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Análisis biogeográfico del género *Quercus* (Fagaceae) y estructura genética de *Q. candicans*, *Q. crassifolia* y *Q. castanea* para establecer áreas prioritarias para la conservación de encinos en el estado de Oaxaca, México.

TESIS

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PRESENTA:

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Por medio de la presente me permito informar a usted que en la reunión ordinaria del Subcomité de (Ecologia y Manejo Integral de Ecosistemas), del Posgrado en Ciencias Biológicas, celebrada el día 31 de octubre de 2016, se acordó poner a su consideración el siguiente jurado para el examen **de DOCTOR EN CIENCIAS** del alumno **RAMÍREZ TORO WILFRIDO** con número de cuenta **510007795,** con la tesis titulada: **"Análisis biogeográfico del género *Quercus* (Fagaceae) y estructura genética de *Q. candicans, Q. crassifolia* y *Q. castanea* para establecer áreas prioritarias para la conservación de encinos en el estado de Oaxaca, México"**, bajo la dirección del **Dr. Alberto Ken Oyama Nakagawa.**

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c.c.p. Expediente de la interesado

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A ti, mi querido Ignacio Josafat.

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RESUMEN

México está en quinto lugar entre los países megadiversos y su porción sur pertenece al hotspot mesoamericano, en donde el estado de Oaxaca contiene el 40% de su flora vascular debido a su intrincada topografía, diversidad de hábitats y de condiciones climáticas. Realizamos un análisis multicriterio (riqueza de especies, rareza, irremplazabilidad, recambio y vulnerabilidad) del género *Quercus* (encinos) además de estudiar la diversidad genética y estructura poblacional de tres especies de encinos rojos (*Quercus candicans*, *Q. crassifolia* y *Q. castanea*) para comprender como la fisiografía dirige la diversidad genética y diferenciación poblacional y priorizar áreas de conservación en Oaxaca. Nuestros resultados indican que la Sierra Madre de Oaxaca (SMOax) es la subprovincia fisiográfica con la mayor riqueza (38 especies), rareza e irremplazabilidad de las especies de encinos, seguida por las Montañas y Valles de Occidente (MVO; 29 especies), la Sierra Madre del Sur (SMS; 25 especies) y las Montañas y Valles del Centro (MVO; 20 especies). Las áreas que han retenido la mayoría de la cubierta vegetal primaria de 2000 a 2010 se encuentran principalmente en SMOax, en el distrito de Ixtlán y en SMS, en el distrito de Miahuatlán. Por otro lado, MVO es el área con el mayor disturbio de hábitat, principalmente en los distritos de Juxtlahuaca y Tlaxiaco. Para las poblaciones de las tres especies de encinos rojos encontramos altos niveles de diversidad genética, algunas de ellas presentan un coeficiente de endogamia de Wright de bajo a moderado. El análisis de varianza molecular (AMOVA) mostro que la mayor parte de la variación ocurre dentro de las poblaciones en las tres especies de encinos rojos. Los análisis de resistencia mostraron conectividad entre casi todas las poblaciones de las tres especies y el análisis de barreras encontró algunas

disrupciones genéticas que limitan el flujo génico entre poblaciones de las tres especies. Aun en un ambiente heterogéneo como el de Oaxaca, las tres especies de encinos presentan altos niveles de diversidad genética y conectividad del paisaje. El estado presenta numerosas áreas sin protección oficial (áreas de conservación indígena y comunal) que juegan un papel central como una alternativa para la conservación para 11 especies de encinos. En conclusión, las áreas prioritarias para la conservación del género se localizan principalmente en SMOax y SMS. Para los encinos blancos, es importante el área semiárida de Coixtlahuaca-Teposcolula-Nochixtlán, mientras que para los encinos rojos las regiones más importantes son las áreas húmedas de Tetotitlán, Sola de Vega y Miahuatlán. También se requiere mantener la conectividad genética a través de la conservación de corredores para mantener la cohesión de las especies de encino.

ABSTRACT

México is in fifth place among megadiverse countries and its southern portion belongs to the Mesoamerican hotspot, where Oaxaca state contains 40% of its vascular flora due to its intricate topography, diversity of habitats and climatic conditions. We performed a multicriteria analysis (species richness, rarity, irreplaceability, replacement and vulnerability) of the genus *Quercus* (oaks) in addition genetic diversity and population structure of three species of red oaks (*Quercus candicans, Q. crassifolia* and *Q. castanea*) were studied in order to understand how physiography directs genetic diversity and population differentiation and to prioritize conservation areas in Oaxaca. Our results indicate that the Sierra Madre de Oaxaca (SMOax) is the physiographic subprovince with the highest richness (38 species), rarity and irreplaceability of oak species, followed by the Western Mountains and Valleys (MVO, 29 species) Sierra Madre del Sur (SMS, 25 species) and the Mountains and Valleys of the Center (MVO, 20 species). Areas that have retained the majority of the primary vegetation cover from 2000 to 2010 are mainly located in SMOax, in Ixtlán district and in SMS, in Miahuatlán district. On the other hand, MVO is the area with the greatest disturbance of habitat, mainly in the districts of Juxtlahuaca-Tlaxiaco. For populations of the three red oaks species we find high levels of genetic diversity, some of which present a low to moderate Wright inbreeding coefficient. The analysis of molecular variance (AMOVA) showed that most of the variation occurred within populations in the three-oak species. Resistance analyses showed connectivity among almost all the populations of the three species, and barrier analysis found some genetic breaks that limited gene flow among populations of the three species. Even in a heterogeneous environment such

as in Oaxaca, the three-oak species have high levels of genetic diversity and landscape connectivity. 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 specie. In conclusion, the priority conservation areas for the genus are mainly located in SMOax and SMS. For the white oaks, the semi-arid area of Coixtlahuaca-Teposcolula-Nochixtlán is important, while for red oaks the most important regions are the humid areas of Tetotitlán, Sola de Vega and Miahuatlán. It is also required the maintenance of genetic connectivity through the preservation of corridors, which is necessary to maintain the cohesiveness of the oak species.

1. INTRODUCCIÓN

La distribución geográfica y la diversidad genética poblacional de las especies de plantas y animales de bosques templados es heterogénea y está espacialmente estructurada a diferentes escalas, desde la local (Holderegger & Wagner, 2008) a la de paisaje (Sork et al., 2010; Ashley et al., 2015) y continental (Petit et al., 2002; Wang et al., 2014; 2015). En cada escala los factores ecológicos y genéticos que estructuran la diversidad genética operan a través de la heterogeneidad ambiental, barreras genéticas, rasgos del ciclo de vida de las especies, la interacción con otros organismos y la fragmentación del hábitat mediada por el ser humano (Bacles et al., 2004; Honnay & Jacquemyn, 2007). También, procesos contemporáneos como la deriva génica y la endogamia podrían afectar la distribución espacial de la variación genética y el tamaño efectivo poblacional (O'Connell et al., 2006; Breed et al., 2012). Características ecológicas como la densidad poblacional, dispersión del polen y el comportamiento de los vectores dispersores de semillas, pueden perturbar la capacidad de los individuos para moverse a través de ambientes y afectar el éxito reproductivo y la aptitud poblacional (Barrett & Schluter, 2008; Craft & Ashley, 2010; Sagnard et al., 2011). Además, las barreras físicas tales como sistemas montanos, grandes cuencas o valles y áreas de hábitat inapropiado, podrían llevar a la alteración del flujo génico entre poblaciones a escala regional (Sork & Waits, 2010; Manel & Holderegger, 2013; Wang et al., 2015; Galván-Hernández et al., 2015). También, la interrupción de la conectividad natural entre poblaciones debido a actividades antropogénicas llevaría a disminuir la variabilidad genética al aumentar la endogamia y la deriva génica y aumentaría la diferenciación genética, resultando en poblaciones fragmentadas aisladas (Vakkari et al., 2006; Farwig et al., 2006; Herrera-Arroyo et al., 2013).

Los actuales patrones distribucionales de especies son el producto de condiciones ambientales y factores históricos que generan diversidad de gradientes en plantas (O'Brien, 1993; Francis & Currie, 2003; Kluge, Kessler & Dunn, 2006; Kessler, Kluge, Hemp & Ohlemüller, 2011), mamíferos (McCain, 2005, 2007), aves (McCain, 2009; Kissling, Sekercioglu & Jetz, 2012) e insectos (Kerr, Vincent & Currie, 1998). A escala regional los gradientes de riqueza de especies se correlacionan con la temperatura, precipitación, productividad, estacionalidad y heterogeneidad del hábitat (Hawkins et al., 2003; Currie et al., 2004; Kissling, Sekercioglu & Jetz, 2012). Muchos estudios muestran una relación entre la riqueza de especies y la altitud (Rahbek, 1997; Kessler, 2000); otros destacan que los patrones más complejos de riqueza en áreas específicas son producto de las historias evolutivas de los taxa (Wiens & Donoghue, 2004; Ricklefs, 2004; Kissling, Sekercioglu & Jetz, 2012). Así, diferencias en las tasas de diversificación pueden proveer alternativas o explicaciones complementarias para comprender los patrones de riqueza.

Miiermeier, Goettsch-Mittermeier & Robles-Gil (1997) encontraron que 70% de la biodiversidad global se concentra solo en 17 países megadiversos entre los que México ocupa el quinto lugar. En nuestro país, uno de los principales hotspots de biodiversidad se localiza en el estado de Oaxaca, que contiene cerca del 40% de la flora vascular de México (García-Mendoza, 2004; Ortiz-Pérez et al., 2004) y que también representa el norte del hotspot mesoamericano en la zona de transición mexicana (Morrone, 2001). 3,762 de las especies de plantas oaxaqueñas son endémicas para México y 732 también lo son para el estado (Villaseñor & Ortíz, 2014). Esta diversidad excepcional está relacionada con la intrincada topografía y diversidad climática de la región, la cual es un área de convergencia de los dos sistemas fisiográficos principales (Sierra Madre Oriental y Sierra Madre del Sur). Esto crea un paisaje complejo con alta biodiversidad a lo largo de montañas, valles y cuencas (Ferrusquía-Villafranca, 1993; Ortiz-Pérez et al., 2004; Trejo, 2004). Particularmente las especies de encinos dominan los bosques templados del estado de Oaxaca con 52 de las 161 especies de *Quercus* reportadas en todo México, 24 perteneces a la sección *Quercus* (encinos blancos) y 28 de la sección *Lobatae* (encinos rojos) (Valencia et al., 2002; Valencia, 2004). Ambas secciones se distribuyen a lo largo de un gradiente altitudinal desde los 150 m en las planicies costeras hasta los 3,300 m en la Sierra Madre de Oaxaca y se distribuyen en al menos cinco de las grandes subprovincias biogeográficas en las que se se divide Oaxaca: Sierra Madre de Oaxaca (SMOax), Montañas y Valles de Occidente (WOMV), Montañas y valles centrales (CMV), Región de los Chimalapas (CHIM) y Sierra Madre del Sur (SMS) (Ortíz-Pérez et al., 2004; Valencia & Nixon, 2004; Vázquez et al., 2004) (Figura 1).

Las especies de encino se caracterizan genéticamente por presentar alta variación dentro y entre poblaciones (Peñaloza-Ramírez et al., 2010; Albarrán-Lara et al., 2010; Aldrich & Cavender-Bares, 2011). Un estudio reciente de Valencia-Cuevas (2014) mostró que la diversidad genética de las poblaciones de *Quercus castanea* parece estar fuertemente relacionada a el número de especies de encino que crecen en simpatría. Por lo tanto, esperamos que la alta biodiversidad de especies en Oaxaca haya sido determinada por la interacción entre la ecología y evolución basados en la fisiografía heterogénea que dirige la variación genética y diferenciación de estas tres especies de encinos.

Algunas estrategias para definir las áreas para la conservación de la biodiversidad asumen que la elección de especies blanco podría proveer una sombrilla protectora para numerosas especies coexistentes. Torres, Luna & Oyama (2011) consideran que las comunidades de encinos constituyen un modelo adecuado para la conservación en los sistemas montanos de los bosques oaxaqueños debido a que los encinos tiene un papel ecológico principal como especie dominante en muchos bosques templados (Valencia, 2004). Además, las especies de encinos juegan un papel clave en el ensamble ecológico de comunidades de organismos tales como hongos ectomicorrizicos (Morris, Pérez, Smith & Bledsoe, 2009), insectos formadores de agallas (Pérez, González, Oyama & Cuevas, 2016) y vertebrados que comen semillas (López & Manson, 2006), entre otros. Los bosques de encinos también proveen hábitat para vertebrados (Brawn, 2006), artrópodos (Tovar, Cano & Oyama, 2004; Tovar & Oyama, 2006) y epífitas (Holz & Gradstein, 2005).

Es por ello que el objetivo principal de este estudio fue identificar áreas prioritarias para la conservación dentro del estado de Oaxaca, México. Para ello aplicamos un análisis multicriterio basado en la riqueza de especies, rareza, recambio, irremplazabilidad y vulnerabilidad de especies de *Quercus* en el estado, además de analizar la estructura y diversidad genética de tres especies de encinos rojos (*Quercus candicans*, *Q. crassifolia* y *Q. castanea*) para comprender como la fisiografía heterogénea determina la conectividad genética entre poblaciones a través de la distribución geográfica de estas especies.

2. ARTÍCULO REQUISITO

A multi-criteria analysis for prioritizing areas for conservation of oaks (Fagaceae: *Quercus*) in Oaxaca, southern México

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Abstract

México 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 multi-criteria analysis (species richness, rareness, irreplaceability, turnover and vulnerability) was used to prioritize conservation areas in Oaxaca, using as model system genus Quercus (the oaks), due to its high diversity and ecological importance in the state. 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 (MVC; 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 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 semi-arid area of Coixtlahuaca-Teposcolula-Nochixtlán 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 (O'Brien, 1993; Francis & Currie, 2003; Kluge, Kessler & Dunn, 2006; Kessler, Kluge, Hemp & Ohlemüller, 2011), mammals (McCain, 2005, 2007), birds (McCain, 2009; Kissling, Sekercioglu & Jetz, 2012), 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 (Hawkins et al., 2003; Currie et al., 2004; Kissling, Sekercioglu & Jetz, 2012). Several studies have also found a clear relationship between species richness and altitude (Rahbek, 1997; Kessler, 2000). Others have also highlighted that more complex patterns of species richness in specific areas is the product of the evolutionary histories of taxa (Wiens & Donoghue, 2004; Ricklefs, 2004; Kissling, Sekercioglu & Jetz, 2012). 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 & Robles-Gil (1997) ascertained that 70% of the world's biodiversity is concentrated in only 17 megadiverse countries. México occupies the fifth place among those megadiverse countries (Mittermeier, Goettsch-Mittermeier & Robles- Gil, 1997). However, most of the biodiversity of México 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 México, with species belonging to both Nearctic and Neotropical biotas (Flores & Gerez, 1994). This state covers only 4.78% of the total surface of the country (García, 2004), but contains around 9019 vascular plant species out of the 21841 species recorded for México (41.3%). Additionally, 3762 of the plant species in Oaxaca are endemic to México, 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). 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 Sierra Madre del Sur (Lorence & García, 1989; García, 2004).

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 & 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, Hernández & Figueroa, 2004; Valencia & Nixon, 2004). Ortiz, Hernández & Figueroa (2004) divided Oaxaca into 12 physiographic sub-provinces: Depresión del Balsas (DB); Depresión ístmica de Tehuantepec (DIT); Fosa de Tehuacán (FT); Montañas y Valles del Centro (MVC); Montañas y Valles del Occidente (MVO); Planicie Costera del Golfo (PCG); Planicie Costera del Pac.fico (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). Both red and white oaks inhabit 10 of the 12 sub-provinces in the state, excluding the PCT and FT (Valencia & Nixon, 2004) (Fig. 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 & 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, 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).

Multi-criteria 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, México, applying a multi-criteria 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: (1) taxonomic richness, defined as the total number of species present in a given area; (2) 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, Luna & Oyama, 2011), (3) species turnover among areas, considering turnover as a measure of the number of different species between two areas, and (4) the estimation of habitat loss for forests where oaks occur, in the context of richness and endemism patterns.

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 & Nixon (2004) and is discussed in detail in Appendix 1. The presence records were obtained from herbarium specimens (MEXU, FCME, OAX, SERO, MO), Global Biodiversity Information Facility (www.gbif.org) and data from monographic and floristic studies reviewed by Torres, Luna & Oyama (2011). The information was condensed into a single database of 2143 non-duplicated georeferenced records. Distributional maps of each of the 54 oak species were obtained using ArcGIS ver. 9.2 (ESRI, 2006).

Study area

Our study covers the entire state of Oaxaca, located in the southern portion of México between 15º 39’ and 18º 42’ N and 93º 52’ and 98º 32’ W, with an area of 95,364 km^2 (Velázquez et al., 2003; Espejo, López, Martínez & Pulido, 2007). The largest number of oak records are located in five regions proposed by Ortíz, Hernández & Figueroa (2004): a) Montañas y Valles del Occidente (MVO), which comprises an area of 21,263 km^2 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 (12-18 ºC annual average, 500-1200 mm annual rainfall), but the western portion receives more precipitation than its eastern sector; b) Sierra Madre de Oaxaca (SMOax), with 17,520 km^2 in area, with a relief amplitude of 2500 m, conspicuous altitudinal fringes, various and asymmetric orographic axes and short and steep slopes. It is characterized by semi-warm 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 2500 mm to 4000 mm); c) Montañas y Valles del Centro (MVC) covers 6663 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 semi-warm semiarid climates. It is the mountain region with higher temperature (annual mean temperature is 22-26 ºC) and lower rainfall (500-800 mm); d) Sierra de los Chimalapas (CHIM) covers 5816 km^2; 20 % of its land surface is mountainous and occurs above 1000 m; 50% are high hills and 30 % are low hills. This subprovince has semi-warm wet to sub-humid climates

(1500-2000 mm annual rainfall) because the Pacific winds; and e) Sierra Madre del Sur (SMS), with 12,350 km^2 in area, characterized by a highly variable relief, with relatively low western mountains (< 2000 m) and higher systems at the Miahuatlán Sierra. The climate is warm and temperate subhumid (1000-1500 mm annual rainfall) (Ortiz, Hernández & Figueroa, 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: (i) 205 grids of 10 x 10 minutes (17.6 x 18.4 km) of latitude and longitude, (ii) 524 grids of 5 x 5 minutes (8.3 x 9.2 km), and (iii) 1316 grids of 2.5 x 2.5 minutes (4.15 x 4.6 km). However, our preliminary results indicated that, even though the results using the three different grid sizes were largely congruent, the 5 x 5 minutes 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 x 5 minutes grid, but the maps for the other two grid sizes are presented in Appendix 2.

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 & 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, Laffan, Linder & Monro, 2001). To obtain a rareness score for a cell, these weights were summarized for all species occurring in the cell (Crisp, Laffan, Linder & Monro, 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, Laffan, Linder & Monro, 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 (GBIF) records. In this matrix, we considered the geographical units identified by Torres-Miranda, Luna-Vega, & Oyama (2013), 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 above 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 (Lennon, Koleff, Greenwood & Gaston, 2001; Koleff, Gaston & Lennon, 2003; Baselga, 2010), using β_{SOR} and β_{JAC} indices. SØrensen index (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, Gaston & Lennon, 2003) while the Jaccard index (βJAC) actually describes the gain or loss of species without the bias of richness (Lennon, Koleff, Greenwood & Gaston, 2001; Koleff, Gaston & Lennon, 2003). β_{SOR} and β_{JAC} 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/presence using intervals of 100 m of altitude across the full elevational distribution for the genus (200 – 3000 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, Velázquez, Palacio, Bocco, Peralta & Prado, 2002; SEMARNAT, 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, Mittermeier, Mittermeier, da Fonseca & Kent, 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, Mittermeier, Mittermeier, da Fonseca & Kent, 2000).

