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Abstract

Mexico has the fifth place among megadiverse countries, and the southern part of the country belongs to the Mesoamerican hotspot, where Oaxaca state has a very rich flora, related to its intricate topography. In this study, a multicriteria analysis (species richness, rareness, irreplaceability, turnover, and vulnerability) was used to prioritize conservation areas in Oaxaca, using as model system the genus Quercus (oaks), due to its high diversity and ecological importance. Our results indicate that the Sierra Madre de Oaxaca (SMOax) is the physiographic subprovince with the highest richness (38 species), rareness and irreplaceability of Quercus species, followed by the Montañas y Valles del Occidente (MVO; 29 species), the Sierra Madre del Sur (SMS; 25 species), and the Montañas y Valles del Centro (20 species). Areas that have retained most primary vegetation cover from 2000 to 2010 are mainly in the SMOax, in the Ixtlán district, and in the SMS, in the Miahuatlán district. On the other hand, MVO is the area with greater habitat disturbance, mainly in the Juxtlahuaca-Tlaxiaco districts. Oaxaca has numerous areas without official protection, named Indigenous Conservation and Community Areas, which play a central role as an alternative for conservation for 11 oak species. In conclusion, the priority conservation areas for the genus are mainly located in the SMOax and in the SMS. For white oaks, the semiarid area of Coixtlahuaca-Teposcolula-Nochitlán is important, while for the red oaks, the most important regions are the humid areas of Teotitlán, Sola de Vega, and Miahuatlán.

Keywords

species richness, rareness, irreplaceability, turnover, vulnerability, Oaxaca, Quercus

Introduction

The geographical distribution of plant and animal species is heterogeneous at all scales. Current distributional patterns are the result of environmental conditions and historical factors that generate diversity gradients in plants (Francis & Currie, 2003; Kessler, Kluge, Hemp, & Ohlemüller, 2011; Kluge, Kessler, & Dunn, 2006; O'Brien, 1993), mammals (McCain, 2005, 2007), birds (Kissling, Sekercioglu, & Jetz, 2012; McCain, 2009), and insects (Kerr, Vincent, & Currie, 1998). Higher species richness is associated with high biomass productivity, an intricate trophic web, and resource specialization of taxa (Francis & Currie, 2003; Hawkins et al., 2003). At the regional level, species richness gradients are correlated with temperature, precipitation, productivity, seasonality, and habitat heterogeneity (Currie et al., 2004; Hawkins et al., 2003; Kissling et al., 2012). Several studies have

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also found a clear relationship between species richness and altitude (Kessler, 2000; Rahbek, 1997). Others have also highlighted that more complex patterns of species richness in specific areas are the product of the evolutionary histories of taxa (Kissling et al., 2012; Ricklefs, 2004; Wiens & Donoghue, 2004). Thus, differences in diversification rates may provide alternative or complementary explanations to the understanding of richness patterns.

Biodiversity hotspots are areas with exceptional concentrations of endemic species which are experiencing remarkable habitat loss (Myers, Mittermeier, Mittermeier, da Fonseca, & Kent, 2000). Among the 25 global biodiversity hotspots, Mesoamerica is the third largest in biodiversity. On the other hand, Mittermeier, Goettsch-Mittermeier, and Robles-Gil (1997) ascertained that 70% of the world's biodiversity is concentrated in only 17 megadiverse countries. Mexico occupies the fifth place among those megadiverse countries (Mittermeier et al., 1997). However, most of the biodiversity of Mexico is located in the southern portion of the country, which also represents the northern part of the Mesoamerican hotspot in the Mexican Transition Zone (Morrone, 2001).

The southern state of Oaxaca has one of the richest floras of Mexico, with species belonging to both Nearctic and Neotropical biotas (Flores Villela & Gerez, 1994). This state covers only 4.78% of the total surface of the country (García-Mendoza, 2004) but contains around 9,019 vascular plant species out of the 21,841 species recorded for Mexico (41.3%). In addition, 3,762 of the plant species in Oaxaca are endemic to Mexico, and 732 of them are endemic to the state, making it the most important region in the country in terms of plant endemism and richness (Villaseñor & Ortiz, 2014). This exceptional diversity is related to the intricate topography and climatic diversity of the region, which is an area of convergence of two major physiographic systems (Sierra Madre Oriental and Sierra Madre del Sur [SMS]). This creates a complex landscape with high biodiversity across the highlands, valleys, and basins (Ortiz, Hernández, & Figueroa, 2004; Trejo, 2004) with endemic species being a crucial component in these biotas. Particularly, the highest levels of richness and endemism for the flora of Oaxaca are found across mountain ranges and valleys such as the Sierra de Juárez, the Río Tomellin canyon, the Tehuantepec Isthmus, the Chimalapas Mountains, and some portions of the SMS (García-Mendoza, 2004; Lorence & García-Mendoza, 1989).

The vegetation of Oaxaca is composed mainly of temperate (40%) and tropical (30%) forests (Velázquez et al., 2003). Particularly, temperate forests include high number of oak species as dominant or codominant elements. Valencia and Nixon (2004) reported 52 species of Quercus for Oaxaca, 24 belonging to the section Quercus (white oaks), and 28 to the section Lobatae (red oaks). Both sections are distributed along an altitudinal gradient from sea level along the coastal plains to 3,300 m in the Sierra Madre de Oaxaca (Ortiz et al., 2004; Valencia & Nixon, 2004). Ortiz et al. (2004) divided Oaxaca into 12 physiographic subprovinces: Depresión del Balsas, Depresión Ístmica de Tehuantepec, Fosa de Tehuacán, Montañas y Valles del Centro (MVC), Montañas y Valles del Occidente (MVO), Planicie Costera del Golfo, Planicie Costera del Pacífico, Planicie Costera de Tehuantepec, Sierra Madre de Oaxaca (SMOax), Sierra Madre del Sur de Oaxaca y Chiapas (SMOC), SMS, and Valles Centrales. Both red and white oaks inhabit 10 of the 12 subprovinces in the state, excluding the Planicie Costera de Tehuantepec and Fosa de Tehuacán (Valencia) & Nixon, 2004; Figure 1).

