens*, *Q. iltisii*, *Q. salicifolia* and *Q. sororia*). The altitudinal C level ranges from 2,300 to > 3,000 m (blue color). Its species richness resulted in 19 species, with four of them exclusive to the level (*Q. acherdophylla*, *Q. crassipes*, *Q. depressa* and *Q. greggii*) and four endemic species to SMS (*Q. macdougallii*, *Q. martinezii*, *Q. nixoniana* and *Q. rubramenta*).

Based on the altitudinal zonation, the oak species richness in the SMS exhibited a maximum of 47 species in the altitudinal B zone showing a unimodal pattern throughout the altitudinal gradient. Therefore, we propose that the SMS has a core altitudinal zone, on an elevation between 1,200 and 2,200 m, which contains the highest amount of species richness and endemic oaks.

Climate differentiation of the altitudinal zones. The results of the discriminant analysis showed that mean diurnal range (Bio2; $P = 0.000$), max temperature of warmest month (Bio5; $P = 0.000$), precipitation of wettest quarter (Bio16; $P = 0.0036$) and precipitation of warmest quarter (Bio18; $P = 0.000$) are the most important variables to discriminate among the three altitudinal zones (Figure 4). The overall model was highly significant (Wilks = 0.68; $P = 0.0001$) and showed a moderate percentage of correct classification of the populations (Altitudinal zone A = 72 %; Altitudinal zone B = 66 %; Altitudinal zone C = 44 %), evidencing the existence of different temperature and precipitation regimes as important factors that contribute to the differentiation of species composition throughout the altitudinal belts.

Discussion

The altitudinal zoning found in this study, reveals the presence of three different altitudinal zones and two important species turnover points. Each of these altitudinal zones showed a particular species richness, as was found by Toledo-Garibaldi & Williams-Linera (2014) who found three groups of sites along an elevation gradient in Veracruz; and also by Olvera-Vargas *et al.* (2010) in a *Quercus* dominated forest located towards the north of the SMS, who also found a floristic gradient with three floristic zones and two important species turnover points. Both studies were conducted including only trees of different species and genus.

Species distribution of *Quercus* reveals altitudinal zonation

Figure 2. Altitudinal pattern of species richness of *Quercus* per altitudinal interval each 100 m in the Sierra Madre del Sur. Blue line = Total richness, Red line = Total richness of *Lobatae*, Green line = Total richness of *Quercus*.

The altitudinal A zone had the least oak diversity, with only 14 species presents. It showed the lowest elevation within the study area, and resulted closely related to tropical and dry climates, which are distinctive of tropical rainforest, dry oak forest, and tropical deciduous forest. This concurs with the presence of certain species such as *Q. crispifolia*, *Q. glaucescens*, *Q. sapotifolia*, *Q. oleoides* and *Q. tuitensis* which are characteristic of these altitudes and type of environment (Rzedowski 1978, González-Villareal 2003, Valencia-A. 2004). The discriminant analysis showed that the altitudinal A zone differs from the others altitudinal zones due mainly to a different precipitation regime during the warmest quarter (Bio 18; Figure 4). This suggests that the differences in the precipitation regimes of the warmest quarter among the different altitudinal zones could be one of the determining factors that limit the distribution of characteristic species in the altitudinal zone A such as *Q. crispifolia*, *Q. glaucescens*, *Q. oleoides*, *Q. sapotifolia* and *Q. tuitensis*.

On the other hand, the altitudinal B zone had the greatest species richness of oaks (47 species), the largest number of exclusive, and endemic species which is why it can be considered as the core region for the genus *Quercus* inside the SMS. In this region, the mean diurnal

range (Bio2) and max temperature of the warmest month (Bio5) were the most important variables. Therefore, the temperature at certain times of year could be considered as an important environmental filter in the distribution of species diversity exclusive to the altitudinal B zone such as *Q. benthamii*, *Q. eduardi*, *Q. hintonii*, *Q. jonesii*, *Q. mulleri*, *Q. pinnativenulosa*, *Q. sebifera*. In the same way, these variables could be acting like environmental barriers that prevent the establishment of species with tropical and xeric affinities in this altitudinal zone.