Prioritizing conservation areas

Conservation priority areas were defined at the statewide level. First, results obtained with grid cells of 5' x 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 & Pressey (2000) and Sarkar et al. (2006) non-protected areas in a network of protected natural areas 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 above. 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 (ESRI, 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 Cuicatlán, 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 20 species. Eleven species are recorded in CHIM (Fig. 2 and 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 theJuxtlahuaca and Mixtepec districts in MVC with six species (Fig. 2). For red oaks, the districts with higher richness are Ixtlán (13 species), Teotitlán (12 species) and Cuicatlán (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 (Fig. 2 and 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 (Juchitán district) (Fig. 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 (Fig. 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 Ixtlán in the SMOax; Yautepec and in the limits between Juquila- Miahuatlán in the SMS, and Juchitán in the CHIM (Fig. 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 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 Fig. 3 and 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 (Fig. 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 (Fig. 3).

Turnover patterns

Turnover patterns for the genus coincide in general with the limits among the physiographic subprovinces (Fig. 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 (Fig. 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 (Fig. 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 (Fig. 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 1800–2200 masl. For white oaks, the highest richness occurs between 2000–2200 masl, while red oaks showed a bimodal pattern with peaks of richness at 1700-2000 and 2200–2400 masl. In this last altitudinal interval, a decrease in the richness of white oaks was observed (Fig. 4).

We also observed that oaks with restricted altitudinal distributions occur mostly between 2000–2500 masl. From 1300 to 2300 masl there is an increase in the rareness index. In the red oaks, altitudes around 1700 masl are also important in terms of rareness. The white oak species that have a very restricted geographic distribution in México are found at 2200 masl, while in the case of the red oaks such species are found between 2200-2400 masl, with the 1000 and 1700 masl altitudes also being important. The greater species turnover was observed at 1100, 1600, 2300, 2600 and 2800 masl. See Fig. 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* occur 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 2010for both the genus and sections levels are located in the north of the Ixtlán district (from the Macuiltianguis to the Santa María Yavesía municipalities) in the SMOax, as well as the border of the Ixtlán district with the Cuicatlán and Tuxtepec districts (Fig. 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, Capul.Ipam, 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 (Fig. 6).

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 (Fig. 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 Lachigurí municipality in the Tehuantepec district (Fig. 6).

For section *Lobatae*, the area with more importance is located 1 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 (Fig. 6).

Discussion

The high biological diversity present in the state of Oaxaca is related to its physiography, which originated 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, 2004). Here, we analyzed at the state level the distribution of 54 oak species, 30 of which are considered endemic to México (55.5%), a higher percentage than for endemic flowering plants present in Oaxaca according to the estimations of Villaseñor & Ortiz (2014). However, there are only two oak species endemic to Oaxaca, even though Valencia & 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 oaks 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, 2004), gymnosperms (Contreras & Luna, 2006) and birds and mammals (Koleff, Gaston, & Lennon, 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 (Bojorquez, Azuara, Ezcurra & Flores, 2005). In the MVO, the Juxtlahuaca area is a priority center for the conservation of oaks and also for terrestrial vertebrates (Bojorquez, Azuara, Ezcurra

& Flores, 2005), 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, what has resulted in little floristic knowledge of this region (García, 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, 2004) mainly due to social conflicts. The SMS and SMOC have been considered priority areas for the conservation of vertebrates and herpetofauna, respectively (Bojorquez, Azuara, Ezcurra & Flores, 2005; 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, Gaston, & Lennon, 2003), and mammals (Iloldi, Fuller, Linaje, Pappas, Sánchez & Sarkar, 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 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 (Iloldi, Fuller, Linaje, Pappas, Sánchez & Sarkar, 2008). The rareness pattern found in the SMOC is similar to that found for mammals (Iloldi, Fuller, Linaje, Pappas, Sánchez & Sarkar, 2008) and birds (Peterson et al., 2003).

Our results showed that the most important altitudinal interval for the white oaks is between 2000-2200 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). In order to make conservation more effective, it is important to consider areas that show a wide altitudinal range as proposed by Zacarías & del Castillo (2010).

Currently, habitat loss is a common phenomenon in all ecosystems, the temperate forests being the most drastically reduced by human influence (Rzedowski, 1978; Challenger, 1998). 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 1400 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 to 21% identified for temperate forests during 1980-2000 (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 semi-arid 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 *Q. frutex* and *Q. 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, 2007), Orchidaceae (Solano, Alonso, Rosado, Aguilar & García, 2008), and several tree species of temperate forest (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 (Bojorquez, Azuara, Ezcurra & Flores, 1995; Peterson et al., 2003), particularly birds (Peterson et al., 2003), mammals (Iloldi, Fuller, Linaje, Pappas, Sánchez & Sarkar, 2008; Briones, Cortés & Lavariega, 2015) 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, Luna & Oyama (2011) proposed that the prioritizing of conservation should focus on those areas without official protection. In general, the system of Protected Natural Areas (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 Tonal. and Hierve el Agua State Park protect a total of 18 oak species.

However, in Oaxaca, there are alternative conservation areas 1 called Indigenous Conservation and Community Areas (ICCAs) (Robson, 2007; Martin, Camacho, del Campo, Fonseca, Mendoza & Ortiz, 2011). According to Martin, Camacho, del Campo, Fonseca, Mendoza & Ortiz (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 protected natural areas (see Table 1 for details). The ICCA system in Oaxaca preserves mostly pine oak-forests as well as cloud forests (Monroy, Sánchez, Briones, Lira & Mass, 2015) what can explain the high number of protected oak species in an area that is about 10% the size of the officially decreed protected natural areas. 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 (UZACHI) and the Union of Communities and Oaxaca Forestry Ejidos (UCEFO) are examples of successful conservation projects in the SMOax in which documented maintenance of primary vegetation and recovery of forest areas exist

(Klooster & Masera, 2000; Bray, Merino, Negreros, Segura, Torres & Vester, 2003; 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, Sánchez, Briones, Lira & Mass, 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 1 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 Yavesía 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 México, 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 & Dur.n, 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.

Acknowledgments

Thanks to Susana Valencia for useful information about the taxonomic and distributional information about the Oaxaca oaks. WRT was supported by CONACYT fellowship 229358 and by the Posgrado en Ciencias Biológicas, UNAM. This project was supported by PAPIIT-DGAPA (UNAM) project RV201015 and IA204615 and CONACYT 240136.

3. TABLAS DEL ARTÍCULO REQUISITO

Table 1. List of oak species recorded for Oaxaca by section. The third and fourth columns indicate if these species are endemic to Mexico or to the state of Oaxaca. Abbreviations: QF = *Quercus* Forest; PQF/ QPF = Mixed Forest; CF = Cloud Forest; S = shrubby vegetation; TF – Tropical Forest; species protected (PRO) in PNA (Protected Natural Areas), in *species protected from the Tehuacán-Cuicatlán Natural Biosphere, or (ICCA) Indigenous and Community Conserved Areas. Growth form: tree or shrub. The two last columns indicate the minimum and maximum elevation in which each species is found.

SECTION	SPECIES	MEXICO	OAXACA	QF	PQF-QPF	CF	S	TF	PNA	ICCA	PRO	tree	shrub	MIN ELEV	MAX ELEV
Lobatae	*Q. acatenangensis*			X	X				X	X	X	X		1500	2900
Lobatae	*Q. acherdophylla*	X				X						X		1800	2100
Lobatae	*Q. acutifolia*	X			X							X		1800	2500
Lobatae	*Q. affinis*	X			X	X				X	X	X		2200	2800
Lobatae	*Q. benthamii*					X						X		1000	1800
Lobatae	*Q. candicans*				X	X						X		1500	2500
Lobatae	*Q. castanea*			X	X				X*		X*	X		1400	2600
Lobatae	*Q. conspersa*			X				X		X	X	X		600	2000
Lobatae	*Q. conzattii*	X		X								X		1600	2400
Lobatae	*Q. cortesii*									X	X	X		500	1500
Lobatae	*Q. crassifolia*				X				X	X	X	X		1700	2800
Lobatae	*Q. crassipes*			X					X*		X*	X		2300	2400
Lobatae	*Q. crispifolia*			X	X			X				X		800	1100
Lobatae	*Q. aff delgadoana*	X		X		X						X		2100	2300
Lobatae	*Q. depressa*	X			X		X					X		2400	3000
Lobatae	*Q. elliptica*			X	X			X		X	X	X		900	2400
Lobatae	*Q. grahamii*	X			X				X*		X*	X		1800	2400
Lobatae	*Q. laurina*	X			X	X			X		X	X		1900	2800
Lobatae	*Q. mulleri*	X	X		X	X						X		1600	2000
Lobatae	*Q. nixoniana*	X				X				X	X	X		2000	2400
Lobatae	*Q. aff ocoteifolia*			X	X							X		1600	2600
Lobatae	*Q. paxtalensis*				X			X				X		800	1200
Lobatae	*Q. pinnativenulosa*	X				X						X		1300	1800
Lobatae	*Q. rubramenta*	X			X	X						X		2200	2600
Lobatae	*Q. salicifolia*	X			X			X				X		800	1000
Lobatae	*Q. sapotiifolia*			X	X			X		X	X	X		400	900
Lobatae	*Q. sartorii*	X				X						X		1400	1700
Lobatae	*Q. scytophylla*	X		X	X	X						X		1600	1900
Lobatae	*Q. skinneri*					X		X		X	X	X		1100	1500
Lobatae	*Q. trinitatis*					X						X		2300	2700
Lobatae	*Q. uxoris*	X				X						X		1500	2000
Quercus	*Q. corrugata*					X				X	X	X		1900	2400

Quercus	*Q. deserticola*	X		X			X		X*		X*	X		2100	2500
Quercus	*Q. frutex*	X		X			X		X*		X*		X	2200	2500
Quercus	*Q. glabrescens*	X			X		X					X		2300	3000
Quercus	*Q. glaucescens*	X		X	X			X		X	X	X		200	1000
Quercus	*Q. glaucoides*	X		X	X		X	X	X	X	X	X		1000	2200
Quercus	*Q. greggii*	X		X			X		X*		X*	X		2100	2300
Quercus	*Q. insignis*				X	X						X		1100	1600
Quercus	*Q. laeta*	X		X	X				X*		X*	X		2000	2400
Quercus	*Q. lancifolia*					X				X	X	X		1000	1400
Quercus	*Q. liebmannii*	X		X	X				X	X	X	X		1600	2400
Quercus	*Q. macdougallii*	*X*	X		X	X						X		2500	2800
Quercus	*Q. magnoliifolia*	*X*		X	X			X	X		X	X		800	2200
Quercus	*Q. martinezii*	X			X	X						X		1800	2200
Quercus	*Q. microphylla*	X					X		X*		X*	X	X	2200	2400
Quercus	*Q. obtusata*	X		X	X		X		X*		X*	X		1500	2500
Quercus	*Q. oleoides*			X	X			X		X	X	X		200	1000
Quercus	*Q. peduncularis*			X	X							X		800	2000
Quercus	*Q. polymorpha*			X		X		X	X*		X*	X		1300	2100
Quercus	*Q. rugosa*			X	X				X		X	X		2000	2800
Quercus	*Q. sebifera*	X					X		X*		X*	X		2000	2200
Quercus	*Q. segoviensis*			X	X							X		1800	2200
Quercus	*Q. splendens*	X			X							X		1000	1900
Section Lobatae		16	1	11	18	15	1	7	6	9	13	31	0	400	3000
Section Quercus		15	1	14	15	6	8	5	12	6	16	22	2	200	3000
Genus Quercus		31	2	25	33	21	9	12	18	15	29	53	2	200	3000

Table 2. Matrix used to correct the rareness index based on the presence/absence of species in 15 geographical units: (SMOcc) Sierra Madre Occidental, (SMOr) Sierra Madre Oriental, (TMVB) Trans-Mexican Volcanic Belt, (MEC) Meseta Central, (SMS) Sierra Madre del Sur, (SMOax) Sierra Madre de Oaxaca, (SMCG) Sierra Madre de Chiapas-Guatemala, (COMA) Montañas de Comayagua. (n-) northern, (s-) southern, (c-) central, (w-) western, (e-) eastern. WF: Weighted factor used to calculate the irreplaceability index. **species endemic to the Oaxaca state, * species endemic to Mexico.

SECTION	SPECIES	n-SMOcc	s-SMOcc	n-SMOr	c-SMOr	s-SMOr	w-TMVB	c-TMVB	e-TMVB	w-MEC	e-MEC	w-SMS	e-SMS	SMOax	SMCG	COMA	TOTAL	**WF**
Lobatae	*Q. acatenangensis*													1	1		2	**9**
Lobatae	*Q. acherdophylla**					1			1					1			3	**8**
Lobatae	*Q. acutifolia**						1	1	1			1	1	1			6	**5**
Lobatae	*Q. affinis**			1	1	1								1			4	**7**
Lobatae	*Q. benthamii*												1		1	1	3	**7**
Lobatae	*Q. candicans*		1			1	1	1	1			1	1	1	1		9	**2**
Lobatae	*Q. castanea*	1	1			1	1	1	1			1	1	1	1		10	**1**
Lobatae	*Q. conspersa*						1	1	1			1	1	1	1	1	8	**3**
Lobatae	*Q. conzattii**		1									1	1	1			4	**7**
Lobatae	*Q. cortesii*												1	1	1	1	4	**7**
Lobatae	*Q. crassifolia*	1	1			1	1	1	1			1	1	1	1		10	**1**
Lobatae	*Q. crassipes**						1	1	1					1			4	**7**
Lobatae	*Q. crispifolia*					1						1	1		1	1	5	**6**
Lobatae	*Q. aff delgadoana**				1	1								1			3	**8**
Lobatae	*Q. depressa**					1			1					1			3	**8**
Lobatae	*Q. elliptica*		1			1	1	1				1	1	1	1	1	9	**2**
Lobatae	*Q. grahamii**											1	1				2	**9**
Lobatae	*Q. laurina**						1	1	1			1	1	1			6	**5**
Lobatae	*Q. mulleri***												1				1	**10**
Lobatae	*Q. nixoniana**						1						1	1			3	**8**
Lobatae	*Q. aff ocoteifolia*					1							1	1	1		4	**7**
Lobatae	*Q. paxtalensis*												1		1		2	**9**
Lobatae	*Q. pinnativenulosa**			1	1	1								1			4	**7**
Lobatae	*Q. rubramenta**											1	1				2	**9**
Lobatae	*Q. salicifolia**						1					1	1				3	**8**
Lobatae	*Q. sapotiifolia*					1							1	1	1	1	5	**6**
Lobatae	*Q. sartorii**		1	1	1									1			4	**7**
Lobatae	*Q. scytophylla**	1	1				1	1				1	1	1	1		8	**3**
Lobatae	*Q. skinneri*													1	1	1	3	**8**
Lobatae	*Q. trinitatis*													1	1		2	**9**
Lobatae	*Q. uxoris**						1					1	1				3	**8**
Quercus	*Q. corrugata*					1							1	1	1	1	5	**5**
Quercus	*Q. deserticola**		1				1	1	1		1			1			6	**5**
Quercus	*Q. frutex**						1	1	1		1			1			5	**6**
Quercus	*Q. glabrescens**							1	1	1	1	1	1	1			7	**4**

Quercus	*Q. glaucescens**		1				1					1	1				4	**7**
Quercus	*Q. glaucoides**		1				1	1	1	1	1	1	1	1			9	**2**
Quercus	*Q. greggii**			1	1	1			1	1	1			1		1	8	**2**
Quercus	*Q. insignis*											1	1	1	1	1	5	**6**
Quercus	*Q. laeta**		1		1	1	1	1	1	1	1	1	1	1			11	**1**
Quercus	*Q. lancifolia*					1								1	1		3	**8**
Quercus	*Q. liebmannii**											1	1	1			3	**8**
Quercus	*Q. macdougallii***													1			1	**10**
Quercus	*Q. magnoliifolia**		1				1	1		1		1	1				6	**5**
Quercus	*Q. martinezii**						1					1	1				3	**8**
Quercus	*Q. microphylla**		1	1	1		1	1	1	1	1		1				9	**2**
Quercus	*Q. obtusata**						1	1	1	1	1	1	1	1			8	**3**
Quercus	*Q. oleoides*				1	1						1	1	1	1	1	7	**3**
Quercus	*Q. peduncularis*						1					1	1	1	1	1	6	**5**
Quercus	*Q. polymorpha*			1	1	1								1	1		5	**6**
Quercus	*Q. rugosa*	1	1	1	1	1	1	1	1	1	1	1	1	1	1		14	**1**
Quercus	*Q. sebifera**			1	1	1								1	1		5	**6**
Quercus	*Q. segoviensis*													1	1	1	3	**8**
Quercus	*Q. splendens**						1					1	1				3	**8**

Table 3. Areas in Oaxaca representing the most important centers of oak species richness, rareness or irreplaceability at the genus and section levels. The number of species (richness), rareness or irreplaceability indices are shown, only for the most important areas. The different physiographic subprovinces are abbreviated as follows: CHIM = Sierra de los Chimalapas; MVO = Montañas y Valles del Occidente; SMOax = Sierra Madre de Oaxaca; and SMS = Sierra Madre del Sur.

Municipalities	District	Richness			Rareness			Irreplaceability		
		Lobatae	*Quercus*	Genus	*Lobatae*	*Quercus*	Genus	*Lobatae*	*Quercus*	Genus
SMOax										
Santa María Teopoxco / San Lucas Zoquiápam	Teotitlán	12	2	14	>0.6		>0.7	> 4		> 5
Santa Ana Cuauhtémoc	Teotitlán	6	6	12						
Teotitlán de Flores Magón	Teotitlán	9						3 - 4		3 - 4
Mazatlán Villa de Flores	Teotitlán							2 - 3		
San Pedro Yólox	Ixtlán	13	6	19	0.4 - 0.5	0.2 - 0.3	>0.7	3 - 4	1 - 2	> 5
Ixtlán de Juárez	Ixtlán	11	6	17		0.2 - 0.3	0.4 - 0.5		1 - 2	3 - 4
Santa María Yavesia	Ixtlán	11	4	15	0.3 - 0.4		0.4 - 0.5	2 - 3		
San Pablo Macuiltianguis	Ixtlán	9	7	16		>0.3	0.4 - 0.5		> 2	3 - 4
Capulálpam de Méndez	Ixtlán	9	4	13						
Cuyamecalco Villa de Zaragoza	Cuicatlán	8								
San Juan Quiotepec	Ixtlán	8	5	13			0.4 - 0.5			
Totontepec Villa de Morelos	Mixe	8								
Santa María Jaltianguis	Ixtlán	6	6	12						
San Juan Atepec	Ixtlán	6	6	12		0.2 - 0.3			> 2	3 - 4
San Andrés Solaga / San Andrés Yaa	Villa Alta	7	5	12					1 - 2	
Tlalixtac de Cabrera	Centro	5	7	12						
San Felipe Usila	Ixtlán				0.3 - 0.4			2 - 3		
San Juan Tepeuxila								2 - 3		
MVO										
Santiago Textitlán	Sola de Vega	8								

Santa María Ixcatlán	Teotitlán		7							
San Juan Teposcolula / San Pedro y San Pablo Teposcolula	Teposcolula	7	6	13		0.2 - 0.3				
San Miguel Chicahua / Santiago Apoala	Nochixtlán		6			0.2 - 0.3	0.4 - 0.5			
Santo Domingo Yanhuitlán	Nochixtlán		6							
Villa de Tamazulapam del Progreso	Teposcolula		6			0.2 - 0.3			1 - 2	
Tepelmeme Villa de Morelos	Coixtlahuaca		6			>0.3			1 - 2	
San juan Bautista Coixtlahuaca	Coixtlahuaca								1 - 2	
San Martín Itunyoso	Tlaxiaco	7	6	13						
CHIM										
Santo Domingo Zanatepec	Juchitán						0.4 - 0.5			
San Miguel Chimalapa	Juchitán	8			0.3 - 0.4		0.4 - 0.5	2 - 3		3 - 4
San Jerónimo Coatlán	Miahuatlán							2 - 3	1 - 2	
SMS										
San Carlos Yautepec	Yautepec				0.4 - 0.5		0.5859	> 4		4 - 5
Santa María Ecatepec	Yautepec				0.3 - 0.4			3 - 4		4 - 5

Table 4. Habitat loss (in ha), disturbance and *Quercus* conservation in Oaxaca, Mexico. Primary vegetation, secondary vegetation and habitat loss (years 2000-2010). Results are shown at genus level and by section.