Some strategies for defining areas for conservation of biodiversity assume that selecting a target species could provide a protective umbrella for numerous co-occurring species. Torres, Luna, and Oyama (2011) considered that oak communities constitute a suitable model for conservation in the mountainous systems of Oaxaca because oaks have a major ecological role as dominant species in several temperate forests (Valencia & Nixon, 2004). Moreover, oak species play a key role in the ecological assembly of communities of organisms such as ectomycorrhizal fungi (Morris, Pérez, Smith, & Bledsoe, 2009), gall-forming insects (Pérez, González, Oyama, & Cuevas, 2016), and seed eating vertebrates (López $\&$ Manson, 2006) among others. The oak forests also provide habitat to vertebrates (Brawn, 2006), arthropods (Tovar, Cano, & Oyama, 2004; Tovar & Oyama, 2006), and epiphytes (Holz & Gradstein, 2005).

Multicriteria analyses provide a systematic approach for integrating risk levels and uncertainty in conservation evaluations, which help decision makers compare and choose among different alternatives (Sarkar et al., 2006). In this study, the main objective was to identify conservation priority areas within the state of Oaxaca, Mexico, applying a multicriteria analysis based on species richness, rareness, turnover, irreplaceability, and vulnerability of *Quercus* species in the state, at the level of the whole genus and for each of the two sections, Lobatae (red oaks) and Quercus (white oaks). The specific criteria used were the following: (a) taxonomic richness, defined as the total number of species present in a given area; (b) endemism, evaluated with two complementary indices: rareness, which increases as the geographic amplitude of a species' distribution decreases; and irreplaceability, which measures the importance of areas that contain unique species and cannot be substituted by other areas (Torres et al., 2011); (c) species turnover among areas, considering turnover as a measure of the number of different species between two areas; and (d) the estimation of habitat loss for forests where oaks occur, in the context of richness and endemism patterns.

Figure I. (a) Physiographic subprovinces of Oaxaca based on Ortiz-Pérez, Hernández-Santana, and Figueroa (2004): Depresión del Balsas (DB), Fosa de Tehuacán (FT), Istmo de Tehuantepec (IT), Montañas y Valles del Centro (MVC), Montañas y Valles del Occidente (MVO), Planicie Costera del Golfo (PCG), Planicie Costera del Pacífico (PCP), Planicie Costera de Tehuantepec (PCT), Sierra Madre de Oaxaca (SMOax), Sierra Madre del Sur de Oaxaca y Chiapas (SMOC), Sierra Madre del Sur (SMS), and Valles Centrales (VC). (b) Distritos administrativos de Oaxaca: Ixtlán (ixt), Centro (cen), Choapam (cho), Coixtlahuaca (coi), Cuicatlán (cui), Ejutla (eju), Etla (etl), Huajuapan (hua), Jamiltepec (jam), Juchitán (juc), Juquila (juq), Juxtlahuaca (jux), Miahuatlán (mia), Mixe (mix), Nochixtlán (noc), Ocotlán (oco), Pochutla (poc), Putla (put), Silacayoapam (sil), Sola de Vega (sol), Tehuantepec (teh), Teotitlán (teo), Teposcolula (tep), Tlacolula (tlc), Tlaxiaco (tlx), Tuxtepec (tux), Villa Alta (vil), Yautepec (yau), Zaachila (zaa), and Zimatlán (zim). Green dots are records of species in the Quercus section, and red dots are records of species in the Lobatae section.

Methods

Distributional Database

We gathered presence records of 54 Quercus species reported for the state of Oaxaca. Thirty-one species were red oaks (section Lobatae), and 23 species were white oaks (section *Quercus*). Our species list (Table 1) somewhat differed from the list compiled by Valencia and Nixon (2004) and is discussed in detail in Appendix A. The presence records were obtained from herbarium specimens (MEXU, FCME, OAX, SERO, MO), Global Biodiversity Information Facility [\(www.gbif.org\)](www.gbif.org), and data from monographic and floristic studies reviewed by Torres et al. (2011). The information was condensed into a single database of 2,143 non-duplicated georeferenced records. Distributional maps of each of the 54 oak species were obtained using ArcGIS ver. 9.2 (Environmental Systems Research Institute, 2006).

Table 1. Continued

Section	Species	Mexico	Oaxaca	OF.	PQF-QPF	CF	S	TF		PNA ICCA PRO		tree	shrub	Min. elevation	Max. elevation
Quercus	Q. microphylla	X					X		X^a		X^a	X	X	2,200	2,400
Quercus	Q. obtusata	X		X.	\times		X		X^a		X^a	X		1,500	2,500
Quercus	Q. oleoides			X	\times			X		X	X	\times		200	1,000
	Quercus Q. peduncularis			X	\times							X		800	2,000
Quercus	Q. polymorpha			X		X		\times	X^a		X^a	X		1,300	2,100
Quercus	Q. rugosa			X.	\times				X		\times	\times		2.000	2,800
	Quercus Q. sebifera	X					X		X^a		X^a	X		2,000	2,200
	Quercus Q. segoviensis			X.	\times							X		1.800	2,200
	Quercus Q. splendens	X			X							X		1.000	1,900
Section Lobatae		16		П	18	15			6	9	13	31	0	400	3,000
Section Quercus		15		4	15	6	8	5.	12	6	16	22	$\overline{2}$	200	3,000
	Genus Quercus		2	25	33	21	9	$\overline{2}$	18	15	29	53	2	200	3,000

Note. QF = Quercus forest; PQF/QPF = mixed forest; CF = cloud forest; S = shrubby vegetation; TF = tropical forest; species protected (PRO) in PNA (Protected Natural Areas). The two last columns indicate the minimum and maximum elevation in which each species is found. ^aSpecies protected in the Tehuacán-Cuicatlán Natural Biosphere or (ICCA) indigenous and community conserved areas. Growth form: tree or shrub.

