American Journal of Botany

American Journal of Botany 98(2): 290–305. 2011.

Conservation biogeography of red oaks (*Quercus*, section *Lobatae*) in Mexico and Central America[1]

Andrés Torres-Miranda[2,3], Isolda Luna-Vega[3,4], and Ken Oyama[2]

[2]Centro de Investigaciones en Ecosistemas, Universidad Nacional Autónoma de México (UNAM), Ant. Carr. a Pátzcuaro 8701, Col. Ex-Hda. de San José de la Huerta, 58190, Morelia, Michoacán, Mexico; [3]Facultad de Ciencias, UNAM, Departamento de Biología Evolutiva, Apartado Postal 70-399, Ciudad Universitaria, México 04510 D.F. Mexico

- *Premise of the study*: Oaks are dominant trees and key species in many temperate and subtropical forests in the world. In this study, we analyzed patterns of distribution of red oaks (*Quercus*, section *Lobatae*) occurring in Mexico and Central America to determine areas of species richness and endemism to propose areas of conservation.
- *Methods*: Patterns of richness and endemism of 75 red oak species were analyzed using three different units. Two complementarity algorithms based on species richness and three algorithms based on species rarity were used to identify important areas for conservation. A simulated annealing analysis was performed to evaluate and formulate effective new reserves for red oaks that are useful for conserving the ecosystems associated with them after the systematic conservation planning approach.
- *Key results*: Two main centers of species richness were detected. The northern Sierra Madre Oriental and Serranías Meridionales of Jalisco had the highest values of endemism. Fourteen areas were considered as priorities for conservation of red oak species based on the 26 priority political entities, 11 floristic units and the priority grid-cells obtained in the complementarity analysis. In the present network of Natural Protected Areas in Mexico and Central America, only 41.3% (31 species) of the red oak species are protected. The simulated annealing analysis indicated that to protect all 75 species of red oaks, 12 current natural protected areas need to be expanded by 120000 ha of additional land, and 26 new natural protected areas with 512500 ha need to be created.
- *Conclusions*: Red oaks are a useful model to identify areas for conservation based on species richness and endemism as a result of their wide geographic distribution and a high number of species. We evaluated and reformulated new reserves for red oaks that are also useful for the conservation of ecosystems associated with them.

Key words: complementarity; conservation biogeography; endemism; *Quercus*; red oaks; simulated annealing analysis; species richness; systematic conservation planning.

The application of biogeographical principles to problems concerning the conservation of biodiversity has emerged as a new line of research (Whittaker et al., 2005). Conservation biologists face several challenges when identifying priority areas that incorporate several biological and environmental patterns and processes. One alternative is to use groups of species that are representative of their ecosystems and could potentially be useful as indicators for conservation assessments. The main goal of conservation biogeography is to select areas that can act as reserves for species, populations, biological assemblages, and ecosystems based on concepts of complementarity, irreplaceability, and vulnerability according to the guidelines of systematic conservation planning (Kirkpatrick, 1983; Vane-Wright et al., 1991; Csuti et al., 1997; Margules and Pressey, 2000; Margules et al., 2002; Sarkar et al., 2006).

[1] Manuscript received 16 June 2010; revision accepted 8 December 2010.

The authors thank J. J. Morrone, S. Valencia-Ávalos, R. Contreras-Medina, C. Ríos-Muñoz, and S. Ramírez for useful comments on previous versions of this manuscript. Two anonymous referees suggested advances in tools to improve our manuscript. O. Alcántara, C. Ríos-Muñoz, and E. Coronado assisted with GIS technical support. They are also indebted to the staff of herbaria cited in the text for their courtesy during our review of specimens. Support from projects DGAPA-PAPIIT (UNAM) IN209108 and IN229803, and SEMARNAT-CONACYT 2004-311, 2004-C01-97 and 2006-23728 are appreciated. The first author was supported by CONACYT fellowship 216036 and by the Posgrado en Ciencias Biológicas, UNAM.

[4] Author for correspondence (e-mail: ilv@hp.fciencias.unam.mx)

doi:10.3732/ajb.1000218

In this study, our goal was to synthesize distributional data of red oaks (section *Lobatae*; genus *Quercus*) and their habitats to identify species-rich and highly endemic areas for conserving red oak species. We calculated and compared species richness, weighted endemism, and corrected weighted endemism indices of the red oaks of Mexico and Central America based on political divisions, floristic provinces, and grid-cell analysis. To determine the most important areas for red oak conservation, we performed complementarity analyses based on species richness and species rarity. A simulated annealing analysis was used to evaluate the efficiency of the current networks of Natural Protected Areas in Mexico and Central America. In this study, we attempted to answer the following questions: (1) How many species of red oaks are protected under the present Natural Protected Areas networks of Mexico and Central America, and (2) which Natural Protected Areas need to be expanded in coverage to efficiently protect oak species and forest stands associated to them?