GROUP	2000	2010	2010 Primary vegetation	2010 Secondary vegetation	LOST	% LOST	% PRIM	% SEC
Quercus (genus)	7,083,990	6,670,867	2,794,115	3,876,751	413,123	5.83%	41.89%	58.11%
Lobatae	3,061,918	2,909,138	1,083,880	1,825,257	152,780	4.99%	37.26%	62.74%
Quercus s. s.	4,022,071	3,761,729	1,710,234	2,051,494	260,342	6.47%	45.46%	54.54%

4. FIGURAS DEL ARTICULO REQUISITO

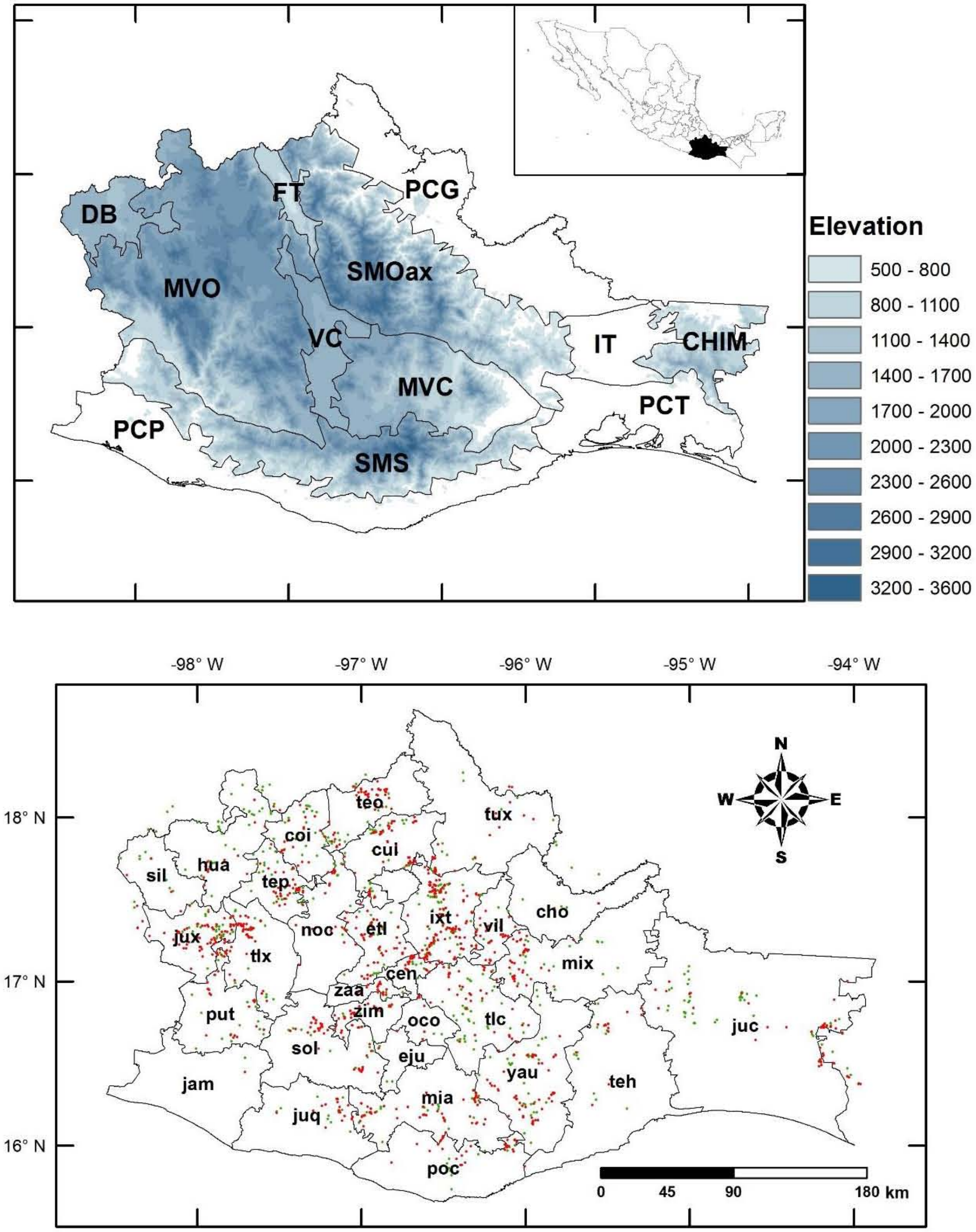


Figure 1. Physiographic sub-provinces of Oaxaca based on Ortiz-Pérez, Hernández-Santana, & Figueroa (2004): Depresión del Balsas (DB); Fosa de Tehuacán (FT); Istmo de Tehuantepec (IT); Montañas y Valles del Centro (MVC); Montañas y Valles del Occidente (MVO); Planicie Costera del Golfo (PCG); Planicie 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). 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); Zimatlán (zim). Green dots are records of species in the *Quercus* section and red dots are records of species in the *Lobatae* section.

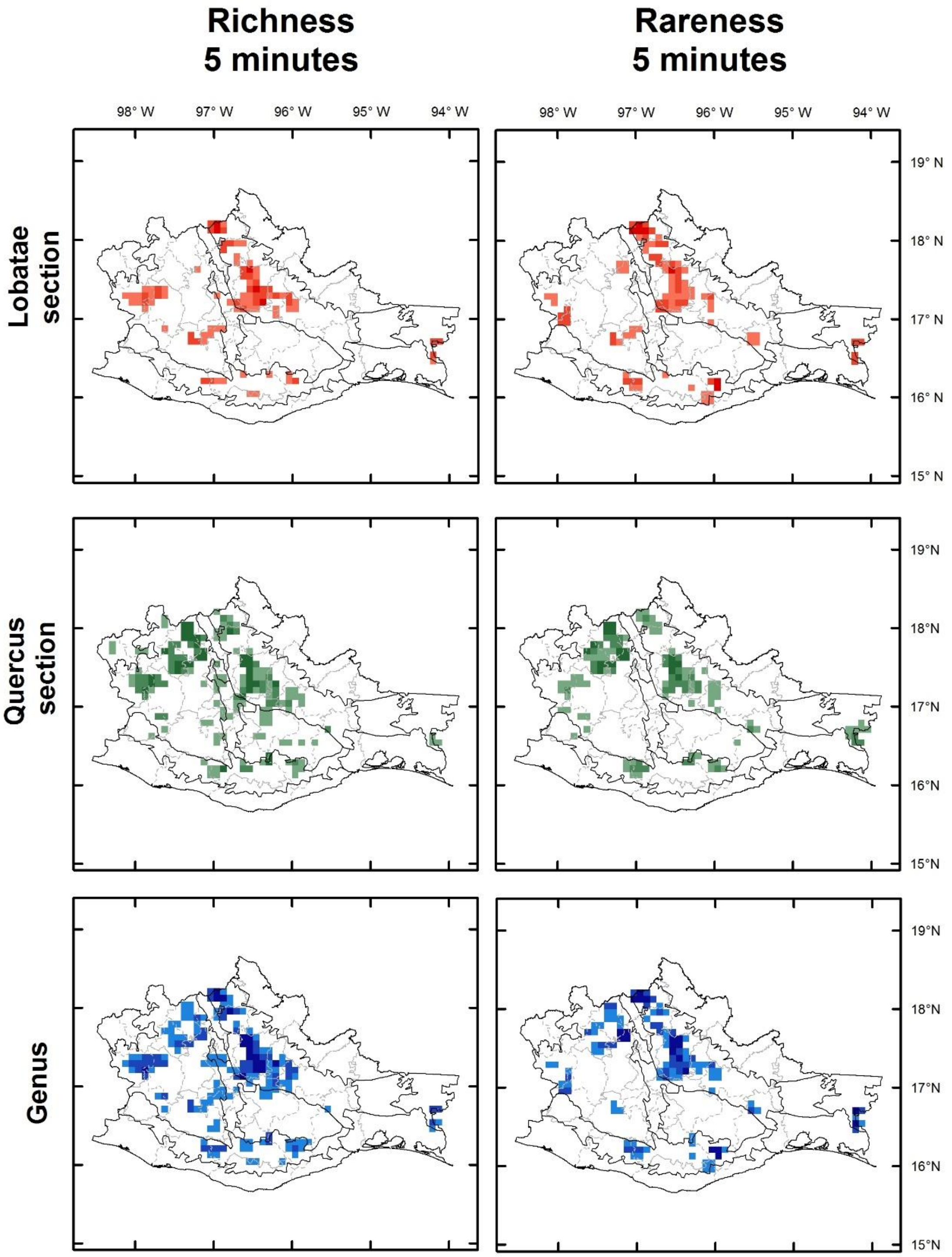


Figure 2. Patterns of richness and rareness for the *Lobatae* section, the *Quercus* section and the whole genus in Oaxaca using a 5 x 5 minutes grid. The cells with greater richness or rareness are indicated in darker colors. Black lines delimit the physiographic subprovinces and gray lines delimit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

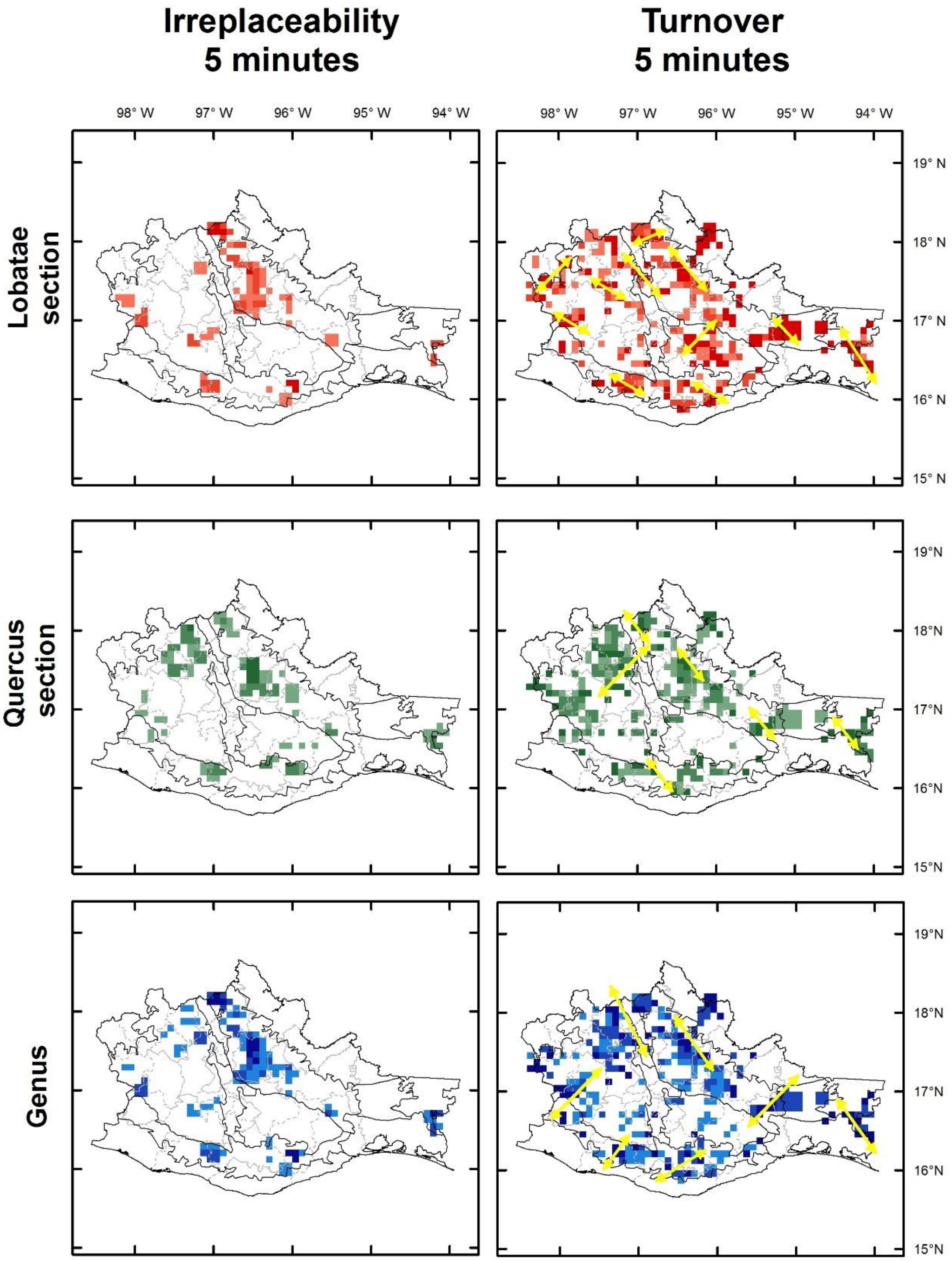


Figure 3. Patterns of irreplaceability for the Lobatae section, the Quercus section and the whole genus in Oaxaca, using a 5 x 5 minutes grid. Darker colors indicate cells with greater indices of irreplaceability or turnover. In the case of turnover, the arrows indicate the areas with highest turnover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

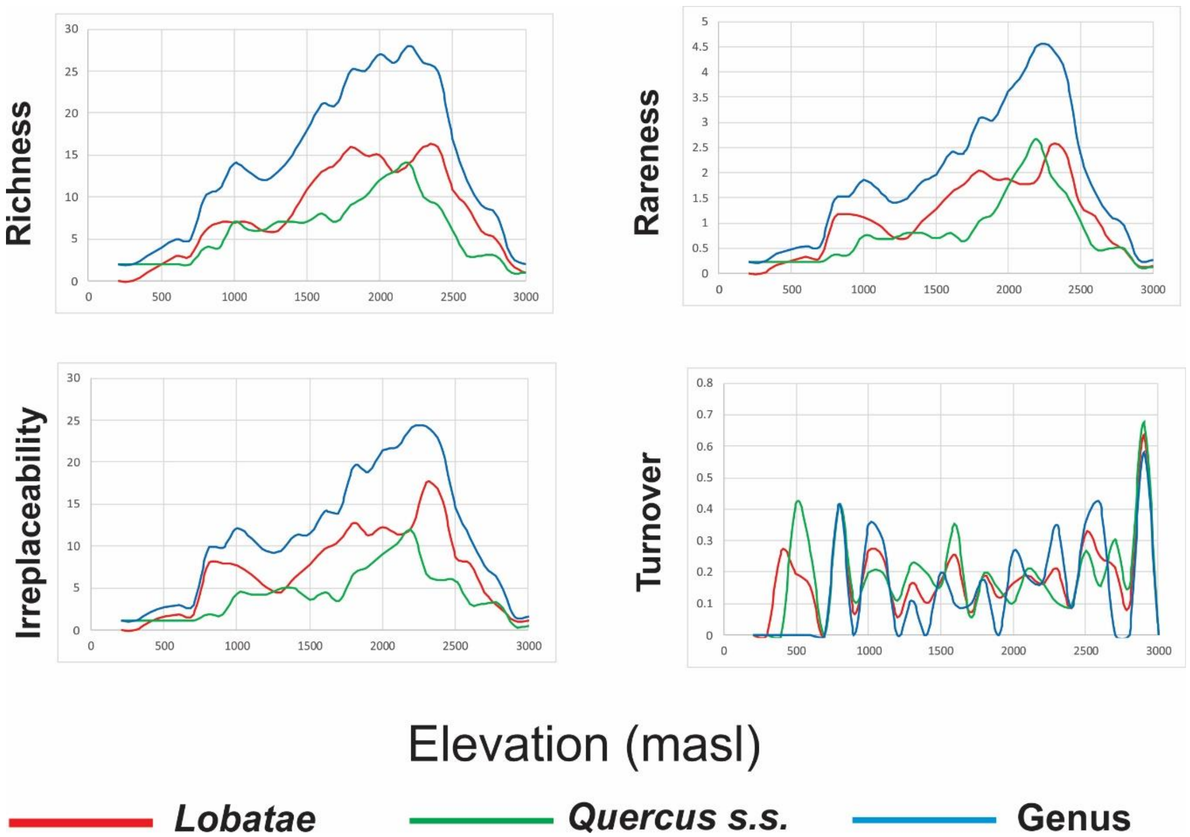


Figure 4. Elevational patterns at section levels and genus. The graph shows the richness, rareness, irreplaceability and turnover indices for each elevation range.

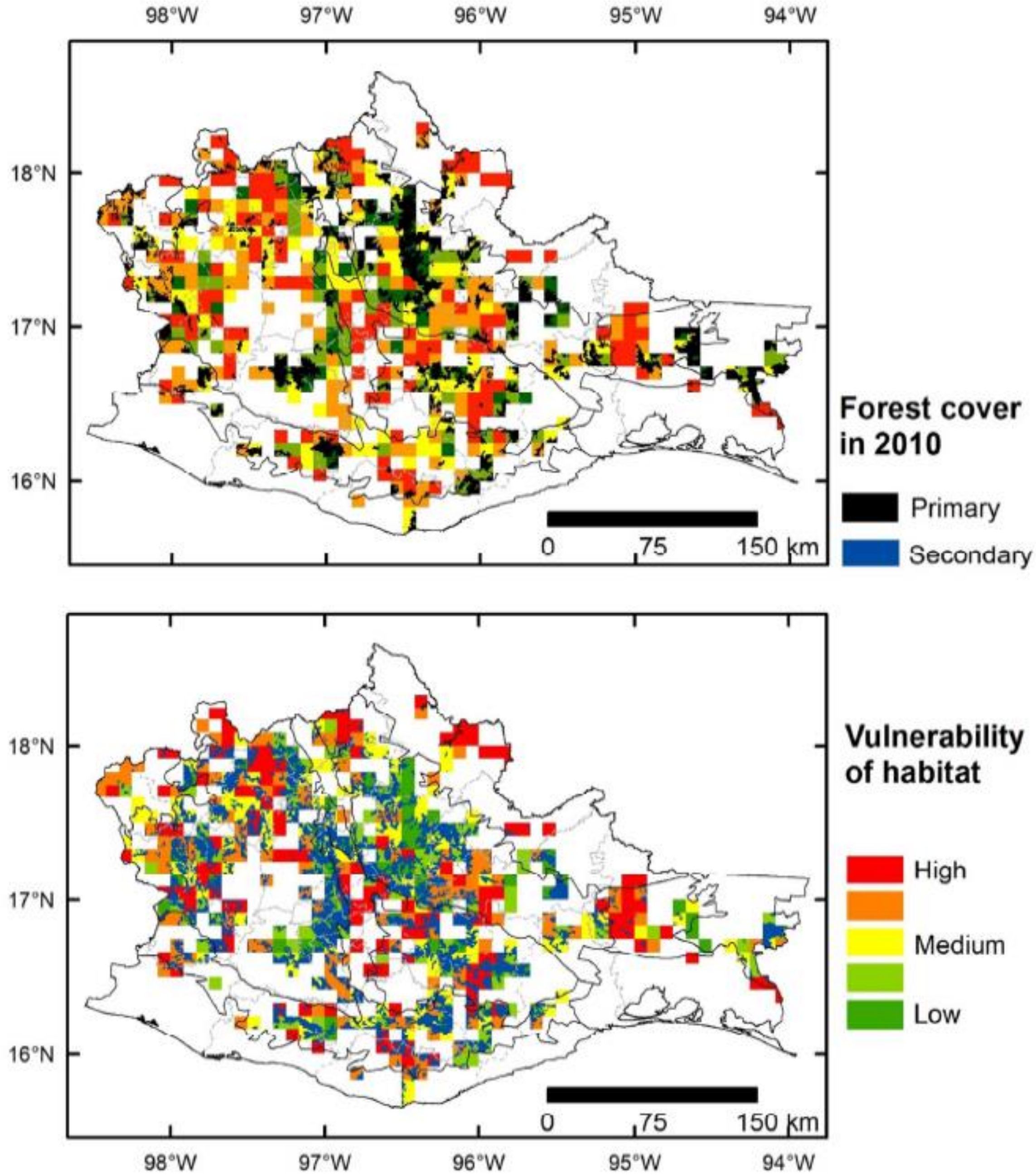


Figure 5. Areas with primary and secondary vegetation cover and vulnerability of habitat for oaks in Oaxaca. The areas that remained with primary vegetation between the years 2000 and 2010 are considered as having a low degree of disturbance (green color) and those that were transformed from primary 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.