Study Area

Our study covers the entire state of Oaxaca, located in the southern portion of Mexico between 15° 39' and 18° 42' N and 93° 52' and 98° 32' W, with an area of 95,364 km² (Espejo, López, Martínez, & Pulido, 2007; Velázquez et al., 2003). The largest number of oak records are located in five regions (biogeographic subprovinces) proposed by Ortíz et al. (2004): (a) MVO, which comprises an area of $21,263$ km² and consists of mountain range systems with tectonic blocks and intermountain depressions that converge to the south in a NNW-SSE orographic axis. This subprovince is characterized by humid temperate climate (12°C-18°C annual average, 500–1,200 mm annual rainfall), but the western portion receives more precipitation than its eastern sector; (b) SMOax, with $17,520 \text{ km}^2$ in area, with a relief amplitude of 2,500 m, conspicuous altitudinal fringes, various and asymmetric orographic axes, and short and steep slopes. It is characterized by semiwarm temperate and humid climates and is the mountain sector with higher rainfall at the statewide level, associated with Gulf trade winds (annual rainfall ranges from 2,500 mm to 4,000 mm); (c) MVC covers $6,663 \text{ km}^2$; the terrain is also complex and the relief amplitude is high and contrasting; valleys and floodplains occur below 1,400 m. It is characterized by humid warm and semiwarm semiarid climates. It is the mountain region with higher temperature (annual mean temperature is 22° C- 26° C) and lower rainfall (500-800 mm); (d) Sierra de los Chimalapas (CHIM) covers 5,816 km^2 ; 20% of its land surface is mountainous and occurs above 1,000 m; 50% are high hills; and 30 % are low hills. This subprovince has semiwarm wet to subhumid climates (1,500–2,000 mm annual rainfall) because the Pacific winds; and (e) SMS, with $12,350 \text{ km}^2$ in area, characterized by a highly variable relief, with relatively low western mountains $\left($ <2,000 m) and higher systems at the Miahuatlán Sierra. The climate is warm and temperate subhumid (1,000–1,500 mm annual rainfall; Ortiz et al., 2004).

Species Richness, Rareness, and Irreplaceability Patterns

The use of equal-area grids has been considered as an important tool for studying biogeographic patterns in biological diversity (McAllister, Schueler, Roberts, & Hawkins, 1994). As the patterns of richness and endemism (as measured with both the rareness and irreplaceability indices) are scale dependent, we initially used three different grid sizes: (a) 205 grids of 10×10 min $(17.6 \times 18.4 \text{ km})$ of latitude and longitude, (b) 524 grids of 5×5 min $(8.3 \times 9.2$ km), and (c) 1,316 grids of 2.5×2.5 min $(4.15 \times 4.6$ km). However, our preliminary results indicated that, even though the results using the three different grid sizes were largely congruent, the 5×5 min was optimal because it does not exaggerate the importance of sites as when a larger grid is used, and minimizes the number of cells lacking data, that increases when the smaller grid is used. Therefore, the results presented are based on the 5×5 min grid, but the maps for the other two grid sizes are presented in Appendix B.

Species richness was measured counting the total number of species within each grid cell (Linder, 2001). To measure rareness, we used the weighted endemism index proposed by Crisp, Laffan, Linder, and Monro (2001), calculated by counting all species in each cell and weighting each species by the inverse of its range. Thus, a single-cell endemic would have the maximum weight of 1, a species occurring in two cells a weight of 0.5, and a species occurring in 100 cells a weight of 0.01 (Crisp et al., 2001). To obtain a rareness score for a cell, these weights were summarized for all species occurring in the cell (Crisp et al., 2001). This index tends to decrease the importance of species with broad distribution.

The measure of irreplaceability was based on the corrected weighted endemism index (Crisp et al., 2001). For this, we constructed a distribution matrix of all oak species at the whole Mexican and Central American level, based on the herbaria, literature, and online (Global Biodiversity Information Facility) records. In this matrix, we considered the geographical units identified by Torres et al. (2011), and we determined the number of units in which each species is recorded (Table 2). The irreplaceability index was calculated by assigning a value from 1 to 10 to each species, depending on the number of geographical units in which it is present. Species restricted to a single unit were weighted with a 10, whereas species present in 10 or more areas were weighted with a 1. In this way, species with local endemism had a high weight factor, while species with a wide geographical distribution had a low weight factor. The weight factor calculated for each species was multiplied by the inverse of their ranges obtained in the previous step. Therefore, the irreplaceability of an area increases when it contains species not found in other geographical units, and it decreases when it contains species found in other geographical units. The weighted irreplaceability values were summed across species to determine the areas with high overall irreplaceability importance.

The patterns of species richness and endemism (rareness and irreplaceability) were examined by mapping the three indices described earlier and detecting in maps the concentration of cells with the highest values.

Species Turnover

Beta diversity, or species turnover, is a measure of differentiation in species composition among distinct areas or along gradients (Koleff, Gaston, & Lennon, 2003; Rodríguez, Oyama, MacGregor, & González, 2015). This measure increases when there are few shared species between two areas. We determined the species turnover patterns based on the proposals of many authors (Baselga, 2010; Koleff et al., 2003; Lennon, Koleff, Greenwood, & Gaston, 2001), using Sørensen index (β_{SOR}) and Jaccard index (β_{JAC}). β_{SOR} is a widely-used measure to reflect the proportion of species shared between two communities (Baselga, 2010), but it is related to species richness (Koleff et al., 2003) while the β_{IAC} actually describes the gain or loss of species without the bias of richness (Koleff et al., 2003; Lennon et al., 2001). β_{SOR} and β_{IAC} indices were computed with the betapart package for the R software (Baselga & Orme, 2012). Both turnover measures were calculated for each pair of cells. The final turnover index for each cell was the average of all turnover values of the cell with the other cells.