This pattern of species richness known as mid-elevation peaks is the most common in the mountains (McCain 2009, McCain & Grytnes 2010), and is generally attributed to the mid-domain effect, which proposes that this pattern is caused by the overlapping of the altitude ranges of the species as it approaches the central part of the mountain system (Sanders 2002, Colwell et al. 2004). For *Quercus* species, a complementary hypothesis is one that is related to climate which state that in the altitudinal B zone there is a higher diversity of temperate and humid climates in relation with altitudinal A and C zones (García-CONABIO 1998). Altogether, these hypotheses, in addition to the great availability of niches occasioned by heterogeneous topography of the zone, would explain

the great richness of the oak species in this altitudinal zone (Hipp *et al.* 2018).

Finally, the altitudinal zone C showed a significant decrease in the species richness of oaks, registering only 19 species (Figure 2). The low similarity coefficient between the altitudinal B and C levels (Figure 3A), reflects a low composition of oak species diversity shared in both levels, being the second important changing point in the species turnover diversity of *Quercus* in the SMS. This important point in the species turnover diversity of *Quercus* is apparently related to differences in the precipitation regime and the mean temperature of the warmest quarter, which prevents a large number of species distributed in the altitudinal B zone from being present in the altitudinal C zone.

Our study found that the largest species richness of species of *Quercus* is concentrated between 1,200 and

2,200 m, which adjusts itself to the pattern of species richness at mid-altitudes (mid-elevation peaks), and it also corresponds to one of the four distribution patterns of species richness proposed by McCain (2009) and re-taken by McCain & Grytnes (2010). A similar pattern with high species richness at mid-altitudes, though with a wider range, was cited by Sabás-Rosales *et al.* (2015) for oaks in the State of San Luis Potosí, where the altitude ranges from 1,201 and 2,700 m, and holds the largest species richness of species of the genus *Quercus*. Such a pattern was also found in the western region of Mexico for tree species (Olvera-Vargas *et al.* 2010) and in a study of six genera of the Mexican cloud forest (Alcántara *et al.* 2002). This pattern corresponds to the one described by Guo *et al.* (2013) for trees, and to the study of Arenas-Navarro *et al.* (2020) who found a similar pattern in Serranías Meridionales de Jalisco for *Quercus* species.

Figure 3. A) Dendrogram produced by the classification of oak distribution based on the Sorensen-Dice index. Altitudinal zone A corresponds to zones ranging from 500 to 1,100 m asl (orange color), altitudinal zone B corresponds to zones ranging from 1,200 to 2,200 m asl (green color), altitudinal zone C corresponds to zones ranging from 2,300 to > 3,000 m asl (blue color), on the X axis = similarity index; B) Altitudinal zonation found in this study for the Sierra Madre del Sur based on the oak distribution; C) A heatmap of the altitudinal distribution for the 61 oak species across the three altitudinal zones. Dark colors represent low percentages of records for each species in each altitudinal zone while light colors represent high percentages of records for each species in each altitudinal zone.

Our results showed that precipitation regime during the warmest quarter, defines the altitudinal A zone. In the altitudinal B zone, the mean diurnal range, and max temperature of warmest month were the most important variables, and in altitudinal C zone were the precipitation regime and the mean temperature of the warmest. Then, different climatic factors are important in driving elevational variation of plant species richness and taxa distribution along elevational gradients. This is a result obtained in other studies such as [Olvera-Vargas *et al.* \(2010\)](#), [Salas-Morales *et al.* \(2015\)](#), [Salas-Morales & Williams-Linera \(2019\)](#) who stated that the climate is fundamentally important in taxa distribution along elevational gradients; and [Arenas-Navarro *et al.* \(2020\)](#) pointed out that temperature and

precipitation are important filters of species distribution along an elevational gradient. *Quercus* has species adapted to different environmental conditions, but this study supports that the main climatic factors driving the elevational distribution of richness oaks at SMS, are those related with temperature and the precipitation regime. However, studies of other environmental factors related to soil, relief, atmospheric moisture, herbivory, dispersion vectors and competition must be conducted in the future to gather more information in order to understand more accurately the environmental limits of oaks species.