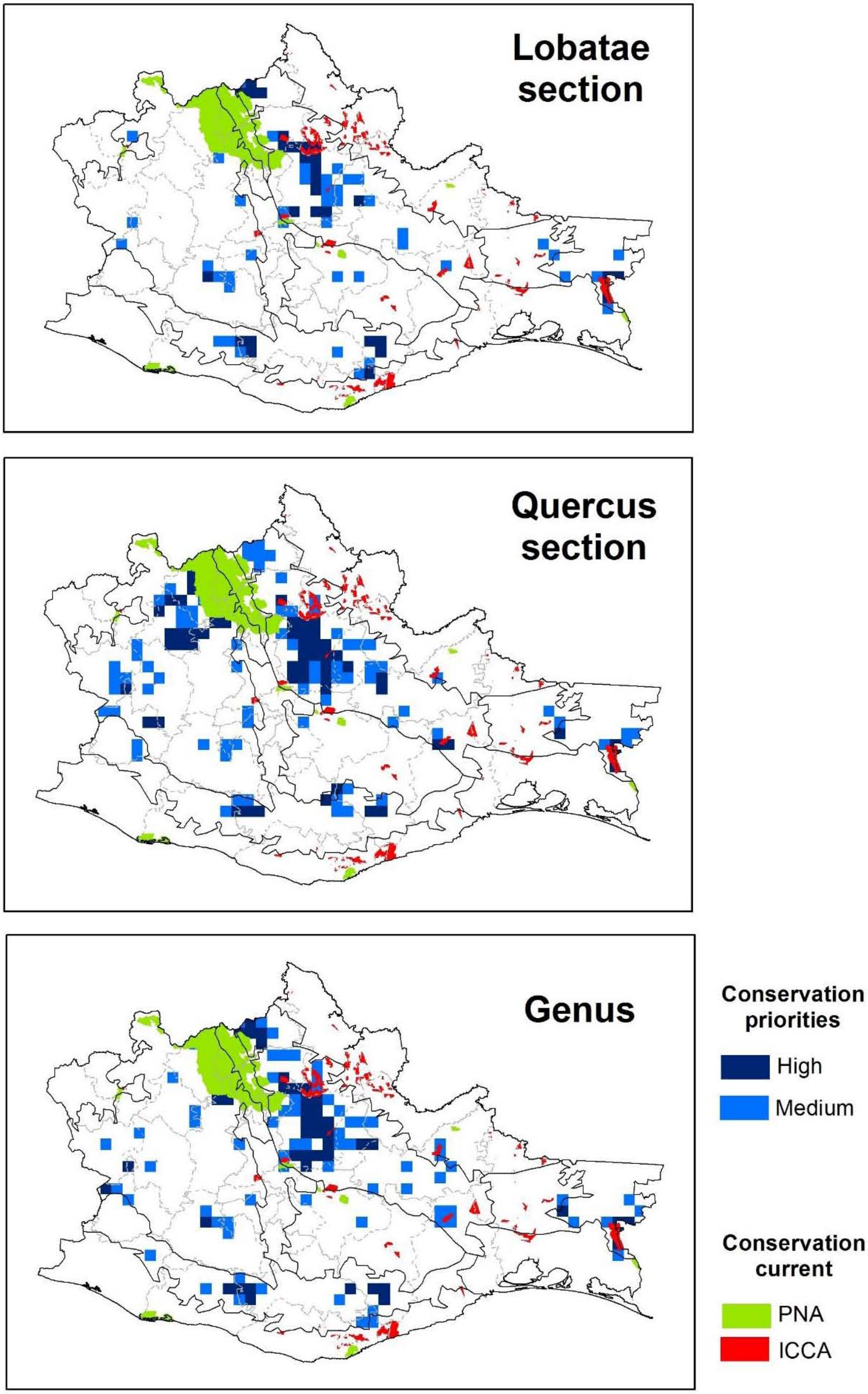


Figure 6. Conservation priority areas in Oaxaca for the *Lobatae* section, the *Quercus* section and the genus *Quercus*. This proposal considers a Systematic Conservation

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.

5. APÉNDICES ARTÍCULO REQUISITO

Appendix 1. Number of records and taxonomic remarks about the oak species included in this study.

Quercus Section
***Endemic to Mexico**
****Endemic to Oaxaca**

Species	Previous record number	Final record number	General remarks	Valencia and Nixon (2004)
*Q. corrugata**	9	28	Valid species. We found more records. Characteristic of cloud forests.	Registered
*Q. deserticola**	10	17	Valid species. We found more records. Characteristic of xeric environments.	Registered
*Q. frutex**	8	12	Some specimens are incorrectly identified as Q. microphylla. Shrubby species.	Registered
*Q. glabrescens**	18	35	Valid species. We found more records. Characteristic of pine-oak forests.	Registered
*Q. glaucescens**	5	64	Valid species. We found more records. It is one of the few species represented in tropical ecosystems.	Registered
*Q. glaucoides**	45	173	Valid species. We found more records. This species has the widest environmental tolerance in Oaxaca, represented in semiarid to subhumid tropical forests to temperate forests.	Registered
*Q. greggii**	2	6	Valid species with few records. Oaxaca constitutes its southern distributional limit.	Registered
Q. insignis		11	Species represented in the montane Gulf region. Registered for cloud forest.	Registered
*Q. laeta**	11	39	Valid species. We found more records.	Registered
*Q. lancifolia**		24	Specimens incorrectly identified as Q. leiophylla.	Not registered
Q. leiophylla	4		Not registered for Oaxaca. The specimens identified as this species belong to Q. lancifolia.	Registered
*Q. liebmannii**	23	52	Valid species. We found more records. Species with morphological similarity with Q. magnoliifolia and Q. obtusata.	Registered
*Q. macdougallii***	11	14	Valid species endemic to Oaxaca.	Registered
*Q. magnoliifolia**	61	144	Valid species. We found more records. Species with morphological similarity to Q.	Registered

			liebmannii, Q. peduncularis and Q. segoviensis. Wide environmental tolerance.	
*Q. martinezii**	2	14	Valid species. We found more records. Characteristic of cloud forest.	Registered
*Q. microphylla**	3	9	Some specimens are incorrectly identified as Q. frutex. Species with shrubby habit.	Registered
*Q. obtusata**	13	98	Valid species. We found more records. Species with morphological similarity to many species, as *Q. laeta*, *Q. liebmanii*, *Q. glabrescens*.	Registered
Q. oleoides	23	45	Valid species. We found more records.	Registered
Q. peduncularis	34	55	Valid species. We found more records. This species is morphologically 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	10	25	Valid species. We found more records. Species inhabiting tropical areas.	Registered
Q. rugosa	13	63	Valid species. We found more records. This species inhabit high mountain areas, mainly in pine-oak forests.	Registered
*Q. sebifera**	4	12	Valid species. We found more records. Species inhabiting semiarid areas.	Registered
Q. segoviensis	11	20	Registered species to Central America, in mixed forests.	Registered
*Q. splendens**	3	22	Some specimens recorded as its synonym, Q. sororia.	Registered
Total	323	982		

6.
7.

Section Lobatae
***Endemic to Mexico**
****Endemic to Oaxaca**

Species	Previous record number	Final record number	General remarks	Valencia and Nixon (2004)
Q. acatenangensis		6	Valid species, many times incorrectly identified as	Not registered

			Q. ocoteifolia. This species inhabits in pine-oak forests from 1100 to 1600 m.	
*Q. acherdophylla**		2	Valid species. Oaxaca is its southern distributional limit. A characteristic species from the Sierra Madre Oriental.	Registered
*Q. acutifolia**	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**	6	10	Valid species. We found other few specimens in herbaria. Its southern 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 characteristic to humid environments, such as cloud and mixed forests.	Registered
Q. castanea	67	169	Valid species. We found more records. This species is characteristic to oak, pine-oak and cloud	Registered

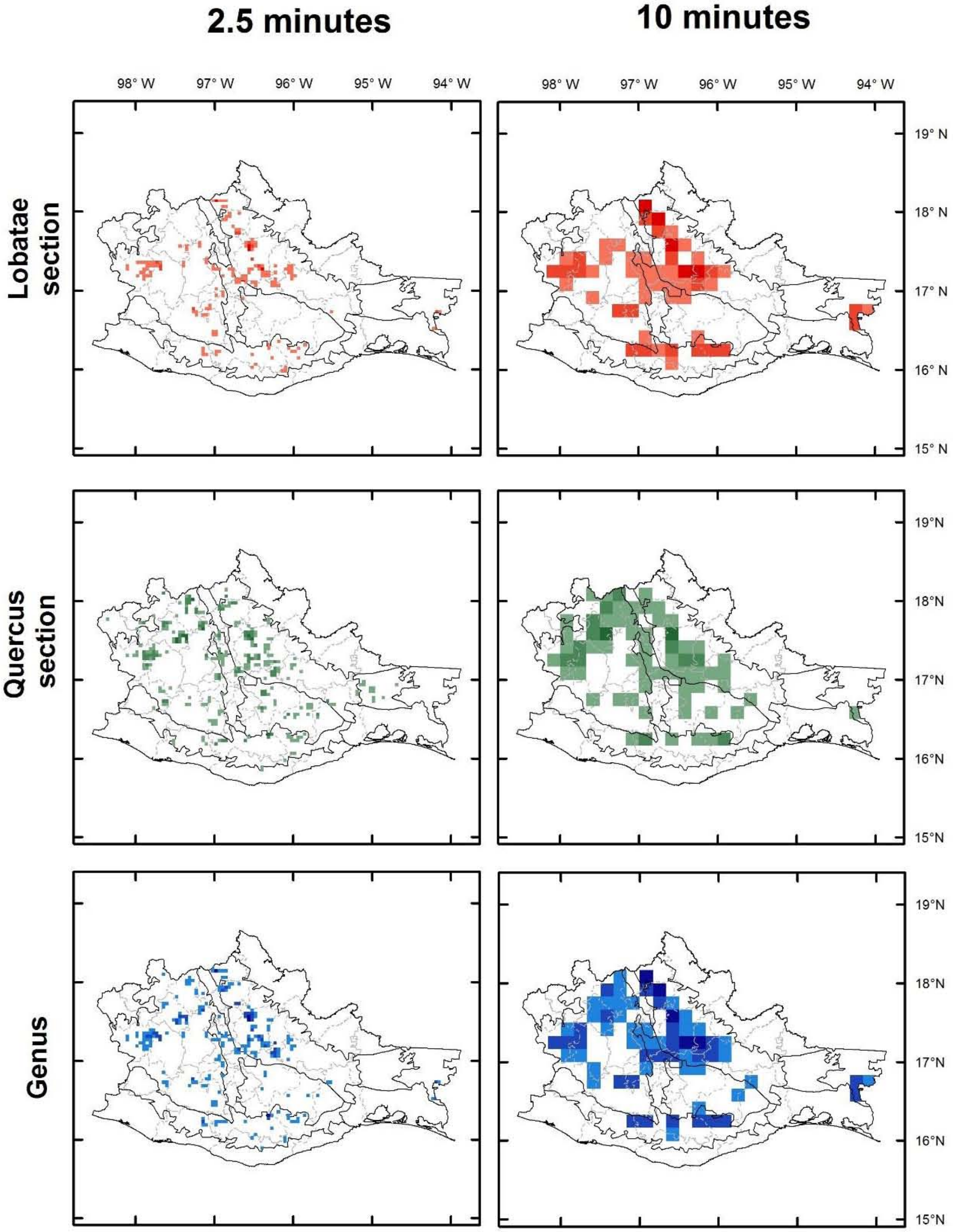
			forests. With a wide environmental tolerance.	
Q. conspersa	51	87	This species is considered as a valid taxon in this study, differently to Valencia et al. (2015), because it inhabits oak and tropical forests, and by genetic evidences. We followed then the proposal of Romero et al. (2000).	Registered
*Q. conzattii**	24	70	Valid species. We found more records. Characteristic species of subhumid oak forests.	Registered
Q. cortesii	4	9	Valid species. We found other few specimens in herbaria. Species with a fragmented distribution in the Sierra Madre del Sur.	Registered
Q. crassifolia	50	120	Valid species. We found more records. Characteristic species of high montane environments, especially in pine-oak forests.	Registered
*Q. crassipes**	4	10	Species represented in pine-oak forests, with southern distributional limit in Oaxaca.	Registered
Q. crispifolia	2	14	Valid species. We found more records. Characteristic of tropical forests in the Sierra Madre del Sur.	Registered
*Q. aff delgadoana**		6		Not registered

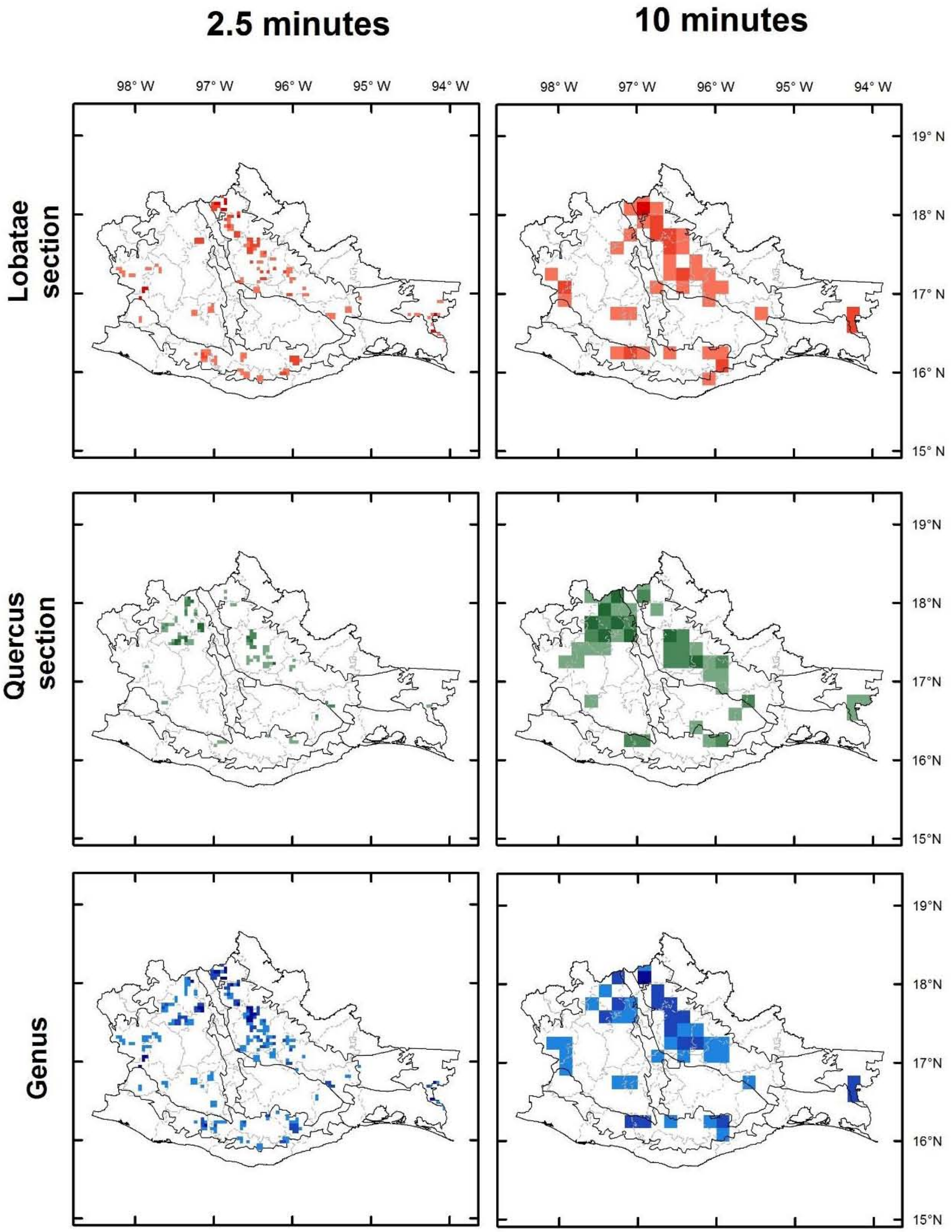
			This species has not been recorded in Oaxaca, but some specimens of cloud forests have morphological similarity with the morphological species described by Valencia et al. (2011).	
*Q. depressa**		11	Valid species for Oaxaca, with its southern distributional limit in Oaxaca. Characteristic species of the Sierra Madre Oriental.	Registered
Q. elliptica	58	114	Valid species. We found more records. Species with tropical affinity represented in a wide altitudinal range.	Registered
*Q. grahamii**		68	Valid species for Oaxaca. Species inhabiting semiarid environments in northwestern Oaxaca. Many specimens were classified as Q. acutifolia.	Not registered
*Q. laurina**	25	95	Valid species. We found more records. Characteristic species of high altitude pine-oak forests.	Registered
*Q. mulleri***	6	9	Valid species, we found few other records. Endemic species to Oaxacan cloud forests.	Registered
*Q. nixoniana**		7	Valid species. Endemic species to cloud forests of the Sierra Madre del Sur.	Registered

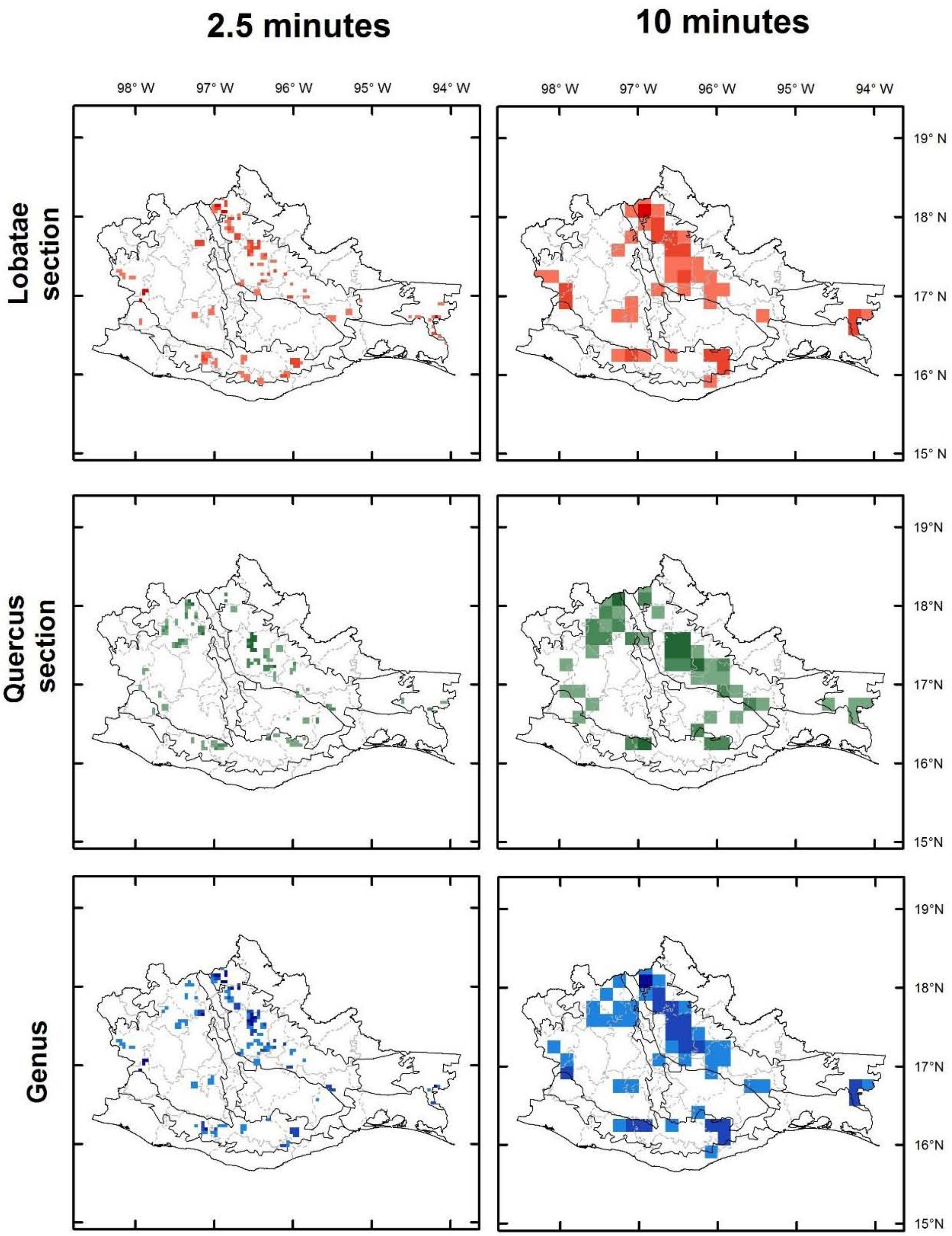
*Q. ocoteifolia**	16	23	Valid species for Oaxaca. Species morphologically similar to Q. laurina, inhabiting lower pine-oak forests (1200-1500 m)	Registered
Q. paxtalensis	3	14	Valid species for Oaxaca. Species also distributed in Chiapas, in lower cloud forests <1200m.	Registered
*Q. pinnativenulosa**		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**	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**		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**	9	9	Valid species. Oaxaca is its southern distributional	Registered