Elevational Patterns

To analyze elevational patterns, we built a matrix of species absence or presence using intervals of 100 m of altitude across the full elevational distribution for the genus (200–3,000 masl). The number of species occurring in each elevational interval was calculated. To evaluate rareness patterns, for each species we counted the number of elevational intervals in which it is present and weighted each species by the inverse of this number. To obtain a rareness score for each elevational interval, these weights were summarized for all species. In the case of irreplaceability, in this second matrix, the weighted inverse of rareness of each species was weighted by the correction factor for each species, and the sum of corrected values of all species for each interval was used to determine its irreplaceability index. The turnover between elevational intervals was computed through β_{SOR} and β_{JAC} indices computed with the betapart package for R (Baselga & Orme, 2012).

Habitat Loss

The amount of habitat loss for oaks was computed by means of cartographic overlaying of two comparable databases (same geographic scale, same vegetation typology) for the most recent decade. For this, we worked with maps in digital format (scale 1:250,000) from the National Forestry Inventory for 2000 (Mas et al., 2002; Secretaría de Medio Ambiente y Recursos Naturales, 2001) and INEGI cartographic data series IV for 2010. Vulnerability was determined separately for the two sections within the genus based on habitat loss percentage or coverage change (primary to secondary; Myers et al., 2000). First, we selected vegetation polygons with presence of oaks (pine forests, pine-oak forests, oak-pine forests, oak forests, mountain cloud forests, high evergreen forests, medium evergreen tropical forests, medium deciduous forests, deciduous forests, and medium deciduous forests) in both 2000 and 2010 inventories and then calculated their areas. Next, we calculated the percentage of habitat loss for the polygons between both interval years. In the 2010 polygons, we also calculated the percentage coverage of secondary and primary vegetation (Myers et al., 2000).

Table 2. Continued Table 2. Continued

bSpecies endemic to the Oaxaca state.

Prioritizing Conservation Areas

Conservation priority areas were defined at the statewide level. First, results obtained with grid cells of $5' \times 5'$ (to minimize biases and overstatement) in the different analyses (for the whole genus and by section) were transformed to a ratio scale along the following lines: (a) Richness, rareness, irreplaceability, and turnover criterion. Values from 0 to 5 were assigned to each cell, where 0 corresponds to cells with low indices (richness, rareness, irreplaceability, or turnover) and 5 corresponds to cells with highest indices in each case. (b) Vulnerability criterion. It was incorporated using a vegetation cover loss index. First, vegetation polygons of the 2000 year with confirmed oaks presences were selected and intersected with the year 2010. The resulting polygons were in turn intersected with the cell grid, and vegetation percentage still classified as primary for 2010 was calculated for each cell. We assigned values from 0 to 5, where 0 corresponds to cells with less primary coverage and 5 to cells with more primary coverage. To do this, we evaluated patterns of richness, rareness, turnover, and habitat loss for the genus and its two sections. (c) Systematic conservation planning. According to the guidelines proposed by Margules and Pressey (2000) and Sarkar et al. (2006), non-protected areas in a network of protected natural areas (PNAs) are priority to conservation, so in this section we used polygons of protected areas enacted at the federal, state, municipal, and community levels. Initially, we gave a protection value of 1 to each cell. Then, we subtracted or added from this value on the basis of their degree of protection. We considered the areas with official decree as having the maximum degree of protection. Therefore, we quantified the area of each cell that has federal protection and, for example, if the percentage of federal protection coverage in a cell is 10%, we subtracted 0.1 from the baseline protection value for the cell. For areas with state or local protection, the coverage percentage was transformed into decimal added to the initial value of each cell. A similar procedure was used for communal protected areas. After the subtraction of costs, the final value of maximum conservation of each cell was transformed into a scale of 0 to 5, where 0 represents those cells whose total surface has federal protection, and 5 represents those cells with no areas under federal or community protection. (d) Areas prioritization. Finally, an average of all the values of all criteria (richness, rareness, turnover, irreplaceability, vulnerability, and effective conservation) was calculated according to each criterion listed earlier. The average value is a direct measure of the prioritization of areas, which was made at both the genus and the section levels. All indices in this study were computed in R software (R Development Core Team, 2011), and the results were visualized in ArcGIS ver. 9.2 (Environmental Systems Research Institute, 2006).

Results

Richness Patterns

The SMOax is the subprovince with the highest richness of oak species (38 species). This subprovince includes the Ixtlán district (with 19 species), the Teotitlán district (with 14 species, mainly in the municipalities of San Francisco Huehuetlán and Santa María Teopoxco), and the Cuicatla´n, Centro, and Villa Alta districts (with 12 species each one). The MVO subprovince has 29 species (the Juxtlahuaca and Tlaxiaco districts have 12 species and the Sola de Vega district 11 species), SMS has 25 species (the Miahuatlán and Yautepec districts have 12 species), and MVC has 20 species. Eleven species are recorded in CHIM (Figure 2; Table 3).

For white oaks, the districts with higher richness are Teposcolula, Coixtlahuaca, and Nochixtlán in MVO with seven species, Ixtlán in SMOax also with seven species, and the Juxtlahuaca and Mixtepec districts in MVC with six species (Figure 2). For red oaks, the districts with higher richness are Ixtlán (13 species), Teotitlán (12 species), and Cuicatla´n (11 species) in the SMOax; Sola de Vega (nine species) and Juxtlahuaca—Mixtepec (seven species) in the MVO; Juchitán (eight species) in CHIM, and Miahuatlán and Yautepec (seven species) in the SMS (Figure 2; Table 3).