Complementarity involves the selection of the fewest areas that preserve all the targeted species and can be estimated with two types of algorithms: (1) richness-based, selecting the first area based on the highest number of species and choosing the second area based on the highest number of complementary species relative to the first area; and (2) rarity-based, selecting areas that contain species unique to one site, then selecting areas that include species represented in only two sites, and then in three sites, and so on (Kirkpatrick, 1983; Margules et al., 1988, 2002; Vane-Wright et al., 1991; Csuti et al., 1997; Margules and Pressey, 2000; Rodrigues and Gaston, 2002; Sarkar et al., 2006). Irreplaceability of areas implies that an area that contains unique species cannot be substituted for another one; without these areas, it would be impossible to achieve the goal of representing all the features of the areas (Margules et al., 2002).

Simulated annealing analysis is a method that finds the lowest number of areas that can include all of the target species studied (Possingham et al., 2000; Pinto and Grelle, 2009). This heuristic method has been used to identify networks of protected areas for a variety of taxa (Cook and Auster, 2005; Shriner et al., 2006; Diniz-Filho et al., 2007; Pearce et al., 2008; Pinto and Grelle, 2009). This method generates a completely random reserve system followed by iterations that explore trial solutions by making sequential, random changes to this system. Either a new randomly selected site is added to the system, or a site already in the system is deleted. At each step, the new solution is compared with the previous solution, and the best one is accepted based on the principle of complementarity (Cook and Auster, 2005); at the same time, these solutions provide a measure of irreplaceability of each area. The most irreplaceable locations are those appearing in the majority of iterations and matching the distribution of those species of restricted ranges. Based on conservation targets (i.e., sets of biodiversity features such as type of vegetation and population density, among others), areas that represent these targets are selected for a minimum total cost, clustering the selected areas spatially (Ball et al., 2009). The program MARXAN produces a single best solution that selects the network that minimized the objective function in most of the iterations; thus, this algorithm meets our conservation goals by identifying the areas (Ball et al., 2009).

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. We chose red oaks as a suitable model for the study of the biogeography of the Mexican and Central American mountainous systems in the Mexican Transition Zone (MTZ: Halffter, 1987; Marshall and Liebherr, 2000; Morrone and Márquez, 2001; Contreras-Medina et al., 2007). Most of the red oaks are endemic and dominant or codominant species in the mountains of Mexico and Central America. These areas have been proposed as main centers of genus diversification of the section *Lobatae* (Manos et al., 1999; Valencia, 2004). The MTZ is a complex zone where Nearctic and Neotropical biotas intersect; it includes the montane areas of the southwestern United States, Mexico, and almost all of Central America.

The genus *Quercus* is one of the most important woody floristic elements in the northern hemisphere with 500–600 species in Asia, Europe, North Africa, and North and Central America (Manos et al., 1999; Manos and Stanford, 2001). The section *Lobatae* (red oaks) is endemic to the New World. Most of the species diversification of red oaks occurred in Mexico (Manos and Stanford, 2001; Valencia 2004; Nixon, 2006), with less occurring in Central America and only one species, *Q. humboldtii*, reaching South America. Most estimates of Mexican *Quercus* have considered species diversity to be high (160–165 species; Nixon, 2006), representing between 25 and 35% of the total oak species in the world. In Mexican temperate forests, oaks form dense stands account for more than 15% of the country's plant cover (Rzedowski, 1978; Challenger, 1998). Recently, Valencia (2004) reported 161 species in Mexico: 4 golden (*Protobalanus*), 81 white (*Quercus*), and 76 red (*Lobatae*) oaks. In Central America, Nixon (2006) reported 34 species; 9 species in Belize, 25–26 in Guatemala, 8–10 in El Salvador, 14 or 15 in Honduras, 14 in Nicaragua, 14 in Costa Rica, and 12 in Panama.