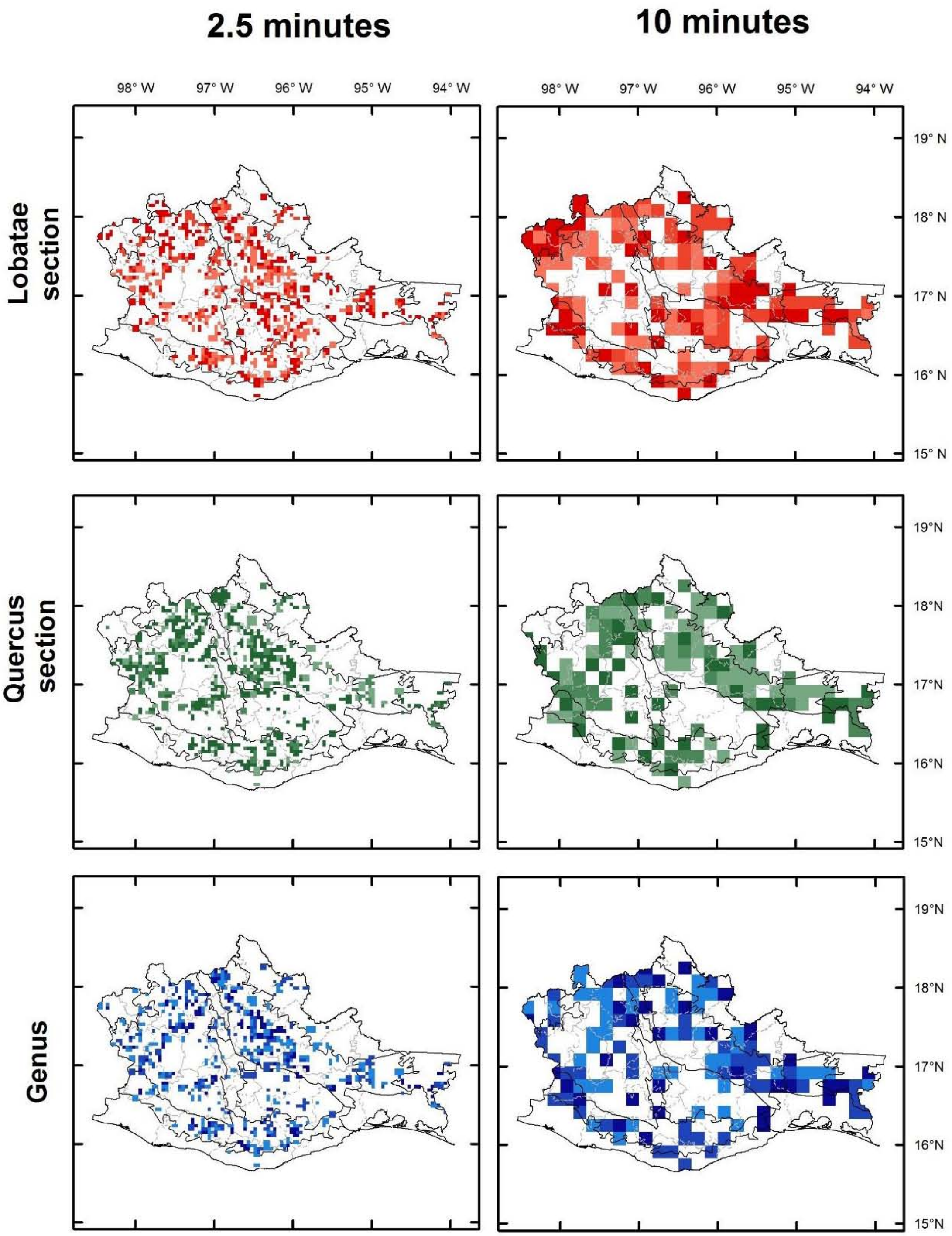
			limit. Endemic to the Sierra Madre Oriental.	
*Q. scytophylla**	14	49	Valid species. We found more records. Species represented in pine-oak and oak forests.	Registered
Q. skinneri	4	13	Valid species. We found more records. Species mainly represented in cloud forests of Central America.	Registered
*Q. trinitatis**		20	Valid species for Oaxaca. Species frequently identified as Q. salicifolia or Q. ocoteifolia. Species inhabiting high cloud forests (2000-2500 m).	Not registered
*Q. uxoris**	8	18	Valid species for Oaxaca. Endemic species to cloud forests of the Sierra Madre del Sur, in altitudes between 1800-2100 m.	Registered
Total	419	1160		

Appendix 2. Richness, rarity, irreplaceability and species turnover, in that order, using 2.5 x 2.5 minutes and 10 x 10 minutes grids.




2.5 minutes
10 minutes
98° W
97° W
96° W
95° W
94° W
19° N
18° N
17° N
16° N
15° N
Lobatae section
Quercus section
Genus


2.5 minutes
10 minutes
Lobatae section
Quercus section
Genus
98° W
97° W
96° W
95° W
94° W
19° N
18° N
17° N
16° N
15° N


2.5 minutes
10 minutes
Lobatae section
Quercus section
Genus
98° W
97° W
96° W
95° W
94° W
19° N
18° N
17° N
16° N
15° N

6. SEGUNDO ARTÍCULO

High genetic diversity and connectivity among populations of *Quercus candicans*, *Q. crassifolia* and *Q. castanea* in a heterogeneous landscape in Mexico

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Abstract

Oaxaca state is one of the main hotspots of biodiversity in Mexico, containing almost 40% of the Mexican vascular flora, due to its high variability in habitats and climatic conditions coupled with high elevations in mountains and low elevations in valleys. We studied the genetic diversity and population structure of three red oak species (*Quercus candicans*, *Q. crassifolia* and *Q. castanea*) across their geographical distribution in Oaxaca to understand how the heterogeneous physiography drives the genetic diversity and population differentiation in these three oak species. We found high levels of genetic diversity in the populations of the three oak species, and some populations had a significant low to moderate Wright's inbreeding coefficient. The analysis of molecular variance (AMOVA) showed that most of the variation occurred within populations in the three oak species. Resistance analyses showed connectivity among almost all the populations of the three species, and barrier analysis found some genetic breaks that limited gene flow among populations of the three species. Even in a heterogeneous environment such as in Oaxaca, the three oak species have high levels of genetic diversity and landscape connectivity. It is necessary to implement urgent conservation practices that include the maintenance of genetic connectivity through the preservation of corridors, which is necessary to maintain the cohesiveness of the oak species. It is also important to preserve some of the centers of species diversity in Oaxaca, such as the subprovinces (i.e., Western Oaxacan Mountains and Valleys, Sierra Madre de Oaxaca and Sierra Madre del Sur) because they harbor most of the genetic diversity and species richness, in order to protect all the communities.

Key words: conservation genetics, genetic connectivity, genetic diversity and structure, Quercus, Mexico

Introduction

The population genetic diversity of temperate forest species is spatially structured at different scales, from the local (Holderegger & Wagner, 2008) to landscape (Sork et al., 2010; Ashley et al., 2015) and continental (Petit et al., 2002; Wang et al., 2014; 2015) scales. At each scale, the ecological and genetic factors that structure the genetic diversity operate through environmental heterogeneity, genetic barriers, species life history traits, the interaction with other organisms and human-mediated habitat fragmentation (Bacles et al., 2004; Honnay & Jacquemyn, 2007). Contemporary processes, such as genetic drift and inbreeding, could eventually affect the spatial distribution of genetic variation and the effective population size (O'Connell et al., 2006; Breed et al., 2012). Ecological characteristics, such as the density of individuals, pollen dispersal and the behavior of seed dispersal vectors, can disturb the capacity of individuals to move throughout environments and affect the reproductive success and population fitness (Barrett & Schluter, 2008; Craft & Ashley, 2010; Sagnard et al., 2011). Additionally, physical barriers, such as mountain systems, large watercourses or valleys and areas of inappropriate habitat, could lead to the disruption of gene flow between populations at a regional scale (Sork & Waits, 2010; Manel & Holderegger, 2013; Wang et al., 2015; Galván-Hernández et al., 2015). In addition, the interruption of natural connectivity between populations due to anthropogenic activities could lead to a decrease in genetic variability through an increase in endogamy and genetic drift and an increase in genetic differentiation, resulting in isolated fragmented populations (Vakkari et al., 2006; Farwig et al., 2006; Herrera-Arroyo et al., 2013).

In Mexico, one of the main hotspots of biodiversity is located in the state of Oaxaca, which contains almost 40% of the vascular flora of Mexico (García-Mendoza, 2004; Ortiz-Pérez et al., 2004). This high species richness is distributed throughout the mountains, valleys and basins in the confluence of three major Mexican physiographic systems, which creates a mosaic of heterogeneous environments (Ferrusquía-Villafranca, 1993; Ortiz-Pérez et al., 2004). In particular, temperate forests in Oaxaca state are dominated by oak species represented by 52 species of *Quercus* out of the 161 reported in all of Mexico (Valencia et al., 2002; Valencia, 2004). Oak species are distributed along an altitudinal gradient from 150 to 3 300 m, and they are distributed in at least five of the large biogeographic subprovinces in which Oaxaca has been divided: Sierra Madre of Oaxaca (SMOax), Western Oaxacan Mountains and Valleys (WOMV), Central Mountains and Valleys (CMV), Región de los Chimalapas (CHIM) and Sierra Madre del Sur (SMS) (Ortíz-Pérez et al., 2004; Vázquez et al., 2004) (Figure 1).

Genetically, oak species are characterized by having high variation within and among populations (Peñaloza-Ramírez et al., 2010; Albarrán-Lara et al., 2010; Aldrich & Cavender-Bares, 2011). Recently, a study by Valencia-Cuevas et al. (2014) showed that the genetic diversity of populations of *Quercus castanea* appears to be strongly related to the number of oak species growing in sympatry. Therefore, we can expect that the higher species biodiversity in Oaxaca has been determined by the interplay between evolution and ecology based on the heterogeneous physiography that drives the genetic variation and differentiation of these three oak species.

The main aim of this study was to analyze the genetic diversity and structure of three red oak species (*Quercus candicans*, *Q. crassifolia* and *Q. castanea*) to understand how the heterogeneous physiography determines the genetic connectivity among populations across the geographical distribution of these species. The specific objectives of this study were to (i) estimate the genetic diversity and differentiation within and among populations of the three red oak species; (2) determine the levels of inbreeding, genetic connectivity and effective population size of the three-oak species; and (3) infer the implications to the conservation of temperate forests at a regional scale.

Materials and Methods

Collecting sites and DNA amplification

Samples of *Quercus candicans* (18 sites)*, Q. crassifolia* (15) and *Q. castanea* (20) were collected in temperate forests across the main physiographic provinces in Oaxaca state, Mexico, (Table 1, Figure 1) along an altitudinal gradient from 150 to 3 300 m. Oaks are mainly distributed in five of the biogeographic subprovinces in which Oaxaca has been divided: Sierra Madre of Oaxaca (SMOax), Western Oaxacan Mountains and Valleys (WOMV), Central Mountains and Valleys (CMV), Región de los Chimalapas (CHIM) and Sierra Madre del Sur (SMS) (Ortíz-Pérez et al., 2004; Vázquez et al., 2004) (Figure 1). We collected leaves of 12 to 20 trees separated by at least 30 m in each location. The samples were frozen until DNA extraction.

Genomic DNA was extracted from 100 mg of fresh leaf material using the protocol proposed by Lefort & Douglas (1996). The isolated DNA was diluted with deionized water to a final concentration of 20 ng/µL and stored at -20°C. For the polymerase chain reactions (PCR), samples of *Q. candicans* and *Q. crassifolia* were amplified with nine nuclear microsatellite loci by multiplexing in two multiplex PCR reactions (QIAGEN Multiplex PCR Kit). The first multiplex included the following five loci: three (quru-GAOA01, quru-GA2M04, quru-GAOM05) developed by Aldrich et al. (2002) and two (QpZAG110, QrZAG4) by Steinkellner et al. (1997) and Kampfer et al. (1998). The second multiplex also included four loci (quru-GAIC08, quru-GA2F05, quru-GAOM07, quru-GAIC06) developed by Aldrich et al. (2002). For *Q. castanea*, nine nuclear microsatellite loci were amplified by multiplexing in two PCR reactions (QIAGEN Multiplex PCR Kit). The first multiplex included five loci: quru-GA2FO5, quru-GAOC19, quru-GAIF02, quru-GAOA01 and quru-GAIF07 (Aldrich et al., 2002). The second multiplex included four loci: quru-GAIC06, quru-GAIC08, quru-GAOC11 and quru-GAOE09 (Aldrich et al., 2002). The PCR was performed using the QIAGEN Multiplex PCR Kit (QIAGEN) in a 5 µl volume containing 1X Multiplex PCR Master Mix, 2 µM of each primer, dH2O, and 20 ng of template DNA. The thermal cycling conditions consisted of 35 cycles of 94°C for 1 min, annealing for 1 min, extension at 72°C for 2 min and final extension at 72°C for 10 min. Multiplex PCR products were combined with a GeneScan-500 LIZ size standard, and the analyses were performed using an ABI-PRISM 3100 Avant sequencer (Applied Biosystems). Fragments were analyzed and recorded using the Peak Scanner program 1.0 (Applied Biosystems).

Genetic diversity

We tested for the presence of null alleles, large-allele dropout and errors due to stuttering in the microsatellite data using the MICRO-CHECKER 2.2.3 program (Van Oosterhout et al., 2006) with 10^2 bootstrap simulations and a 95% confidence interval. For each of the three oak species, we estimated the following genetic diversity parameters: number of alleles per locus (A), observed heterozygosity (H_O) and expected heterozygosity (H_E), using the GENETIX 4.02 software (Belkhir et al., 2004).

Genetic structure and Bayesian analysis

The genetic ancestry of each individual plant and the three species separately was analyzed with the STRUCTURE 2.3.4 software (Pritchard et al., 2000; Falush et al., 2003; Hubisz et al., 2009). STRUCTURE uses a Bayesian clustering model to determine the proportion of each individual's ancestry originating from different populations (Evanno et al., 2005). The optimal number (K) of groups was determined by varying K from 1 to 10 and running the analysis ten times for each K value to find the maximum posterior likelihood [LnP (D)]. Each run was performed using 10^6 Markov chain Monte Carlo (MCMC) repetitions following a burn-in period of 50^4 iterations. We used an admixture model that allows the correlation of allele frequencies without any *a priori* information. Following Evanno et al. (2005), we determined the most likely value of K based on the maximum value of ΔK as implemented in the Structure Harvester 0.6.9 software (Earl & von Holdt, 2012).

A hierarchical test of population structure was conducted using the stepwise mutation model (SMM) with AMOVA in ARLEQUIN 3.5. (Excoffier & Lischer, 2010). We grouped the populations by taking account the genetic groups previously identified with STRUCTURE for the populations of the three-oak species and grouping the populations of the three oak species according to their geographical distributions (physiography). Statistical significance was tested using 10^4 permutations.

To identify geographic barriers and genetic breaks among populations of *Q. candicans, Q. crassifolia and Q. castanea*, we used the Monmonier's maximum difference algorithm with the BARRIER version 2.2 software (Manni et al., 2004). BARRIER creates a map of the sampling locations from their geographical coordinates. Barriers are then represented on the map by identifying the maximum values within the population-pairwise genetic distance matrix. We used a pairwise matrix of average square distances (ASD) (Goldstein et al., 1995; Slatkin, 1995) estimated for the populations of *Q. candicans, Q. crassifolia* and *Q. castanea*. Resampling random subsets of individuals within populations with the MSA program (Dieringer & Schotterer, 2003) provided 100 bootstrap replicate distances that were used to achieve statistical significance for the predicted barriers.

Demographic analysis

We estimated the effective size (*Ne*) of populations of *Q. candicans, Q. crassifolia* and *Q. castanea* using the LDNe software (Waples & Do, 2008). This program implements the bias-correction method developed by Waples (2006) to obtain *Ne* from a sample of S individuals. We set Pcrit = 0.02 (i.e., alleles with a frequency < 0.02 are excluded), which generally provides a good balance between accuracy and bias (Waples & Do, 2008). Confidence intervals (CIs) for *Ne* were calculated with the chi-square approximation implemented in LDNe (Waples & Do, 2008).

Ecological niche modeling and spatial connectivity

A database with georeferenced occurrence data for *Quercus candicans, Q. castanea* and Q. *crassifolia* was built. The presence records were obtained from herbarium specimens (CHAP, ENCB, FCME, IEB, IZTA, LL, MEXU, MO, XAL and UNL), the Global Biodiversity Information Facility (www.gbif.org) and data from monographic and floristic studies reviewed by Torres-Miranda et al. (2011). A total of 26 presence records were gathered for *Q. candicans*, 67 for *Q. castanea* and 50 for *Q. crassifolia*; these records were used to build the ecological niche model for each species in Oaxaca state.

To characterize the environmental niches, we used the 19 bioclimatic variables obtained from the WorldClim Project (www.worldclim.com; Hijmans et al., 2005), with a spatial resolution of 0.0083° (~1 km^2), and the result of interpolating monthly averages from weather stations throughout the world from 1950 to 2000. Then, we defined a polygon that covers Oaxaca state to establish the area of accessibility in order to run the ecological niche model (ENM). We used the algorithm MAXENT v. 3.3.3k (Phillips et al., 2006) to model ENM performance, which uses the maximum entropy principle to estimate, from the existing values in the records of climate layers, a probability distribution that ranges from 0 to 1 for each pixel, which can be interpreted as an index of habitat suitability for the population being modeled (Elith et al., 2011). The algorithm compensates for co-linearity between variables using a regularization method that addresses feature selection; therefore, there is less need to remove correlated variables (Elith et al., 2011) because the contribution of each one is ranked through the analysis. For model performance, we used 75% of the occurrence records for each of the three oak species for training, and the remaining percentage was used for testing. We used 1000 iterations to limit convergence and a 0.00001 convergence limit during modelling, as this is the default level used by background test models. We also used a regularization value of 1. The options for extrapolation and clamping were disabled.

For the performance of MAXENT models, we used the AUC values of the receiver operating characteristic (ROC) curve (Phillips et al., 2006), which allows the evaluation of the correspondence of the climatic suitability generated by the model with the known occurrences, ranging from zero to one, where 1 indicates perfect discrimination between presences and absences.

To generate spatial resistance distances for dispersal among sites based on habitat suitability maps (conductance grid), we imported the potential current distribution map for the three *Quercus* species separately into Circuitscape 4.0 (McRae & Beier, 2007). This program calculates pairwise resistance to gene flow among populations based on all possible paths, not just the least-cost path, thus better explaining the movement of genes among widely separated regions over many generations (McRae & Beier, 2007; McRae et al., 2008). The input for Circuitscape is a raster dataset (habitat map) in which each cell is assigned a conductance value corresponding to the probability of the study organism moving through the habitat type encoded by the cell. We chose a conductance grid in which higher cell values denote greater ease of movement and applied a connection scheme that allowed gene flow among the four nearest cells. We used the potential distribution map rasters as input maps to quantify pairwise resistance distances between *Q. candicans*, *Q. castanea* and *Q. crassifolia* populations across their distributions in Oaxaca state. We evaluated the connectivity between the three species separately using the results of Circuitscape, where low resistance distances between pairs of nodes indicate effective dispersal between them, suggesting major connectivity between the populations of each oak species (McRae et al., 2008).