Rareness Patterns

We found five main rareness regions at the level of the whole *Quercus* genus, that in order of importance are two districts in the SMOax (Ixtlán and Teotitlán), one in the MVO (in the border between the Coixtlahuaca and Nochixtlán districts), one in the SMS (Yautepec district), and one in CHIM (Juchitan district; Figure 2; Table 3). For the section Quercus, we identified five areas with importance for rareness: one in the north of the Ixtlán district, and four areas located within the Coixtlahuaca, Nochixtlán, and Teposcolula districts (Figure 2). For section Lobatae, the regions with high rareness values are located in order of importance in the following districts: Teotitlán, in the limits between Ixtlán and Cuicatlán, and in the south of Ixtlan in the SMOax; Yautepec, in the limits between Juquila-Miahuatlán in the SMS; and Juchitan, in the CHIM (Figure 2). The highest rareness index represented those areas where there are species with a restricted distribution within Oaxaca but without considering if those species occur in other biogeographic regions outside of Oaxaca.

Irreplaceability Patterns

The irreplaceability measure obtained considered if species occur, besides Oaxaca, in other regions. In this way, we recognized the areas with greater value in terms of

Figure 2. Patterns of richness and rareness for the Lobatae section, the Quercus section, and the whole genus in Oaxaca using a 5×5 min grid. The cells with greater richness or rareness are indicated in darker colors. Black lines delimit the physiographic subprovinces, and gray lines delimit the districts of Oaxaca.

irreplaceability at the level of the whole Quercus genus, that in order of importance are located in Teotitlán and Ixtlán (mainly in the northern region) in the SMOax, Yautepec and borders between Juquila-Miahuatlán in the SMS and the CHIM (see Figure 3; Table 3). For white oaks, the areas in order of importance are in the following districts: northern Ixtlán in the SMOax; Coixtlahuaca, Teposcolula, and Nochixtlán in the MVO; Villa Alta in the SMOax; and Miahuatlán in the SMS (Figure 3). For red oaks, the districts with higher importance are Teotitlán in the SMOax; Yautepec in the

SMS, the limits between Cuicatlán and Ixtlán in the SMOax; Juchitán in CHIM; and the border between Juquila and Miahuatlán in the SMS (Figure 3).

Turnover Patterns

Turnover patterns for the genus coincide in general with the limits among the physiographic subprovinces (Figure 3). Also, high turnover values were observed between the Teotitlán district and the rest of the SMOax subprovince. A similar case was observed for

the Nochixtlán district when compared with the Teposcolula and Coixtlahuaca districts (Figure 3). The areas of higher turnover for the white oaks are almost the same as those observed at the whole genus level, but the highest turnover values were found at the limits between the districts of Coixtlahuaca, Teposcolula, and Nochixtlán (Figure 3). However, in the case of the red oaks, the area with the higher turnover was localized at the Isthmus of Tehuantepec. There are also important turnover areas between the districts of Tepescolula-Tlaxiaco in the MVO, and Juquila and Putla in the SMS (Figure 3). Also, a high turnover value was observed between the SMOax and the MVO, which was not detected at the genus level or for the white oaks.

Altitudinal Patterns

The highest species richness at the whole genus level was found between 1,800 and 2,200 masl. For white oaks, the highest richness occurs between 2,000 and 2,200 masl, while red oaks showed a bimodal pattern with peaks of richness at 1,700 to 2,000 and 2,200 to 2,400 masl. In this last altitudinal interval, a decrease in the richness of white oaks was observed (Figure 4).

We also observed that oaks with restricted altitudinal distributions occur mostly between 2,000 and 2,500 masl. From 1,300 to 2,300 masl, there is an increase in the rareness index. In the red oaks, altitudes around 1,700 masl are also important in terms of rareness. The white oak species that have a very restricted geographic distribution in Mexico are found at 2,200 masl, while in the case of the red oaks, such species are found between 2,200 and 2,400 masl, with the 1,000 and 1,700 masl altitudes also being important. The greater species turnover was observed at 1,100, 1,600, 2,300, 2,600, and 2,800 masl (see Figure 4 for details).

Habitat Loss

Vegetation fragments with presence of oak species in Oaxaca have lost 5.83% of their original area between 2000 and 2010 (413,123 ha). From the remaining area, 41.89% and 58.11% correspond to primary and secondary vegetation, respectively (Table 4). By section, Quercus showed a higher loss of habitat (6.47%) ; however, the percentage of remnants representing primary and secondary vegetation is almost equal (45.46% and 54.54%, respectively). In contrast, areas where section Lobatae occurs have been transformed into secondary vegetation at a higher percentage (62.74%).

Areas that have retained most of their primary vegetation cover from 2000 to 2010 for both the genus and sections levels are located in the north of the Ixtlan district (from the Macuiltianguis to the Santa María Yavesía municipalities) in the SMOax, as well as the border of the

Table 3. Continued

Continued

Figure 3. Patterns of irreplaceability for the Lobatae section, the Quercus section, and the whole genus in Oaxaca, using a 5×5 min grid. Darker colors indicate cells with greater indices of irreplaceability or turnover. In the case of turnover, the arrows indicate the areas with highest turnover among cells. Black lines delimit the physiographic subprovinces, and gray lines delimit the districts of Oaxaca.

Ixtlán district with the Cuicatlán and Tuxtepec districts (Figure 5). The importance of other districts is evident, as, for example, Sola de Vega-Zimatlán, Etla, northern Tlacolula, Mixe, and western Miahuatlán. In the rest of the districts, most of the vegetation where oaks occur is secondary.

Prioritizing Conservation Areas

According to our analysis, the most important conservation areas for the genus and both sections are mainly located in the SMOax, including the municipalities of San Pedro Yolox, Macuiltianguis, San Juan Quiotepec, Ixtlán, Comaltepec, Capulálpam, Santa Catarina Ixtepeji, and Santa María Yavesía; all in the Ixtlán district, and municipalities in the Cuicatlán district, as San Felipe Usila and San Juan Tepeuxila. In the Teotitlán district, Santa María Teopoxco, San Lucas Zoquiapam, and Mazatlán are important. In the south of the SMOax, the San Andrés Yaa and Totontepec municipalities are important for conservation, in the limits between the Villa Alta and Mixe districts (Figure 6).