In addition to the ecological factors mentioned above, particularly those climatic, which in part explain the unimodal pattern of oaks in the SMS, there are historical and

Figure 4. Sample ordination produced by the discriminant analysis. The ellipses represent the 95 % confidence. Each point represents a species records for the different altitudinal zones.

evolutionary factors that allow proposing an explanation for the emergence of this pattern. These can be grouped into three: I) The main affinity of *Quercus* for temperate climates; II) the middle lands as receptors of multiple arrival events originated by the glacial cycles during the Pleistocene, and the permanence in situ of taxa that they found in the middle land refuges; and III) the ability of species of *Quercus* to colonize new habitat.

I) The genus *Quercus* has a northern temperate affinity (Hipp *et al.* 2018) and is widely distributed in the northern hemisphere in a wide range of habitats and climates. Despite this ecological diversity even in tropical lands like section *Virentes* (Cavender-Bares *et al.* 2015), the species show several traits that recall their temperate origin (Cavender-Bares 2019). After their possible origin in North America in the Eocene, American oaks diversified southward, and they arrived in Mexico in the Miocene, where their speciation rate increased in Mexican mountains (Hipp *et al.* 2018), and reached the highest world diversity, currently exceeding 160 species (Valencia-A 2004).

II) Climate changes during Pleistocene had great impact in all existing biota, provoking its latitudinal and altitudinal migration, reduction or fragmentation of species, but also its survival in refugia, expansion, extinction and diversification of taxa (Hewitt 2004, Turner 2004, Ramírez-Barahona & Eguiarte 2013). During the coldest periods of the Pleistocene, many tropical species became extinct, creating available habitats for species with temperate affinities that could migrate towards lower latitudes and altitudes, and that could persist due to their preadaptation to certain environmental changes, and their ability for rapid migration (Kremer & Hipp 2019), reaching altitudes near to sea level, which is the case of some oak species (Hewitt 2004, Turner 2004, Soltis *et al.* 2006, Cavender-Bares 2016) such as *Q. oleoides* and *Q. sapotifolia*. During the interglacial periods, temperature raised to the current temperature or even 3 degrees above (Caballero *et al.* 2010), provoking new migrations to greater altitudes and latitudes (Bush *et al.* 2004, Caballero *et al.* 2010, Ramírez-Barahona & Eguiarte 2013).

Mastreta-Yanes *et al.* (2015) indicated that Mexican mountains presented minor climatic changes during Pleistocene compared to those global, which provoked that temperate and semi warm-humid climates (which are preferred by oaks) were temporarily displaced. This enables organisms to migrate, primarily along an altitudinal gradient rather than a latitudinal one (McGlone 1996, Jetz *et al.* 2004, Turner 2004) and survive the oscillations in the same region (Hewitt 2004).

Palynological studies mention the presence of montane taxa (*Quercus*, *Alnus*, *Juglans*, *Liquidambar*, *Magnolia* and *Podocarpus*) growing at lower altitudes than the present ones during the coldest periods of the Pleistocene (Bush & Colinvaux 1990, Colinvaux *et al.* 1996, Hodel *et al.* 2008, Bush *et al.* 2009).

The mid altitudes acted as corridors or paths and even as transition zones between the highest and lowest lands and received multiple taxa arrival events. Some biota went across the mid regions as many times as climatic changes took place, that is, twice the cycles there existed. Another biota found in this middle zone a niche or shelters where they could settle, these migrations or stays increased the specific diversity in this level.

III) *Quercus* species are characteristic for presenting high genetic diversity produced by frequent hybridization among species (Petit *et al.* 2003, Hipp *et al.* 2020), which can produce not only preadaptations, specific diversification, and high rates of evolutionary divergence (Kremer & Hipp 2019), favoring species migration into new and different habitats (Cavender-Bares 2016, Hipp *et al.* 2020), so they went up and down during the climatic changes. If slope differences and orientation, micro-orography, topography, soil, solar exposition, wind, precipitation, evaporation and the diversity of climates in this zone are considered, a vast collection of very heterogeneous habitats in the mid regions were produced (Turner 2004, Martinelli 2007, Espinosa *et al.* 2016, Sam *et al.* 2019). According to Tews *et al.* (2004), there is a positive correlation between habitat heterogeneity and species diversity. These habitats become available for organisms and their heterogeneity is greater than in higher and lower altitudes, which is an advantage for species with great genetic variation and temperate affinity (such as many of the American species of *Quercus*), and also with the ability to establish themselves in new habitats.