RESULTS

Genetic diversity

No evidence of null alleles was found in any of the sample-loci combinations. The tests for errors due to stuttering and large-allele dropout yielded negative results in all cases. The values of the genetic diversity parameters estimated and grouped into biogeographical regions (i.e., subprovinces) were high for all the species (Table 1). For the populations of *Q. candicans*, Ne ranged from 6.8 to 12.11 and heterozygosity ranged from 0.67 to 0.87 (Table 1). *Quercus crassifolia* also had high values of genetic diversity; the Ne ranged from 5.5 to 10.0 and heterozygosity from 0.792 to 0.920. Finally, *Q. castanea* also had high values of genetic diversity; the Ne ranged from 6.1 to 8.0 and heterozygosity ranged from 0.643 to 0.881. Wright's inbreeding coefficient within populations (F_{IS}) showed positive values in the majority of cases, denoting heterozygote deficiency, although most of the values were not significant using a jackknife test (Table 1).

Genetic structure and Bayesian analysis

The AMOVA performed for the stepwise mutation model (i.e., SMM, R_{ST}) comparing the genetic clustering (structure) and biogeographic subprovinces showed significant differences; most of the variation occurred within populations in the three oak species (Table 2).

The maximum posterior likelihood [LnP (D)] and the maximum Δ*K* value showed that *K* = 3 is the optimum number of genetic groups for *Q. candicans* and *Q. castanea* and *K* = 2 for *Q. crassifolia* (Figure 2). The pie charts in Figure 3A show the distribution of ancestry proportions for *Q. candicans* at each collection site. Cluster 1 (red) is widespread across the Oaxaca subprovinces but only present in one population of WOMV. Cluster 2 (green) is consistently structured across the three subprovinces. Cluster 3 (blue) has a wider distribution (Figure 3A). For *Q.*

crassifolia, the effective number of genetic groups was *K* = 2. Both clusters (red and green) are widely distributed across the three provinces (Figure 3B). Finally, for *Q. castanea*, cluster 1 (red), cluster 2 (green) and cluster 3 (blue) are widespread across the Oaxaca subprovinces (Figure 3C).

The BARRIER analysis performed using 100 bootstrap replicates for *Q. candicans* (Figure 3A) showed five main breaks or genetic discontinuities. The first break (B1), with 95% bootstrap support (BS), separated the populations of SMOax from those in WOMV. B2 (89%, BS) separated the Tlazoyaltepec population from the rest of the populations in WOMV. B3 and B4 (79%, BS) separated populations on the edge of the distribution from neighboring populations located in SMS and SMOax. B5 split populations in SMS and CMV (Figure 3A). For *Q. crassifolia*, six breaks were identified (Figure 3B). B1 and B4 (90%, BS) separated the eastern from the western part of WOMV and SMOax. B2 (80%, BS) divided the Paxtlan population from the rest of the populations in the eastern portion of SMS. B3 (75%, BS) separated the Coatlan population from the populations located in the southeastern portions of SMS. B5 (62%, BS) separated the populations from the eastern portion of WOMV from Tlaxiaco and Juxtlahuaca in the western portion of WOMV (Figure 3B). For *Q. castanea*, four breaks were identified (Figure 3C). B1 and B2 (95-90%, BS) separated the populations from the eastern portion of WOMV from Tlaxiaco and Juxtlahuaca in the western portion of WOMV. B3 (70%, BS) divided the Colorada population from the rest of the populations in the southeastern portion of SMS. B4 (62%, BS) separated the populations in northwest SMOax from those in the northeastern portion of SMOax (Figure 3C).

Demographic analysis

Estimates of effective population size were performed using the subprovinces to get an idea about changes in population size across the landscape. The effective population size (N_e) obtained using LDNe for *Q. candicans* populations showed that SMOax group had the highest value (N_e = 118 individuals), followed by WOMV (N_e = 62) and SMS (N_e = 61). For *Q. crassifolia*, the populations showed that the estimates of Ne in the WOMV group had the highest value (N_e = 167 individuals), followed by SMOax (N_e = 123) and SMS (N_e = 122). Finally, for the *Q. castanea* populations, the SMOax group had the highest value (N_e = 374 individuals), followed by the WOMV (N_e = 296) and SMS (N_e = 83) groups. All N_e estimates had high jackknife support and a good confidence interval (CI) (Table 3).

Ecological niche modeling and spatial connectivity

The total number of occurrences allowed us to develop with good performance with high AUC values (0.862, 0.927 and 0.921) for *Quercus candicans*, *Q. castanea* and *Q. crassifolia*, respectively. The climatic spatial resistance surface for *Q. candicans* (Figure 4D) showed major connectivity among populations in WOMV, SMOax and SMS, leaving one unconnected population in western WOMV, with a resistance value ranging from 0 to 6.97 and an average resistance distance of 3.66 among populations. For *Q. castanea*, the climatic spatial resistance surface (Figure 4E) showed major connectivity between WOMV and SMOax, leaving unconnected populations to the west of the WOMV and SMS, with resistance values ranging from 0.48 to 15.23 and an average resistance distance of 3.30 among populations. Finally, the climatic spatial resistance surface for *Q. crassifolia* (Figure 4F) showed major connectivity among WOMV, SMOax and SMS, leaving two unconnected populations to the west of the WOMV, with resistance values ranging from 0.42 to

6.99 and an average resistance distance of 3.36 among populations. The average resistance values among the three oak species were quite similar.

Discussion

Genetic diversity

Genetic variation is necessary for the future viability of populations (Vellend, 2005). In general, we found high genetic variation in the populations of the three red oak species (Q*. candicans, Q. castanea* and *Q. crassifolia*) distributed in three biogeographic subprovinces (SMOax, SMS and WOMV) of Oaxaca state, Mexico (Table 1). The genetic diversity observed in the populations could be related to the biological traits of long-lived species, such as wind pollination, outcrossing, large effective population size and extensive pollen flow among populations (Sork et al., 2002; Sork & Smouse 2006; Breed et al., 2012). In general, the values of genetic diversity found in several Mexican oak species were higher than those reported in other *Quercus* species in North America and Europe (Fernández-Manjarrés & Sork, 2006; Craft & Ashley, 2010; Aldrich & Cavender-Bares, 2011; Vranckx et al., 2014; Ashley et al., 2015).

Oak species in Oaxaca have been subject to a long process of adaptation to microclimatic heterogeneity coupled with a very complex geological history, generating a heterogeneous matrix of species richness in different regions through the state (Valencia, 2004). Interestingly, populations with high genetic diversity coincide with areas of high oak species richness according to a recent biogeographic study of oaks in Oaxaca (Ramirez-Toro et al., unpublished data).

Inbreeding and population size

Natural forests in Oaxaca state have been dramatically diminishing over at least the past 50 years (Velázquez et al., 2003; Gomez-Mendoza et al., 2006). Most of the deforested areas occur in temperate forests that produce 46% of the pine and 85% of the oak wood (Palacio-Prieto et al., 2000; Velázquez et al., 2003). The three oak species have been threatened throughout their ranges in Oaxaca as a result of habitat destruction. Despite the high rates of deforestation of temperate forests, there is still not strong evidence of inbreeding in the oak populations as has been observed in other species (Sork & Smouse, 2006; Craft & Ashley, 2010; Herrera-Arroyo et al., 2013). In some cases, few populations showed significant positive F_{IS} values in *Q. candicans* and *Q. castanea* in WOMV and in *Q. crassifolia* and *Q. castanea* in SMOax (Table 1). However, significant effects were observed in the reductions in population size in WOMV (N_e = 62.4) and SMS (N_e = 61.5) for *Q. candicans* and (N_e = 83.9) *Q. castanea* (Table 3). It has been suggested that even in wind-pollinated and mostly outcrossing species such as oaks, decreasing the local tree density in a community might alter mate availability such that the number of nearby pollen sources surrounding a mother tree decreases and the pollination distance between mates increases (Sork et al., 2002; Bacles et al., 2004; Eckert et al., 2010; Breed et al., 2012; Frankham et al., 2013; Vranckx et al., 2014). Additionally, seed dispersal in oaks is limited because the acorns lack adaptations for long-distance dispersal (e.g., acorns germinate closely to the mother tree) or transport by birds (Jump & Penuelas, 2006; Sork & Smouse 2006; Fernández-Manjarrés & Sork, 2006; Sagnard et al., 2011).

Genetic structure, Bayesian admixture analysis, breaks in gene flow and connectivity

We did not find genetic structure in the populations of any of the three oak species; most of the genetic variation was explained within populations (Table 2). We also found a great amount of connectivity between the populations located in the WOMV and the SMOax but leaving unconnected populations of the three-oak species in the western WOMV and SMS. Differences in land cover and elevation may create multiple climatic zones across the Oaxaca region, characterized by variation in climate, topography and vegetation; therefore, it is possible that habitat discontinuity and physical geographical barriers both play a substantial role in genetic differentiation and genetic inbreeding.

Oaxaca state has an intricate landscape, with mountains with high peaks crossed by valleys and canyons. Heterogeneous environments promote the maintenance of high genetic diversity as well as deep processes of divergence between populations of species (Ferrusquía-Villafranca, 1993; García-Mendoza, 2004; Ortiz-Pérez et al., 2004). Additionally, we observed evidence of landscape differentiation in the barriers to gene flow between *Q. candicans* and *Q. crassifolia* (barriers B5, B6, B2, B1) that split the western and the eastern portions of WOMV subprovince. This evidence agrees with the climatic spatial resistance surface, which showed less connectivity between *Q. candicans* and *Q. crassifolia*, leaving unconnected populations in the western and eastern portions of WOMV. From a biogeographic viewpoint, both western and eastern sides of the zones host pine-oak forest flora in a series of linear mountainous ranges with a maximum elevation of 3 200 –3 400 m, and they are separated by inter-montane valleys covered with tropical deciduous forests in the central portion of the province (Ortiz-Pérez et al., 2004). We suggest that the inter-montane valleys with tropical deciduous forests possibly act as a geographical barrier for the disjunct distribution of the three species in the zone.

Due to the small and isolated distributions, limited gene flow and genetic drift may contribute to the high inbreeding within both sides of the WOMV region.

We also detected another geographic barrier to gene flow between populations indicated by B1, B4, B4, B1, B4 (*Q. candicans, Q. crassifolia* and *Q. castanea*) that separate populations located in the northeastern part of SMOax from those in the northwestern WOMV. The spatial resistance surface showed less connectivity among *Q. candicans, Q. crassifolia* and *Q. castanea* between WOMV and SMOax. As the desert zone developed in the Tehuantepec depression in Oaxaca, forests contracted or fragmented or disappeared, which affected the species composition on both sides of WOMV and SMOax (García-Mendoza et al., 2004; Ortiz-Pérez et al., 2004). This valley is located in the northern portion of the SMOax to the east and the northeastern portion of the WOMV. Most of the valley lies at elevations below 1 000 m but rises to slightly more than 1 400 m toward the south elevations, where it is covered by xerophytic vegetation and many succulents, such as cacti and *Mammillaria*, and acts as an additional great barrier to gene flow for *Q. candicans, Q. crassifolia* and *Q. castanea* in the WOMV and SMOax (Ortiz-Pérez et al., 2004). Therefore, we suggest that high variability in habitat and climatic conditions combined with high elevations and large geographic distances may explain the moderated genetic differentiation and the inbreeding of some isolated populations (Sork & Waits, 2010; Manel & Holderegger, 2013).

Implications for conservation

We studied the genetic structure of populations of Q*. candicans*, *Q. crassifolia* and *Q. castanea* in Oaxaca, one of the areas with high biodiversity in Mexico. High levels of genetic diversity were observed in populations of these species across their distribution along some of the main physiographic subprovinces (i.e., WOMV, SMOax and SMS), indicating that sites with high oak species richness (Ramírez-Toro et al., unpublished data) also had high genetic diversity. Recent studies have suggested that species diversity and genetic diversity could be interconnected as a consequence of a process acting in parallel at these two levels (Vellend, 2005; Papadopoulou et al., 2011). However, this biological richness is threatened by the effects of land cover changes, such as deforestation; Oaxaca state has lost over half a million hectares of forested areas during the last 20 years (Velázquez et al., 2003; Gómez-Mendoza et al., 2006).

The conservation of forests in Oaxaca is necessary because most of the natural areas are not currently protected by the government. There are only five natural protected areas in this state. In Oaxaca, the initiative called Indigenous Conservation and Community Areas (ACIC) is another alternative to manage and preserve the remaining natural areas with different levels of disturbance (Robson, 2007; Anta-Fonseca & Sanchez, 2009; Martin et al., 2011). However, according to Martin et al. (2011), 126 ACIC protect 375,457 ha, but only 22 include forests with oak species. Therefore, it is necessary to implement diverse conservation practices that include areas with high species richness and high genetic diversity as well as areas that could serve as natural corridors to maintain natural biological processes, such as dispersal and pollination (Herrera-Arroyo et al., 2013; Oyama et al., 2017).

Acknowledgments

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7. TABLAS DEL SEGUNDO ARTÍCULO

Table1. Locality name, sample size, N/W geographical coordinates (degrees), altitude, mean number of alleles (N_a), mean number of effective alleles per locus (N_e), mean observed heterozygosity (H_O), mean expected heterozygosity (H_E), for populations of *Quercus candicans, Q. crassifolia* and *Q. castanea* in the Oaxaca, Mexico. Standard errors are included in parenthesis and P-value for F_{IS} within samples based 1004 randomizations adjusted to P= 0.05 in parenthesis.

Locality	**Sample size**		**Genetic diversity**		
	Coordinates	N_e	H_O	H_E	F_{IS}
Q. candicans					
SMOaX					
1. Atepec	17.421/ -96.497	8.00 (2.07)	0.852 (0.10)	0.808 (0.08)	0.014 (0.093)
2. Comaltep	17.561/ -96.542	6.88 (2.53)	0.675 (0.11)	0.757 (0.14)	0.244 (0.003)
3. Jaltiangu	17.369/ -96.513	9.00 (3.03)	0.835 (0.12)	0.817 (0.10)	0.063 (0.078)
4 Yolox	17.571/ -96.550	8.66 (0.98)	0.827 (0.16)	0.814 (0.10)	0.044 (0.135)
5 Talea	17.379/ -96.236	12.11 (2.31)	0.841 (0.16)	0.848 (0.10)	0.056 (0.045)
WOMV					
6. SantiaA	17.233/ -97.005	9.55 (2.07)	0.818 (0.10)	0.832 (0.08)	0.077 (0.029)
7 SantiaB	17.233/ -97.004	6.22 (2.78)	0.853 (0.24)	0.781 (0.17)	0.027 (0.295)
8. PeNoles	17.095/ -96.936	5.55 (0.98)	0.628 (0.16)	0.713 (0.10)	0.272 (0.002)
9 Tlazoyalte	17.073/ -96.927	11.33 (2.66)	0.812 (0.08)	0.851 (0.08)	0.084 (0.004)
10 Yucunico	17.200/ -97.884	6.22 (2.07)	0.879 (0.10)	0.757 (0.07)	0.052 (0.807)
SMS					
11. Juquila	16.235/ -97.197	6.88 (2.08)	0.811 (0.08)	0.794 (0.07)	0.077 (0.059)
12. Coatlan	16.189/ -96.812	6.22 (2.78)	0.866 (0.24)	0.724 (0.17)	0.088 (0.937)
13. Pacifico	16.147/ -96.500	5.11 (2.66)	0.793 (0.08)	0.642 (0.08)	-0.160 (0.99)
14 SuchixteA	16.078/ -96.468	8.88 (2.53)	0.881 (0.11)	0.854 (0.14)	0.043 (0.118)
15 SuchixteB	16.078/ -96.468	6.88(3.03)	0.791 (0.12)	0.794 (0.10)	0.095 (0.040)
16 SuchixteC	16.072/ -96.490	6.77 (2.08)	0.785 (0.08)	0.796 (0.07)	0.106 (0.027)
17. Riohon	16.007/ -96.523	6.00 (2.07)	0.777 (0.10)	0.730 (0.07)	0.011 (0.488)
18. Loxicha	15.993/ -96.532	6.77 (2.31)	0.828 (0.16)	0.778 (0.10)	0.046 (0.194)
Q. crassifolia					
SMOaX					
19. Comaltep	17.559/ -96.541	5.55 (2.40)	0.828 (0.12)	0.720 (0.07)	0.038 (0.303)
20. Llanotie	17.554/ -96.536	10.66 (2.31)	0.889 (0.10)	0.857 (0.07)	0.016 (0.302)
21. Atepec	17.421/ -96.497	10.00 (1.21)	0.792 (0.10)	0.837 (0.03)	0.117 (0.002)
22. Jaltiangu	17.366/ -96.513	8.55 (1.94)	0.820 (0.21)	0.824 (0.10)	0.125 (0.001)
23 Xiacui	17.270/ -96.424	8.33 (1.26)	0.920 (0.05)	0.846 (0.01)	-0.015 (0.65)
WOMV					
24 Santiago	17.233/ -97.005	5.44 (1.94)	0.764 (0.21)	0.704 (0.10)	0.077 (0.164)
25. NuxINo	17.223/ -97.033	10.11(1.26)	0.795 (0.05)	0.842 (0.01)	0.109 (0.005)
26 PeNoles	17.095/ -96.936	6.11 (2.06)	0.825 (0.16)	0.761 (0.12)	0.016 (0.371)
27 Tlaxiaco	17.190/ -97.796	8.11 (2.31)	0.864 (0.10)	0.809 (0.07)	0.003 (0.451)
28. Juxtlahua	17.344/ -97.948	12.11(1.37)	0.863 (0.14)	0.865 (0.03)	0.043 (0.075)
SMS					
29. Coatlan	16.225/ -96.886	5.22 (2.06)	0.770 (0.16)	0.750 (0.12)	0.144 (0.103)
30 Paxtlan	16.233/ -96.525	11.33 (1.21)	0.959 (0.10)	0.888 (0.03)	-0.012 (0.92)
31 Pinabete	16.116/ -96.477	8.33 (2.40)	0.873 (0.12)	0.826 (0.07)	0.020 (0.304)
32. Pacifico	16.147/ -96.500	5.00 (1.94)	0.801 (0.21)	0.708 (0.12)	0.018 (0.397)
33 Suchixte	16.077/ -96.465	6.12 (1.37)	0.852 (0.14)	0.781 (0.03)	0.041 (0.234)

Locality	**Sample size**		**Genetic diversity**		
	Coordinates	N_e	H_{O}	H_{E}	F_{IS}
Q. castanea					
SMOaX					
34 Ixtlan	17.330/ -96.456	7.55 (1.26)	0.787 (0.05)	0.815 (0.01)	0.100 (0.015)
35 Capulal	17.270/ -96.424	7.00 (2.31)	0.804 (0.10)	0.781 (0.07)	0.031 (0.255)
36 Ixtepeji	17.259/ -96.540	7.22 (2.08)	0.881 (0.08)	0.799 (0.07)	-0.030 (0.73)
37 Yatzachi	17.240/ -96.220	6.00 (3.03)	0.746 (0.12)	0.749 (0.10)	0.112 (0.055)
38 Cerezal	17.235/ -96.567	6.11 (2.66)	0.619 (0.08)	0.729 (0.08)	0.210 (0.006)
WOMV					
39 Nochixtl	17.327/ -97.119	8.00 (2.07)	0.768 (0.10)	0.787 (0.08)	0.082 (0.032)
40 Sosola	17.303/ -97.084	7.00 (2.78)	0.746 (0.24)	0.773 (0.17)	0.094 (0.032)
41 Capilla	17.258/ -97.041	8.22 (2.31)	0.728 (0.16)	0.826 (0.10)	0.176 (0.003)
42 Nuxino	17.224/ -97.030	6.55 (2.53)	0.643 (0.11)	0.761 (0.14)	0.240 (0.003)
43 Tejalapa	17.118/ -96.920	7.44 (2.66)	0.729 (0.08)	0.809 (0.08)	0.154 (0.006)
44 Penoles	17.117/ -96.928	6.66 (2.31)	0.738 (0.16)	0.790 (0.10)	0.127 (0.006)
45 Tlazoyal	17.072/ -96.924	6.33 (3.03)	0.599 (0.12)	0.721 (0.10)	0.235 (0.003)
46 Cuilapam	17.072/ -96.866	6.44 (2.08)	0.845 (0.08)	0.760 (0.07)	-0.056 (0.85)
47 Tlaxiaco	17.190/ -97.796	6.55 (0.98)	0.798 (0.16)	0.778 (0.10)	0.054 (0.148)
48 Juxtlahua	17.175/ -97.825	5.88 (2.78)	0.833 (0.24)	0.755 (0.17)	-0.004 (0.51)
SMS					
49 Juquila	16.249/ -97.179	6.66 (2.53)	0.738 (0.11)	0.785 (0.14)	0.127 (0.010)
50 Colorada	16.573/ -96.939	7.55 (0.98)	0.788 (0.16)	0.751 (0.10)	0.002 (0.518)
51 SolaVega	16.555/ -96.957	6.88 (2.07)	0.747 (0.10)	0.803 (0.07)	0.140 (0.006)
52 Mihuatla	16.470/ -97.015	7.11 (2.07)	0.780 (0.10)	0.810 (0.07)	0.107 (0.018)
53 Portillo	16.453/ -97.003	6.11 (2.07)	0.800 (0.10)	0.777 (0.08)	0.065 (0.114)

Table 2. Analysis of molecular variance (AMOVA) performed on the nSSR data and using R_{ST} for the three group genetic clusters obtained by means of STRUCTURE and grouped according to Physiographical Provinces for populations of *Q. candicans, Q. crassifolia and Q. castanea.* Asterisks indicate statistically significant values ($P < 0.01$). Tests were based on 10^4 random permutations.