Figure 4. Elevational patterns at section levels and genus. The graph shows the richness, rareness, irreplaceability, and turnover indices for each elevation range.

Note. Primary vegetation, secondary vegetation, and habitat loss (years 2000–2010). Results are shown at the genus level and by section.

In the east of the SMS, there are important areas in the municipalities of San Carlos Yautepec, Santa María Ecatepec, and San Pedro Mixtepec, in the limits between the Yautepec and Miahuatlán districts; in the west, the municipalities of San Jerónimo Coatlán and San Juan Lachao in the limits between the Juquila and Miahuatlán districts. In the MVO, the area between the municipalities of Putla and Juxtlahuaca is important, as well as the Santiago Textitlán municipality in the Sola de Vega district. In CHIM, the area with greater importance for conservation is in the San Miguel Chimalapa municipality in the Juchitán district (Figure 6).

In the analysis for the *Quercus* section, other additional areas were identified, as: the Tepescolula and San Pedro Nopala municipalities in the Teposcolula district, San Andrés Cabecera Nueva in the Putla district, San Miguel Chicahua in the Nochixtlán district, and the Tepelmeme municipality in the Coixtlahuaca district.

In the SMOax, the municipalities of Talea de Castro, Juquila-Vijanos, and Tanatze in the Villa Alta district are also of importance, as well as the Santiago Lachiguri municipality in the Tehuantepec district (Figure 6).

For section Lobatae, the area with more importance is located in SMOax in the Teotitlán district, including Santa María Teopoxco and San Lucas Zoquiapam. The rest of the priority sites are located, in order of importance, in the SMOax, SMS, CHIM, and MVO, but in this last physiographic province the only important municipality is Santiago Textitlán, in the Sola de Vega district (Figure 6).

Discussion

The high biological diversity present in the state of Oaxaca is related to its physiography, which originated

Figure 5. Areas with primary and secondary vegetation cover and vulnerability of habitat for oaks in Oaxaca. The areas that remained with primary vegetation between the year 2000 and 2010 are considered as having a low degree of disturbance (green color) and those that were transformed from primary to secondary vegetation during the same period are considered as showing a high disturbance (red color). Black lines delimit the physiographic subprovinces, and gray lines delimit the districts of Oaxaca.

through complex geological processes. In turn, the Oaxacan physiography has given rise to a high diversity of soil and climate types that allowed the establishment of a rich flora and different types of ecosystems (García-Mendoza, 2004). Here, we analyzed at the state level the distribution of 54 oak species, 30 of which are considered endemic to Mexico (55.5%), a higher percentage than for endemic flowering plants present in Oaxaca according to the estimations of Villaseñor and Ortiz (2014). However, there are only two oak species endemic to Oaxaca, even though Valencia and Nixon (2004) mention the presence of other three endemic oaks in Oaxaca, which have not been formally described yet.

Oaxaca is divided in 12 physiographic subprovinces, 10 of which have records of oak species, the SMOax being the region with the highest oak richness. A high richness also has been found in this subprovince for vascular plants in general (García-Mendoza, 2004), gymnosperms (Contreras & Luna, 2006), and birds and mammals (Koleff et al., 2003). Furthermore, the SMOax has been identified as the area of convergence of vertebrate species belonging to different assemblages as a result of historical and ecological changes (Bojórquez, Azuara, Ezcurra, & Flores, 1995). In the MVO, the Juxtlahuaca area is a priority center for the conservation of oaks and also for terrestrial vertebrates (Bojo´rquez et al., 1995), especially for herpetofauna (Urbina & Flores, 2010). On the other hand, most of the oak species that occur in the SMS have few records and fragmented distributions. The scarcity of records may be due in part to the difficulty of accessing these areas, that has resulted in little floristic knowledge of this region (García-Mendoza, 2004; Solano, Alonso, Rosado, Aguilar, & García, 2008; Zacarías & del Castillo, 2010). As in the SMS, botanical sampling efforts in the SMOC have been insufficient (García-Mendoza, 2004) mainly due to social

Figure 6. Conservation priority areas in Oaxaca for the Lobatae section, the Quercus section, and the genus Quercus. This proposal considers a systematic conservation planning approach based on a multicriteria analysis. The protected natural areas (PNA) are shown in green and in red the indigenous conservation and community areas (ICCA). Black lines delimit the physiographic subprovinces, and gray lines delimit the districts of Oaxaca.

conflicts. The SMS and SMOC have been considered priority areas for the conservation of vertebrates and herpetofauna, respectively (Bojórquez et al., 1995; Urbina & Flores, 2010).

The municipality of Macuiltianguis and nearby areas were the most important regions in terms of rareness patterns at both the whole genus level and for white oaks,

whereas the most important rareness region for red oaks was located in the SMS (Yautepec and Coatlán). These rareness patterns are also similar to those patterns reported for gymnosperms (Contreras & Luna, 2006), amphibians and reptiles (Koleff et al., 2003), and mammals (Illoldi et al., 2008). Located at the northeast of the MVO, the major rareness regions for white oaks are

Tepelmeme and Teposcolula. These regions have relatively low rainfall (<800 mm) with temperate subhumid to semiarid climates. In contrast, the rareness centers of red oaks were identified at sites with high annual precipitation $(>\!\!800 \,\mathrm{mm})$ in the south of this subprovince, particularly in the Juxtlahuaca-Mixtepec, Santa María Peñoles, and Zimatlán regions. The latter is also a priority area according to the rareness of mastofauna (Illoldi et al., 2008). The rareness pattern found in the SMOC is similar to that found for mammals (Illoldi et al., 2008) and birds (Peterson et al., 2003).