Red oaks occur in many temperate and subtropical forests such as oak, pine–oak, and cloud forests, as well as in prairies, scrublands, and evergreen and deciduous tropical forests, where they can be present as shrubs or small or large trees. Oaks play a major ecological role as dominant species and have diverse types of interactions with ectomycorrhizal fungi (e.g., Smith and Read, 1997), gall-forming insects (e.g., Walker et al., 2002), and seed-eating vertebrates (e.g., Vander-Wall, 2001), among others. Oak forests also provide habitats for a diverse group of other organisms including vertebrates (Brawn, 2006), arthropods (Tovar-Sánchez et al., 2004; Tovar-Sánchez and Oyama, 2006a), and epiphytes (Holz and Gradstein, 2005).

MATERIALS AND METHODS

Distributional data—Distributional data for 75 red oak species from Mexico and Central America were obtained from herbarium specimens in the following collections: MEXU, ENCB, IEB, XAL, UANL, CHAP, LL-TEX, and MO. Only 69 of the 76 species reported for Mexico by Valencia (2004) were used for this analysis because it was not possible to obtain herbarium specimens for *Q. aerea*, *Q. cupreata*, *Q. furfuraceae*, *Q. mulleri*, *Q. pachucana*, *Q. runcinatifolia*, and *Q. tardifolia*. We also included *Q. acatenangensis* (sensu Nixon [2006] but not recognized by Valencia [2004]), which occurs from Chiapas to Nicaragua, as a species different from *Q. ocoteifolia* distributed in eastern Mexico. In total, we had a database composed of 70 species of red oaks for Mexico and 17 species for Central America (Appendix S1, see Supplemental Data with the online version of this article). In addition, taxonomic treatments, monographs, and floristic studies were reviewed for distributional data (Muller, 1942, 1951; Martínez, 1951, 1953, 1954, 1959, 1965, 1966, 1974; Standley and Steyermark, 1952; McVaugh, 1974; Burger, 1977; Espinosa, 1979; Valdez and Aguilar, 1983; González-Villarreal, 1986, 2003a, b; Bello and Labat, 1987; de la Cerda, 1989; Spellenberg, 1992; Vázquez, 1992, 2000, 2006; Nixon and Muller, 1993; Valencia, 1995, 2004, 2005, 2007; Valencia and Jiménez, 1995; Spellenberg and Bacon, 1996; Romero et al., 2000a, b, 2002; Breedlove, 2001; Encina and Villarreal, 2002; Valencia and Cartujano, 2002; Valencia et al., 2002; Valencia and Lozada, 2003; Santacruz and Espejel, 2004; Valencia and Nixon, 2004; Vázquez et al., 2004; Romero, 2006). With this information, a database including 13 502 georeferenced records was constructed. Data occurrence was visualized using the program GIS ArcView ver. 3.2 (ESRI, 1999); distributional maps were built in vector format for each of the 75 species for Mexico and Central America on a scale of 1 : 250 000.

Study area—The biogeographic analysis was performed using three different units: political divisions, floristic provinces, and latitude × longitude grid cells.

Political divisions—We used political divisions of Mexico and the countries of Central America as follows: 28 states for Mexico, 3 districts for Belize, 6 provinces for Costa Rica and 3 for Panama, 20 departments for Guatemala, 7 for El Salvador, 9 for Honduras, and 9 for Nicaragua. In total, 85 political entities were used for all of these countries (Fig. 1A). We decided to use political divisions because in Mexico and some countries of Central America, conservation decisions are undertaken considering political boundaries rather than natural criteria. Furthermore, conservation policies are implemented independently by each country or state in the same country (Dávila-Aranda et al., 2004).

Floristic provinces—We used floristic provinces proposed by Rzedowski (1978) for Mexico with some modifications including those suggested for adjacent areas of Central America (Morrone, 2001) and southern North America (Takhtajan, 1986). We considered 15 floristic provinces: (i) California Peninsula (CALI), (ii) Sierra La Laguna (LAGU), (iii) northern Altiplano Mexicano (NALT), (iv) southern Altiplano Mexicano (SALT), (v) Tamaulipas (TAM), (vi) Sierra Madre Oriental (SMOR), (vii) Sierra Madre Occidental (SMOC), (viii) Serranías Meridionales (MERI), (ix) Valle de Tehuacán-Cuicatlán (VTC), (x) Depresión del Balsas (BAL), (xi) Sierra de los Tuxtlas (TUX), (xii) Planicie Costera del Golfo (PCG), (xiii) Planicie Costera del Pacífico (PCP), (xiv) Serranías Transístmicas (STI), and (xv) Sierra de Talamanca (TALA). The same floristic provinces were used previously by Contreras-Medina et al. (2007) for gymnosperms, but in this work we included an additional analysis in which we