Source of variation	S	Variance components	Percentage of variation	Fixation index
Q. candicans Physiography				
Among groups	53.773	0.0298	0.99	Φ_{CT} = 0.009**
Among populations within groups	39.537	0.1253	4.25	Φ_{SC} = 0.042**
Within populations	844.04	2.794	94.76	Φ_{ST} = 0.052**
Total	937.35	2.949		
Q. candicans Structure				
Among groups	56.045	0.2408	7.97	Φ_{CT} = 0.073**
Among populations within groups	37.265	0.0172	0.59	Φ_{SC} = 0.006**
Within populations	844.0	2.7948	92.62	Φ_{ST} = 0.079**
Total	937.3	3.0174		
Q. crassifolia Physiography				
Among groups	8.901	0.0208	0.92	Φ_{CT} = 0.090**
Among populations within groups	2.525	0.0956	4.24	Φ_{SC} = 0.040**
Within populations	664.7	2.332	94.84	Φ_{ST} = 0.080**
Total	676.1	2.257		
Q. crassifolia Structure				
Among groups	5.446	0.035	1.57	Φ_{CT} = 0.010**
Among populations within groups	5.980	0.094	4.16	Φ_{SC} = 0.040**
Within populations	664.7	2.332	94.27	Φ_{ST} = 0.090**
Total	676.1	2.173		
Q. castanea Physiography				
Among groups	28.863	0.021	0.71	Φ_{CT} = 0.007**
Among populations within groups	50.472	0.051	1.75	Φ_{SC} = 0.010**
Within populations	1042	2.89	97.64	Φ_{ST} = 0.090**
Total	1123	2.96		
Q. castanea Structure				
Among groups	25.21	0.077	2.61	Φ_{CT} = 0.030**
Among populations within groups	55.11	0.018	0.62	Φ_{SC} = 0.060**
Within populations	1041	2.98	96.78	Φ_{ST} = 0.096**
Total	1121	2.98		

Table 3. Analysis results obtained for the estimation of the population effective size, tested for the three physiographic groups, values obtained with the program LDNe, for *Q. candicans, Q. crassifolia and Q. castanea* populations in the Oaxaca Mexico.

Models	*SMOAx*	*WMOMV*	*SMS*
Q. candicans			
LDNe	118.5	62.4	61.5
Q. crassifolia			
LDNe	123.7	167.6	122.5
Q. castanea			
LDNe	374.3	296.6	83.9

8. FIGURAS DEL SEGUNDO ARTICULO

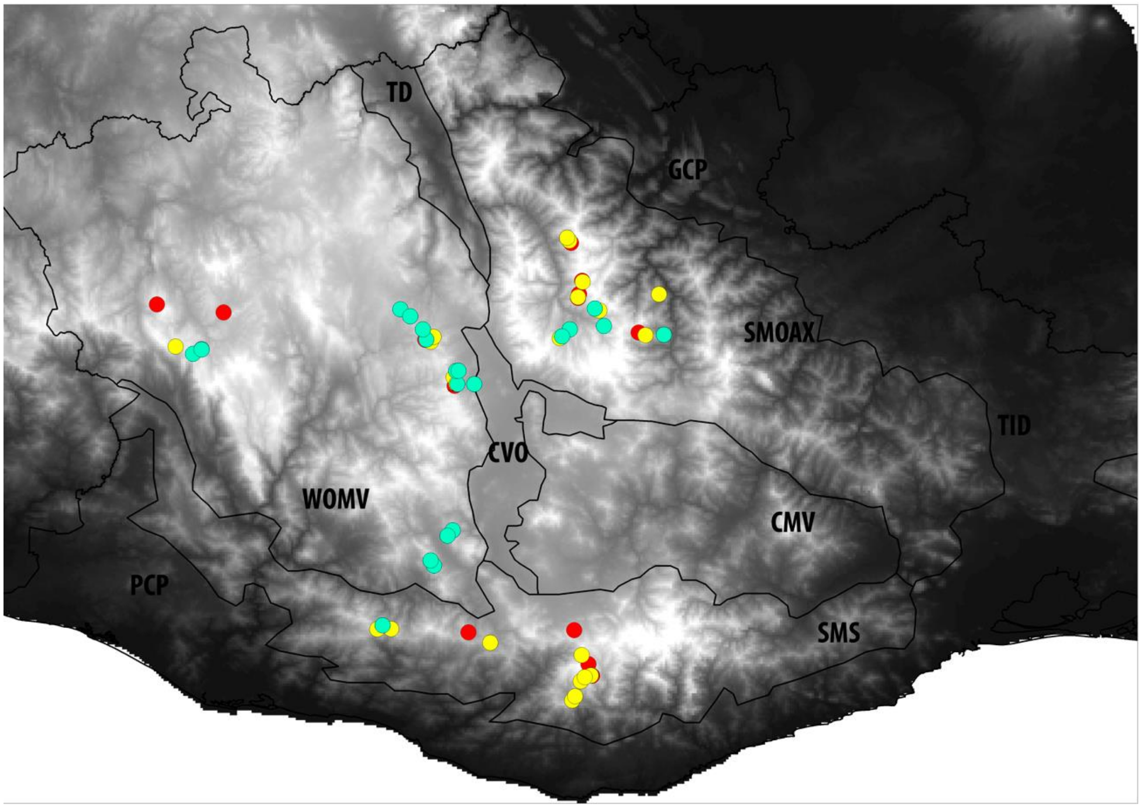

Figure 1. The physiographic provinces of the state of Oaxaca (drawn from Ortiz-Perez et al. 2004). The names of the numbered provinces and their abbreviations are as follows: 1, Western Oaxacan Mountains and Valleys (WOMV); 2, Tehuacan Depression (TD); 3, Sierra Madre of Oaxaca (SMOax); 4, Gulf Coastal Plain (GCP); 5, Central Valleys of Oaxaca (CVO); 6, Central Mountains and Valleys (CMV); 7, Tehuantepec Isthmic Depression (TID); 8, Sierra Madre del Sur (SMS); 9, Pacific Coastal Plain (PCP) ; 10, Tehuantepec Coastal Plain (TCP). Points represented the localities of Q. candicans (Yellow), Q. crassifolia (Red) and Q. castanea (Blue).

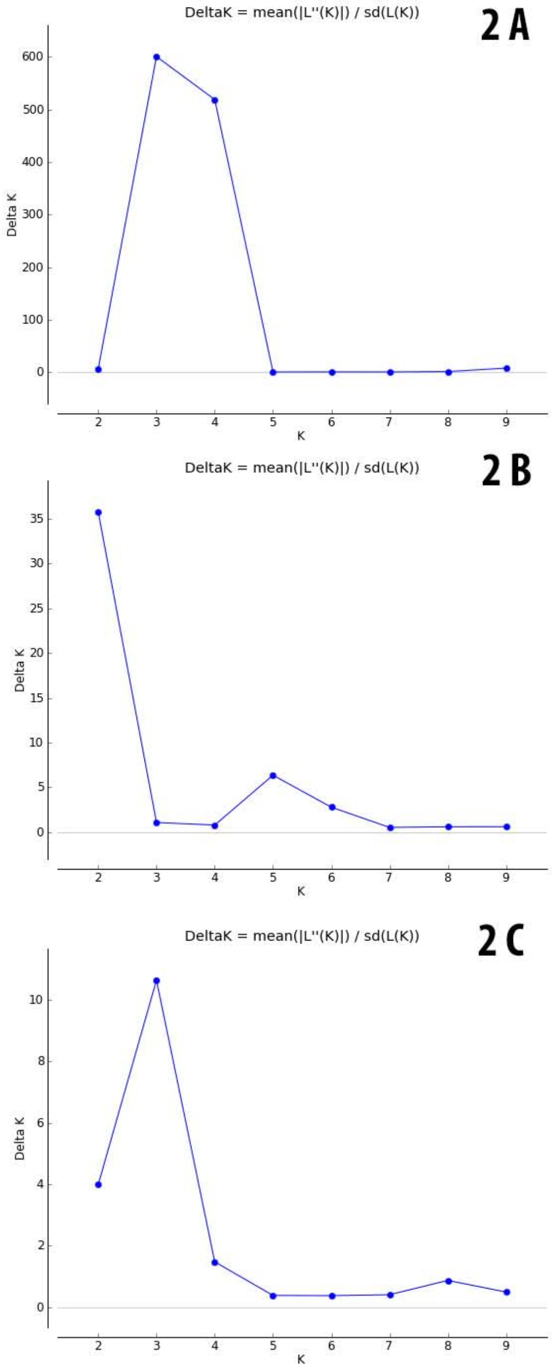

Figure 2. Maximum probability to the most probable genetic group of *Q. candicans* 2 (A) *Q. crassifolia* 2(B) and *Q. castanea* 2(C).

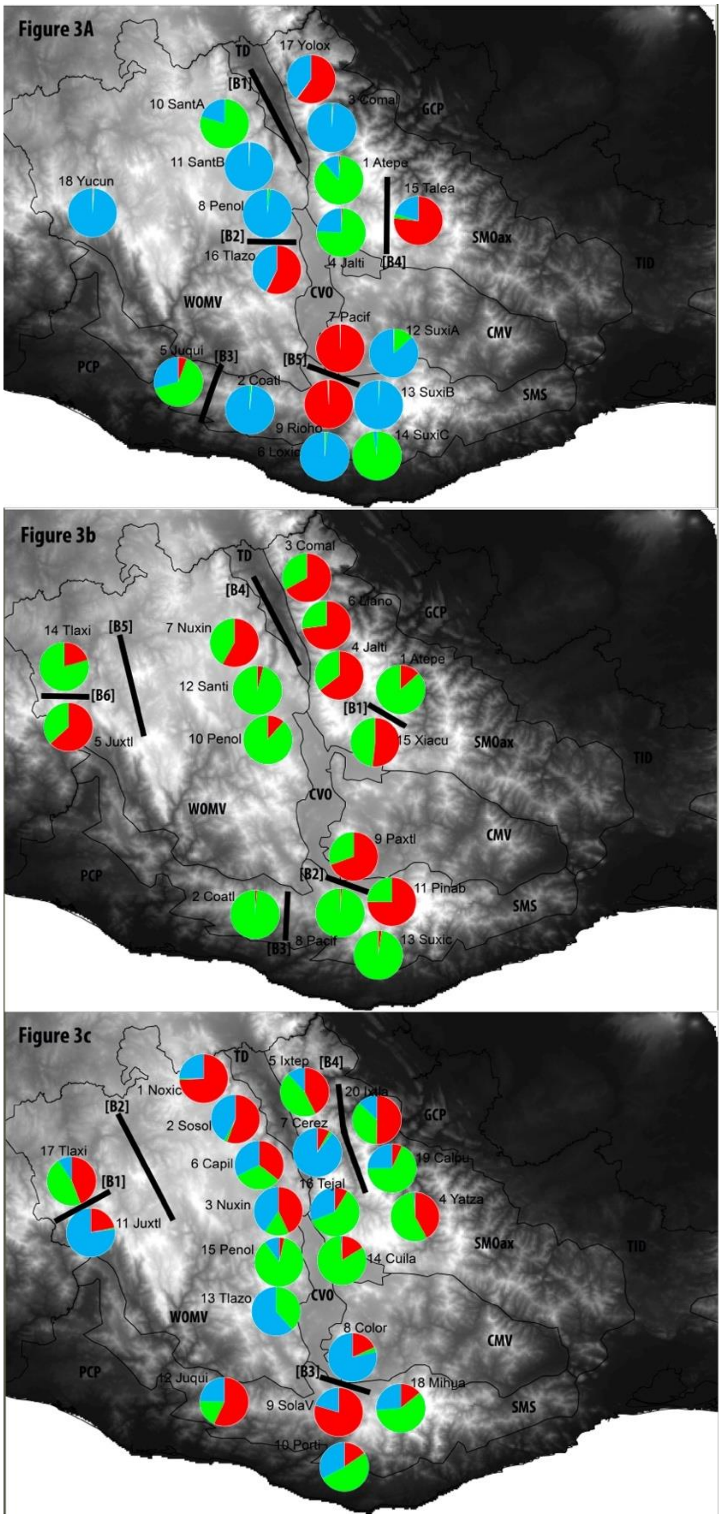

Figure 3. Distribution of genetic ancestry proportion groups corresponding to *Q. candicans* 3(A), *Q. crassifolia* 3(B) and for *Q. castanea* 3 (C) populations across physiographic regions in Oaxaca. Black bars mean the barriers detected with the BARRRIERS program.

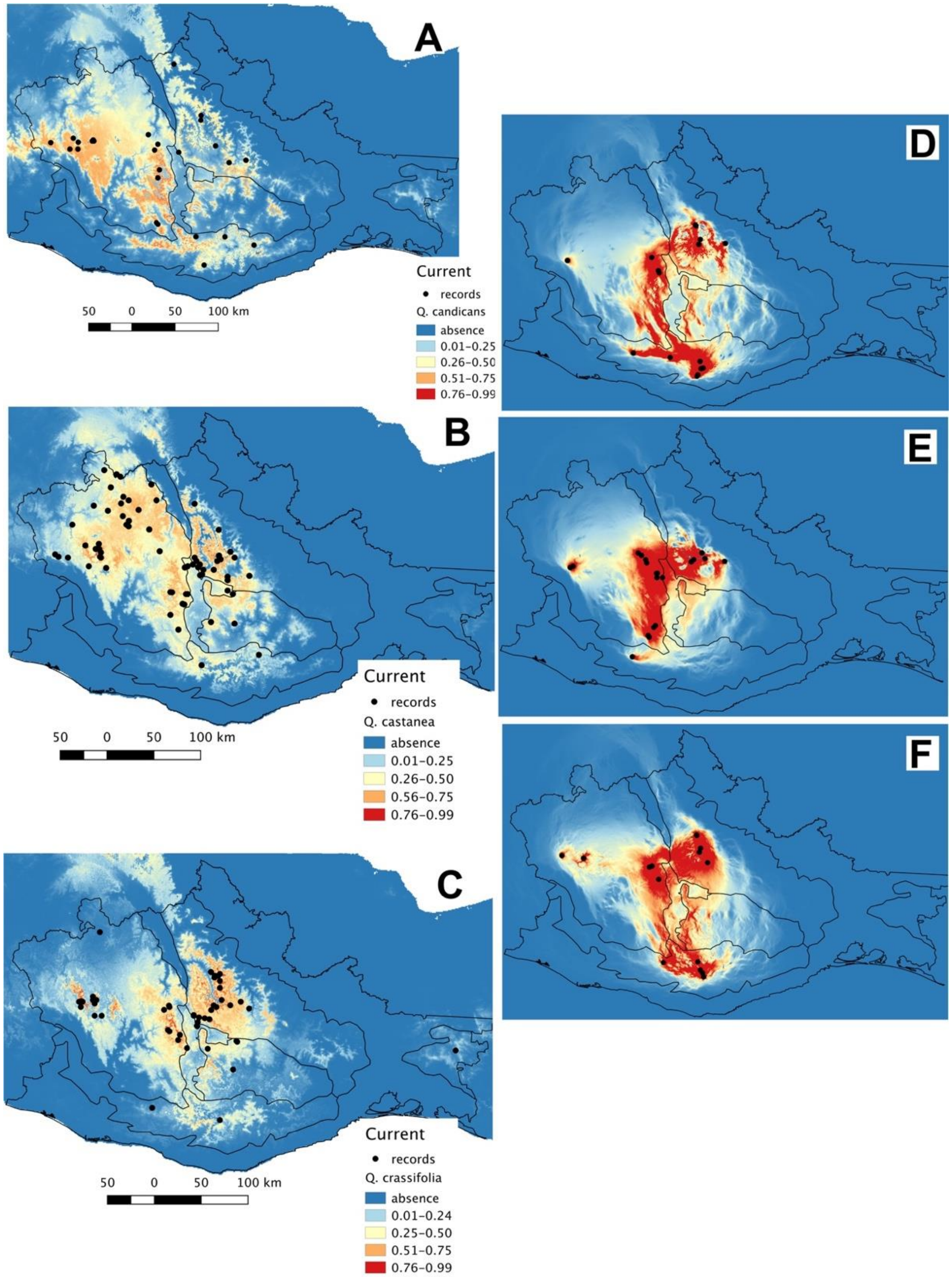

Figure 4. Potential distribution of Quercus candicans A. Q. castanea B. and C. Q. crassifolia identified using ecological niche modeling, prediction of suitable habitat in the current environment. Black dots are the presence records used to build the ecological niche model. D. Connectivity map among populations of Q. candicans. E. Connectivity map among populations of Q. castanea and F. Connectivity map among populations of Q. crassifolia. Black dots are the populations records used for each species in the genetic analyses to build the connectivity maps.

9. DISCUSIÓN GENERAL Y CONCLUSIONES

9.1. Patrones de riqueza y rareza de encinos

La alta diversidad biológica presente en el estado de Oaxaca está relacionada a su fisiografía, que se originó a través de complejos procesos geológicos. A su vez, la fisiografía oaxaqueña ha dado lugar a una alta diversidad de tipos de suelos y climas que permitieron el establecimiento de una rica flora y diferentes tipos de ecosistemas (García, 2004). Aquí analizamos a nivel estatal la distribución de 54 especies de encinos, 30 de las cuales está consideradas endémicas para México (55.5%), un porcentaje mayor que para plantas con flores presentes en Oaxaca de acuerdo a las estimaciones de Villaseñor & Ortíz (2014). Sin embargo, solo hay dos especies de encinos endémicas para Oaxaca, aunque Valencia & Nixon (2004) mencionan la presencia de otros tres encinos endémicos en Oaxaca que aún no han sido formalmente descritos.