Our results showed that the most important altitudinal interval for the white oaks is between 2,000 and 2,200 masl, but the case of the red oaks is more complex since at least three altitudinal intervals with high richness were identified. The analysis also indicated that the altitudinal intervals where the highest turnover occurs are at lower or higher altitudes with respect of the intervals with highest richness. The pattern of turnover also coincides with the transition between different types of vegetation. For example, we found high species turnover that matches the transition from tropical forest vegetation to cloud or oak forests, and from those to pine-oak forests. This pattern was also identified in the state of Jalisco by Vázquez and Givnish (1998). To make conservation more effective, it is important to consider areas that show a wide altitudinal range as proposed by Zacarías and del Castillo (2010).

Currently, habitat loss is a common phenomenon in all ecosystems, the temperate forests being the most drastically reduced by human influence (Challenger, 1998; Rzedowski, 1978). According to Velázquez et al. (2003), 40% of Oaxaca's surface is covered by temperate forests, of which 21% have been altered to secondary vegetation from 1980 to 2001. In 2001, 70% of the secondary temperate forests recorded in 1980 had been converted to grasslands. The temperate forests in Oaxaca lost about 1% of their area annually, meanwhile the increase of secondary vegetation is higher than this 1% (Velázquez et al., 2003). Robson (2007) suggested that an additional problem for conservation is that 80% of the biodiverse forests in Oaxaca are near human settlements, whose lands are the heritage of 1,400 indigenous communities and ejidos (Moguel & Toledo, 1999; Sarukhan & Larson, 2001).

Temperate subhumid forests mainly in the MVO and southwestern of the SMO and semiarid temperate forests of the MVC had deforestation rates of 0.5% per year, less than 2% reported for oak forests (Gómez, Vega, Ramírez, Palacio, & Galicia, 2006). However, the conversion rate from primary to secondary vegetation in this same period (70%) is higher in the subhumid forests of the MVO, compared with 21% identified for temperate forests during 1980 to 2000 (Velázquez et al., 2003). On the other hand, although habitats associated with the MVC have suffered habitat loss and transformation processes, there still remain large areas of predominantly monospecific forests, as well as in semiarid regions of the SMS, MVO, and SMOax.

Implications for Conservation

According to Peterson et al. (2003), the indicator group concept is a useful tool to match the richness and endemism values of different groups in a given area. Oaks are dominant species in the main temperate vegetation types. In Oaxaca, most oak species are trees, except Quercus frutex and Quercus microphylla, which inhabit the Tehuacán-Cuicatlán Valley. Therefore, oaks can be considered important elements in almost all forest types. In this study, we have shown that patterns of richness for oaks are similar to those obtained for other plants groups. The SMOax is considered by several authors as a richness center for gymnosperms (Contreras & Luna, 2006), Orchidaceae (Solano et al., 2008), and several tree species of temperate forests (Zacarías & del Castillo, 2010). Most of these studies coincide on the importance of humid mountain ecosystems in explaining the high diversity observed at the limits between the Ixtlán-Cuicatlán and Tuxtepec districts, which we also identified as areas of high oak richness. A similar result has also been observed for other groups such as vertebrates (Bojo´rquez et al., 1995; Peterson et al., 2003), particularly birds (Peterson et al., 2003), mammals (Briones, Cortés, & Lavariega, 2015; Illoldi et al., 2008), and reptiles (Urbina & Flores, 2010). Undoubtedly, the recent interest in the botanical exploration of Oaxaca through projects such as the ethnofloristic inventory in regions with high biodiversity has significantly increased the number of records for plant species, allowing us to describe the distribution of oak species in detail.

Torres et al. (2011) proposed that the prioritizing of conservation should focus on those areas without official protection. In general, the system of PNAs of Oaxaca is deficient in terms of the conservation of ecosystems where oaks occur. Four PNAs, the Tehuacán-Cuicatlán Biosphere Reserve, Benito Juárez National Park, Boquerón of Tonalá, and Hierve el Agua State Park protect a total of 18 oak species.

However, in Oaxaca, there are alternative conservation areas called indigenous conservation and community areas (ICCAs; Martin et al., 2011; Robson, 2007). According to Martin et al. (2011), statewide overall 126 ICCAs preserve 375,457 ha, of which only 22 include forests where oaks occur. However, this conservation system protects around 15 species of oaks, many of them not present in the official PNAs (see Table 1 for details). The ICCA system in Oaxaca preserves mostly pine oakforests as well as cloud forests (Monroy, Sánchez, Briones, Lira, & Maass, 2015) what can explain the high number of protected oak species in an area that is about 10% the size of the officially decreed PNAs. Together, PNAs and ICCAs in Oaxaca protect 29 oak species (53.7% of the total), of which 16 are white oaks and 13 are red oaks.

Despite not being considered as ICCAs, the Union of Zapoteca-Chinanteca Communities and the Union of Communities and Oaxaca Forestry Ejidos are examples of successful conservation projects in the SMOax in which documented maintenance of primary vegetation and recovery of forest areas exist (Bray et al., 2003; Klooster & Masera, 2000; Robson, 2007). Conversely, MVO has less ICCAs; particularly the Juxtlahuaca-Mixtepec region has few community-protected areas, and oak species in this region are those with higher rate of habitat loss. Given the considerable number of species and the high rate of transformation of the vegetation cover, which has increased because of the presence of pests (Monroy et al., 2015), a conservation system involving the participation of the local communities should be promoted, following the ICCA model. A similar case is presented in the SMS that has the fewest number of ICCAs, almost all concentrated in the Coatlán region. However, in the SVO, SMS, and CHIM, the main problems for conservation of natural areas are those associated with social disputes over land ownership (Peterson et al., 2003). Currently, in the Chimalapas conservation strategies based on the ICCA model have been adopted, allowing the conservation of forest areas and even contributing to attenuate conflicts over land ownership (Monterrubio & Newing, 2013).