Finally, we want to point out that the number of altitudinal zones, species turnover points, and the richness pattern found in this study depend on the method being used (Bach & Gradstein 2011), the site of study (Mastreta-Yanes *et al.* 2018) and the analyzed taxa (Arenas-Navarro *et al.* 2020). However, a similar altitudinal pattern and altitudinal zones could be possibly found in the case of temperate taxa and those associated with oaks in the SMS. On the other hand, according to the limited available resources for the management and conservation of biodiversity, it is important to prioritize certain regions and to

consider the importance of oaks in montane ecosystems of the northern hemisphere. Therefore, it is estimated that it would be a good starting point for further studies in management and conservation of species.

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Species distribution of *Quercus* reveals altitudinal zonation

Appendix I. Species of *Quercus* found in the Sierra Madre del Sur. Asterisk show endemic species to SMS and the sign + show endemic species to Mexico.

Section *Lobatae*

1. *Q. acatenangensis* Trel.
2. + *Q. acherdophylla* Trel.
3. *Q. acutifolia* Née
4. + *Q. aristata* Hook. & Arn.
5. *Q. benthamii* A. DC.
6. *Q. calophylla* Schltdl. & Cham.
7. + *Q. castanea* Née
8. + *Q. conzattii* Trel.
9. *Q. crassifolia* Bonpl.
10. + *Q. crassipes* Bonpl.
11. *Q. crispifolia* Trel.
12. +**Q. cualensis* L.M. González
13. + *Q. depressa* Bonpl.
14. + *Q. eduardi* Trel.
15. *Q. elliptica* Née
16. + *Q. confertifolia* Bonpl.
17. + *Q. grahamii* Benth.
18. + *Q. hintonii* E.F. Warb.
19. +**Q. iltisii* L.M. González
20. + *Q. jonesii* Trel.
21. + *Q. laurina* Bonpl.
22. +**Q. mexiae* L.M. González
23. +**Q. mulleri* Martínez
24. +**Q. nixoniana* S. Valencia & Lozada-Pérez
25. + *Q. pinnativenulosa* C.H. Mull.
26. + *Q. planipocula* Trel.
27. +**Q. rubramenta* Trel.
28. +**Q. salicifolia* Née
29. *Q. sapotifolia* Liebm.
30. + *Q. sartorii* Liebm.
31. + *Q. scytophylla* Liebm.

32. *Q. skinneri* Benth.
33. +**Q. tuitensis* L.M. González
34. + *Q. trinitatis* Trel.
35. + *Q. urbanii* Trel.
36. +**Q. uxoris* McVaugh

Section *Quercus*

1. + **Q. centenaria* L.M. González
2. *Q. corrugata* Hook.
3. + *Q. deserticola* Trel.
4. + *Q. frutex* Trel.
5. + *Q. glabrescens* Benth.
6. + *Q. glaucescens* Bonpl.
7. + *Q. glaucoides* M. Martens & Galeotti
8. + *Q. greggii* Trel.
9. *Q. insignis* M. Martens & Galeotti
10. + *Q. laeta* Liebm.
11. + **Q. liebmanii* Oerst. Ex Trel.
12. + **Q. macdougallii* Martínez
13. + *Q. magnoliifolia* Née
14. + **Q. martinezii* C. H. Mull
15. + *Q. microphylla* Née
16. + *Q. obtusata* Bonpl.
17. *Q. peduncularis* Née
18. *Q. polymorpha* Schltdl. & Cham.
19. + *Q. resinosa* Liebm.
20. *Q. rugosa* Née
21. + *Q. sebifera* Trel.
22. *Q. segoviensis* Liebm.
23. + *Q. sororia* Liebm.
24. + *Q. subspathulata* Trel.

Section *Virentes*

1. *Q. oleoides* Schltdl. & Cham.