Oaxaca se divida en 12 sub-provincias fisiográficas, 10 de las cuales contienen registros de especies de encinos, SMOax es la región con la mayor riqueza de encinos. En general, también se encontró una alta riqueza de plantas vasculares para esta subprovincia (García, 2004), gimnospermas (Contreras & Luna, 2006) y aves y mamíferos (Koleff, Gaston, & Lennon, 2003). Además, SMOax ha sido identificada como el área de convergencia de especies de vertebrados que pertenecen a diferentes ensambles como resultado de cambios históricos y ecológicos (Bojorquez, Azuara, Ezcurra & Flores, 2005). En MVO, el área de Juxtlahuaca es un centro prioritario para la conservación de encinos y también para vertebrados terrestres (Bojorquez, Azuara, Ezcurra & Flores, 2005), especialmente para la herpetofauna (Urbina & Flores, 2010). Por otro lado, muchas de las especies de encinos que habitan en SMS tienen pocos registros y distribuciones fragmentadas. La pobreza de registros se puede deber en parte a la dificultad de acceder a estas áreas, lo que ha resultado en escaso conocimiento florístico de la región (García, 2004; Solano, Alonso, Rosado, Aguilar & García, 2008; Zacarías & del Castillo, 2010). Como en SMS, los esfuerzos de muestreo en SMOC han sido insuficientes (García, 2004) debido principalmente a conflictos sociales. SMS y SMOC han sido consideradas áreas prioritarias para la conservación de vertebrados y herpetofauna, respectivamente (Bojorquez, Azuara, Ezcurra & Flores, 2005; Urbina & Flores, 2010).

El municipio de Macuiltianguis y áreas cercanas fueron las regiones más importantes en términos de patrones de rareza tanto para todo el género como para encinos blancos, mientras que la región más importante en rareza para encinos rojos se localizó en SMS (Yautepec y Coatlán). Estos patrones de rareza también son similares a aquellos patrones reportados para gimnospermas (Contreras & Luna, 2006), anfibios y reptiles (Koleff, Gaston, & Lennon, 2003), y mamíferos (Iloldi, Fuller, Linaje, Pappas, Sánchez & Sarkar, 2008). Las principales regiones de rareza para encinos blancos se localizan al noreste de MVO en Tepelmeme y Teposcolula. Estas zonas presentan lluvias relativamente bajas (<800 mm) con climas templados subhúmedos a semiáridos. En contraste, los centros de rareza de encinos rojos fueron identificados como sitios con alta precipitación anual (>800 mm) al sur de esta subprovincia, particularmente en las zonas de Juxtlahuaca-Mixtepec, Santa María Peñoles y Zimatlán. La anterior también es un área prioritaraia de acuerdo a la rareza de mastofauna (Iloldi, Fuller, Linaje, Pappas, Sánchez & Sarkar, 2008). El patrón de rareza encontrado en SMOC es similar al encontrado para mamíferos (Iloldi, Fuller, Linaje, Pappas, Sánchez & Sarkar, 2008) y aves (Peterson et al., 2003).

9.2. Patrones de recambio de especies de encinos

Nuestros resultados muestran que el intervalo altitudinal más importante para los encinos blancos está entre 2000-2200 msnm, pero en el caso de los encinos rojos es más complejo ya que se identificaron al menos tres intervalos altitudinales con alta riqueza. El análisis también muestra que los intervalos altitudinales donde ocurre el mayor recambio se localizan a altitudes más bajas o más altas con respecto a los intervalos de mayor riqueza. El patrón de recambio también coincide con la transición entre diferentes tipos de vegetación. Por ejemplo, encontramos un alto recambio de especies que coincide con la transición de vegetación de bosque tropical a la de bosques mesófilos o de encinos, y de estos a bosques de pino-encino. Este patrón también fue identificado en el estado de Jalisco por Vásquez y Givnish (1998). Para que la conservación sea más eficaz, es importante considerar áreas que muestran un amplio rango altitudinal tal como lo propone Zacarías & Del Castillo (2010).

9.3. Pérdida de hábitat asociado a encinos

Actualmente la pérdida de hábitat es un fenómeno común en todos los ecosistemas, siendo los bosques templados los más drásticamente reducidos por la influencia humana (Rzedowski, 1978; Challenger, 1998). De acuerdo con Velázquez et al. (2003), 40% de la superficie de Oaxaca está cubierta por bosques templados, de los cuales 21% ha sido alterado a vegetación secundaria de 1980 a 2001. En el 2001, 70% de los bosques templados secundarios registrados en 1980 se habían convertido a pastizales. En Oaxaca los bosques templados pierden cerca del 1% de su área anualmente, mientras que el aumento de la vegetación secundaria es mayor a ese 1% (Velázquez et al. 2003). Robson (2007) sugiere que un problema adicional para la conservación es que 80% de los bosques biodiversos en Oaxaca están cerca de asentamientos humanos, cuyas tierras son la herencia de 1400 comunidades indígenas y ejidos (Moguel & Toledo, 1999; Sarukhan & Larson, 2001).

Los bosques templados subhúmedos principalmente en MVO y el suroeste de SMO y los bosques semiáridos templados de MVC tienen tasas de deforestación de 0.5% por año, menos del 2% reportado para bosques de encinos (Gómez, Vega, Ramírez, Palacio & Galicia, 2006). Sin embargo, la tasa de conversión de vegetación primaria a secundaria en el mismo periodo (70%) es mayor en los bosques subhúmedos de MVO, comparada al 21% identificada para bosques templados durante 1980-2000 (Velázquez et al., 2003). Por otro lado, aunque los hábitats asociados con MVC han sufrido pérdida de hábitat y procesos de transformación, aún mantiene grandes extensiones de bosques predominantemente monoespecíficos, así como también en regiones semiáridas de SMS, MVO y SMOax.

9.4. Diversidad genética

La variación genética es necesaria para el futuro de la viabilidad de las poblaciones (Vellend, 2005). En general, encontramos alta variación genética en las poblaciones de tres especies de encinos rojos (*Q. candicans*, *Q. castanea* y *Q. crassifolia*) distribuidas en tres subprovincias biogeográficas (SMOax, SMS y MVO) del estado de Oaxaca, México (Tabla 1). La diversidad genética observada en las poblaciones podría relacionarse a rasgos biológicos de especies de larga vida, tales como la polinización por el viento, cruzamiento, gran tamaño efectivo poblacional y flujo génico extensivo entre poblaciones (Sork et al., 2002; Sork & Smouse 2006; Breed et al., 2012). En general, los valores de diversidad genética encontrados en varias especies de encinos mexicanos fueron más altos que los reportados en otras especies de *Quercus* en Norteamérica y Europa (Fernández-Manjarrés & Sork, 2006; Craft & Ashley, 2010; Aldrich & Cavender-Bares, 2011; Vranckx et al., 2014; Ashley et al., 2015). Las especies de encinos en Oaxaca han estado sujetas a un largo proceso de adaptación a una heterogeneidad microclimática acoplada a una historia geológica muy compleja, generando una matriz heterogénea de riqueza de especies en diferentes regiones a través del estado (Valencia, 2004). Curiosamente, las poblaciones con alta diversidad genética coinciden con áreas de alta riqueza de especies de encinos de acuerdo a un reciente estudio biogeográfico de encinos en Oaxaca (Ramirez-Toro et al., datos aún no publicados).

9.5. Endogamia y tamaño poblacional

Los bosques naturales en el estado de Oaxaca han disminuido dramáticamente por lo menos en los últimos 50 años (Velázquez et al., 2003; Gomez-Mendoza et al., 2006). La mayoría de las áreas deforestadas ocurren en bosques templados que producen 46% de la madera de pino y 85% de la de encino (Palacio-Prieto et al., 2000; Velázquez et al., 2003). Las tres especies de encinos han sido amenazadas a través de su distribución en Oaxaca como resultado de la destrucción del hábitat. A pesar de las altas tasas de deforestación de bosques templados, aún no hay fuerte evidencia de endogamia en las poblaciones de encinos como se ha observado en otras especies (Sork & Smouse, 2006; Craft & Ashley, 2010; Herrera-Arroyo et al., 2013). En algunos casos, pocas poblaciones mostraron valores significativamente positivos de F_{IS} en *Q. candicans* y *Q. castanea* en MOV y en *Q. crassifolia* y *Q. castanea* en SMOax (Tabla 1). Sin embargo, efectos significativos se observaron en la reducción del tamaño efectivo poblacional en MVO (N_e = 62.4) y SMS (N_e = 61.5) para *Q. candicans* y (N_e = 83.9) para *Q. castanea* (Tabla 3). Se ha sugerido que aún en especies polinizadas por el viento y principalmente con cruzamiento externo tales como los encinos, la disminución de la densidad de árboles en una comunidad podría alterar la capacidad de apareamiento, de manera que el número de fuentes de polen cercanas a un árbol madre disminuye y la distancia de polinización entre parejas aumenta (Sork et al., 2002; Bacles et al., 2004; Eckert et al., 2010; Breed et al., 2012; Frankham et al., 2013; Vranckx et al., 2014). Además, la dispersión de semillas en encinos está limitada debido a que las bellotas carecen de adaptaciones para la dispersión a grandes distancias (p. ej., las bellotas germinan cerca del árbol madre) o son transportadas por aves (Jump & Penuelas, 2006; Sork & Smouse 2006; Fernández-Manjarrés & Sork, 2006; Sagnard et al., 2011).

9.6. Estructura genética, análisis bayesiano de mezclas, disrupciones en el flujo génico y conectividad.

No encontramos estructura genética en ningunas de las tres poblaciones de especies de encinos; la mayor parte de la variación genética se encontró dentro de las poblaciones (Tabla 2). También encontramos una gran cantidad de conectividad genética entre poblaciones localizadas en MVO y SMOax excepto las poblaciones al oeste de MVO y SMS para las tres especies. Diferencias en la cobertura y en la elevación del terreno pueden crear múltiples zonas climáticas a través de la región de Oaxaca, caracterizada por la variación en climas, topografía y vegetación; por lo tanto, es posible que tanto la discontinuidad del hábitat como las barreras geográficas físicas jueguen un papel importante en la diferenciación genética y la endogamia.

El estado de Oaxaca posee un paisaje intrincado con montañas con picos altos cruzadas por valles y cañones. Los ambientes heterogéneos promueven el mantenimiento de una alta diversidad genética, así como también procesos profundos de divergencia entre poblaciones de especies (Ferrusquía-Villafranca, 1993; García-Mendoza, 2004; Ortiz-Pérez et al., 2004). Además, observamos evidencia de diferenciación del paisaje en las barreras para el flujo génico entre *Q. candicasn* y *Q. crassifolia* (barreras B5, B6, B2 y B1) que dividen las pociones este y oeste de MVO. Esta evidencia coincide con la superficie de resistencia climática espacial entre *Q. candicans* y *Q. crassifolia*, manteniendo poblaciones aisladas en las porciones este y oeste de MVO. Desde el punto de vista biogeográfico, tanto las zonas occidentales como las orientales de las regiones que albergan una flora de bosques de pino-encino en una serie de cordilleras lineales montanas con una elevación máxima de 3200-3400 m, están separados por valles intermontanos cubiertos con bosques tropicales deciduos en la porción central de la provincia (Ortiz-Pérez et al., 2004). Suponemos que los valles inter-montanos con bosques tropicales deciduos actúan como una barrera geográfica para la distribución disyuntiva de las tres especies en la zona. Debido a las distribuciones pequeñas y aisladas, el flujo génico limitado y la deriva génica pueden contribuir a una alta endogamia dentro de ambos lados de la región MVO.

También detectamos otra barrera geográfica para el flujo génico entre las poblaciones señaladas por B1, B4 (*Q. candicans*, *Q. crassifolia* y *Q. castanea*) que separan las poblaciones localizadas al noreste de SMOax de aquellas en el noroeste de MVO. La superficie de resistencia espacial mostró menor conectividad entre *Q. candicans*, *Q. crassifolia* y *Q. castanea* entre MVO y SMOax. A medida que se desarrolló la zona desértica en la depresión de Tehuantepec en Oaxaca, los bosques se contrajeron o fragmentaron o desaparecieron, lo que afecto la composición de especies en ambos lados de MVO y SMOax (García-Mendoza et al., 2004; Ortiz-Pérez et al., 2004). Este valle se localiza al norte de SMOax, al este y noreste de MVO. La mayor parte del valle se encuentra a elevaciones por debajo de los 1000 m, pero se eleva a poco más de 1400 m hacia las elevaciones sureñas, donde está cubierta por vegetación xerófila y muchas suculentas tales como cactus y *Mammillaria* y actúa como una gran barrera adicional al flujo génico para *Q. candicans*, *Q. crassifoliarassifolia* y *Q. castanea* en MVO y SMOax (Ortiz-Pérez et al., 2004). Por lo tanto, sugerimos que una alta variabilidad en hábitat y condiciones climáticas combinadas con altas elevaciones y grandes distancias geográficas pueden explicar la diferenciación genética moderada y la endogamia de algunas poblaciones aisladas (Sork & Waits, 2010; Manel & Holderegger, 2013).

9.7. Implicaciones para la conservación

De acuerdo con Peterson et al. (2003) el concepto de grupo indicador es una herramienta útil para empatar los valores de riqueza y endemismo de diferentes grupos en un área dada. Los encinos son especies dominantes en los principales tipos de vegetación. En Oaxaca, la mayoría de especies de encinos son árboles, excepto *Q. frutex* y *Q. microphylla*, que habitan el valle de Tehuacán-Cuicatlán. Por lo tanto, puede considerarse a los encinos como elementos importantes en casi todos los tipos de bosques. En este estudio, hemos mostrado que los patrones de riqueza para encinos son similares a aquellos obtenidos para otros grupos de plantas. SMOax es considerada por muchos autores como un centro de riqueza para gimnospermas (Contreras & Luna, 2007), Orchidaceae (Solano, Alonso, Rosado, Aguilar & García, 2008) y varias especies de árboles de bosques templados (Zacarías & del Castillo, 2010). Muchos de estos estudios coinciden en la importancia de ecosistemas montanos húmedos para explicar la alta diversidad observada en los límites entre los distritos de Ixtlán-Cuicatlán y Tuxtepec, los que también identificamos como áreas de alta riqueza de encinos. Un resultado similar se ha observado también para otros grupos tales como vertebrados (Bojorquez, Azuara, Ezcurra & Flores, 1995; Peterson et al., 2003), particularmente aves (Peterson et al., 2003), mamíferos (Iloldi, Fuller, Linaje, Pappas, Sánchez & Sarkar, 2008; Briones, Cortés & Lavariega, 2015) y reptiles (Urbina & Flores, 2010). Indudablemente, el reciente interés en la exploración botánica de Oaxaca a través de proyectos tales como el inventario etnoflorístico en regiones con alta biodiversidad ha aumentado significativamente el número de registros para especies de plantas, permitiéndonos describir la distribución de especies de encinos en detalle.

Encontramos elevados niveles de diversidad genética de las poblaciones estudiadas de *Q. candicans*, *Q. crassifoliafolia* y *Q. casatanea* a lo largo de su distribución en las principales subprovincias fisiográficas de Oaxaca (MVO, SMOax y SMS) demostrando que los sitios con mayor riqueza también lo son en diversidad genética. Recientemente se ha sugerido que la diversidad genética y la de especies podrían estar interconectadas debido a un proceso que actúa en paralelo a estos dos niveles (Vellend, 2005; Papadpoulou et al., 2011). Actualmente esta riqueza biológica está amenazada por los efectos de procesos de cambio de uso del suelo, tales como la deforestación; en los últimos 20 años Oaxaca ha perdido más de medio millón de hectáreas boscosas (Velázquez et al., 2003; Gómez-Mendoza et al., 2006).

Torres, Luna & Oyama (2011) propusieron que la priorización de la conservación debería enfocarse en aquellas áreas sin protección oficial. En general, el sistema de Areas Naturales Protegidas (ANP) de Oaxaca es deficiente en términos de la conservación de ecosistemas donde habitan los encinos. Cuatro ANP, la Reserva de la Biosfera de Tehuacán-Cuicatlán, el Parque Nacional Benito

Juárez, el Boquerón de Tonala y el Parque Estatal de Hierve el Agua protegen un total de 18 especies de encinos.

Sin embargo, en Oaxaca, hay áreas alternativas de conservación llamadas Áreas de Conservación Indígena y Comunal (ACIC) (Robson, 2007; Martin, Camacho, del Campo, Fonseca, Mendoza & Ortiz, 2011). De acuerdo con Martin, Camacho, del Campo, Fonseca, Mendoza & Ortíz (2011), a nivel estatal un total de 126 ACIC conservan 375,457 ha, de las cuales sólo 22 incluyen bosques donde habitan los encinos. Sin embargo, este sistema de conservación protege cerca de 15 especies de encinos, muchas de estas no presentes en las áreas naturales protegidas oficiales (véase la tabla 1 para más detalles). El sistema de ACIC en Oaxaca conserva principalmente bosques de pino-encino, así como también bosques mesófilos (Monroy, Sánchez, Briones, Lira & Mass, 2015) lo que explica el elevado número de especies de encinos protegidas en un área cercana al 10% del tamaño de las áreas naturales oficialmente decretadas como protegidas. En conjunto, ANP y ACIC protegen 29 especies de encino en Oaxaca (53.7% del total), de las cuales 16 son encinos blancos y 13 rojos.

A pesar de no ser considerada como ACIC, la Unión de Comunidades Zapoteca-Chinantecas (UZACHI) y la Unión de Comunidades y Ejidos Forestales Oaxaqueños (UCEFO) son ejemplos de proyectos exitosos de conservación en SMOax en las que se ha documentado el mantenimiento de la vegetación primaria y la recuperación de áreas boscosas existentes (Klooster & Masera, 2000; Bray, Merino, Negreros, Segura, Torres & Vester, 2003; Robson, 2007). Por el contrario, MVO tiene menos ACIC; particularmente la región de Juxtlahuaca-Mixtepec tiene pocas áreas comunales protegidas y las especies de encinos en esta región son aquellas con la mayor tasa de pérdida de hábitat. Dado el número considerable de especies y su alta tasa de transformación de la cubierta vegetal, que ha aumentado debido a la presencia de plagas (Monroy, Sánchez, Briones, Lira & Mass, 2015), debería promoverse un sistema de conservación que involucre la participación de comunidades locales, siguiendo el modelo de ACIC. Un caso similar se presenta en SMS que tiene el menor número de ACIC, casi todas concentradas en la región de Coatlán. Sin embargo, en SVO, SMS y CHIM los principales problemas para la conservación de áreas naturales son aquellos asociados con disputas sociales sobre la propiedad de la tierra (Peterson et al., 2003). Actualmente, en los Chimalapas se han adoptado estrategias de conservación basadas en ACIC, permitiendo la conservación de áreas boscosas e incluso contribuyendo a atenuar conflictos sobre la propiedad de la tierra (Monterrubio & Newing, 2013).

En todos los casos, la creación de sistemas de áreas protegidas en SMOax, un sitio identificado como una prioridad en todos los análisis, es importante. La conservación de esta área debería confirmar la importancia del sistema ACIC creado para formar corredores comunales a lo largo de municipios en esta región que permiten aumentar el área comunal protegida, desde San Felipe Usila-San Francisco Texmelucán en el noroeste hasta Santa María Ixtepeji-Santa María Yavesía al sur. Es innegable que la vocación de conservación de los dueños de las tierras ha demostrado ser efectiva para el desarrollo humano y el mantenimiento de los servicios ecosistémicos, y esta región de SMOax ha sido reconocida como una de los mejores ejemplos de conservación y uso sustentable de recursos en México, incluso permitiendo aumentar la cubierta forestal. El éxito de este tipo de proyectos se debe a la amplia conciencia de sus habitantes acerca de los problemas ambientales Van Vleet, Bray & Durán, 2016).

Finalmente, es claro que el diseño de áreas de conservación debería considerar las diferencias ecológicas entre las secciones *Quercus* y *Lobatae*, ya que para los encinos blancos algunas áreas idetificadas como prioritarias se encuentran en regiones áridas al norte de MVO, mientras que las regiones prioritarias para los encinos rojos están principalmente localizadas en las partes húmedas de SMOax, SMS y CHIM.

Debe considerarse la protección oficial en algunas regiones de SMS y MVO debido a la pérdida significativa en la cubierta vegetal y la pobre organización entre los dueños de las tierras en estas áreas. Sin embargo, el extenso número de comunidades complica la creación de áreas naturales sin protección gubernamental, ya que en estas áreas debería diseñarse, como en SMOax, una red de corredores alternos que conecten diferentes tierras comunales y que formen una red extensiva para proteger bosques montanos de Oaxaca.

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