In all cases, the creation of systems of protected areas in the SMOax, a site identified as a priority in all

analyses, is important. The conservation of this area should reassert the importance of the ICCA system created to form community corridors along the municipalities in this region that allow to increase the protected community area, from San Felipe Usila-San Francisco Texmelucán at the northwest to Santa María Ixtepeji-Santa Maria Yavesia at the south. It is undeniable that the vocation of conservation of landholders has proven effective for human development and maintenance of ecosystem services, and this region of the SMOax has been recognized as one of the best examples of conservation and sustainable use of resources in Mexico, even allowing to increase the forest cover. The success of this type of projects is due to the ample awareness of the inhabitants about environmental problems (Van Vleet, Bray, & Durán, 2016).

Lastly, it is clear that the design of conservation areas should consider the ecological differences between the Quercus and Lobatae sections, since for the white oaks some areas identified as priority are found in the arid regions to the north of the MVO, while priority regions for the red oaks are mainly located in the humid parts of the SMOax, SMS, and CHIM.

Official protection in some regions of the SMS and MVO should be considered due to significant losses in forest cover and poor organization among landholders in these areas. However, the large number of rural communities complicates the creation of natural areas with government protection, so in these areas, as in the SMOax, alternatively a network of corridors connecting different community lands and forming an extensive network to protect the montane forests of Oaxaca could be designed.

Appendix A. Number of Records and Taxonomic Remarks About the Oak Species Included in This Study

(continued)

18 Tropical Conservation Science **18** Transfer Conservation Science **18** Transfer Conservation Science 19

Continued

Continued

Species	Previous record number	Final record number	General remarks	Valencia and Nixon (2004)
Q. peduncularis	34	55	Valid species. We found more records. This species is morpho- logically similar to Q. segoviensis and Q. magnoliifolia, but different in the size of the peduncle and because it inhabits in humid low montane areas.	Registered
Q. polymorpha	$\overline{10}$	25	Valid species. We found more records. Species inhabiting tropi- cal areas.	Registered
Q. rugosa	3	63	Valid species. We found more records. This species inhabit high mountain areas, mainly in pine- oak forests.	Registered
Q. sebifera ^a	4	12	Valid species. We found more records. Species inhabiting semi- arid areas.	Registered
Q. segoviensis	\mathbf{H}	20	Registered species to Central America, in mixed forests.	Registered
Q. splendens ^a	3	22	Some specimens recorded as its synonym, Q. sororia.	Registered
Total	323	982		
Section Lobatae				
Q. acatenangensis		6	Valid species, many times incor- rectly identified as Q. ocoteifolia. This species inhabits in pine-oak forests from 1100 to 1600 m.	Not registered
Q. acherdophylla ^a		2	Valid species. Oaxaca is its southern distributional limit. A character- istic species from the Sierra Madre Oriental.	Registered
Q. acutifolia ^a	25	59	This species is considered as a valid taxa in this study, differently to Valencia et al. (2015), because it inhabits mixed and oak forests. and by genetic evidences. We followed then the proposal of Romero et al. (2000).	Registered
Q. affinis ^a	6	$\overline{10}$	Valid species. We found other few specimens in herbaria. Its south- ern distributional limit is Oaxaca. A characteristic species from the Sierra Madre Oriental.	Registered
Q. benthamii		9	Valid species for Oaxaca. Represented in cloud and pine- oak forests.	Registered
Q. candicans	26	78	Valid species. We found more records. This species is charac- teristic to humid environments, such as cloud and mixed forests.	Registered

Continued

Continued

Species	Previous record number	Final record number	General remarks	Valencia and Nixon (2004)
Q. mulleri ^b	6	9	Valid species, we found few other records. Endemic species to Oaxacan cloud forests.	Registered
Q. nixoniana ^a		7	Valid species. Endemic species to cloud forests of the Sierra Madre del Sur.	Registered
Q. ocoteifolia ^a	16	23	Valid species for Oaxaca. Species morphologically similar to Q. laurina, inhabiting lower pine-oak forests (1200-1500 m)	Registered
Q. paxtalensis	3	4	Valid species for Oaxaca. Species also distributed in Chiapas, in lower cloud forests \langle 1200m.	Registered
Q. pinnativenulosa ^a		9	Valid species for Oaxaca, with its southern distributional limit in this Mexican state. Characteristic species of cloud forests in the Sierra Madre Oriental.	Registered
Q. rubramenta ^a	5	9	Valid species with few more records. Endemic species to the cloud and pine-oak forests of the Sierra Madre del Sur.	Registered
Q. salicifolia ^a		6	Valid species for Oaxaca. Endemic species to the lowlands of the Sierra Madre del Sur.	Not registered
Q. sapotiifolia	12	37	Valid species. We found more records. Species also represented in Central America, inhabiting tropical environments of low montane vegetation types.	Registered
Q. sartorii ^a	9	9	Valid species. Oaxaca is its southern distributional limit. Endemic to the Sierra Madre Oriental.	Registered
Q. scytophylla ^a	14	49	Valid species. We found more records. Species represented in pine-oak and oak forests.	Registered
Q. skinneri	4	13	Valid species. We found more records. Species mainly repre- sented in cloud forests of Central America.	Registered
Q. trinitatis ^a		20	Valid species for Oaxaca. Species frequently identified as Q. salicifo- lia or Q. ocoteifolia. Species inha- biting high cloud forests (2000- $2500 \,\mathrm{m}$).	Not registered
Q. uxoris ^a	8	8	Valid species for Oaxaca. Endemic species to cloud forests of the Sierra Madre del Sur, in altitudes between 1800-2100 m.	Registered
Total	419	1,160		

^aSpecies endemic to Mexico.

^bSpecies endemic to Oaxaca.

Appendix B. Richness, Rarity, Irreplaceability, and Species Turnover, in That Order, Using 2.5×2.5 Min and 10×10 Min Grids

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