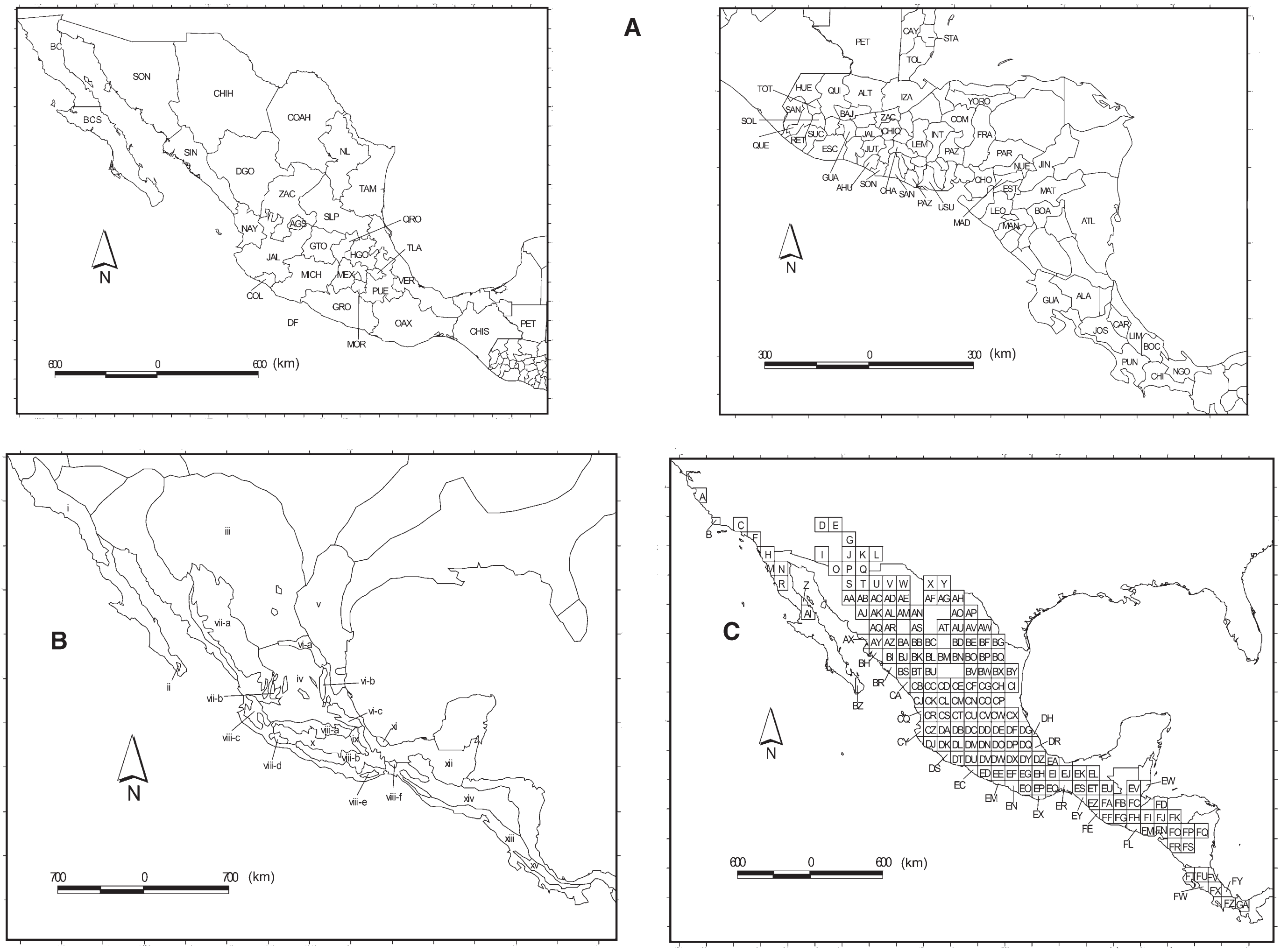

Fig. 1. Units used in biogeographic analysis: (A) Political division for Mexico: AGS Aguascalientes, BC Baja California, BCS Baja California Sur, CHIS Chiapas, CHIH Chihuahua, COAH Coahuila, COL Colima, DF Distrito Federal, DGO Durango, GTO Guanajuato, GRO Guerrero, HGO Hidalgo, JAL Jalisco, MEX México, MICH Michoacán, MOR Morelos, NAY Nayarit, NL Nuevo León, OAX Oaxaca, PUE Puebla, QRO Querétaro, SLP San Luis Potosí, SIN Sinaloa, SON Sonora, TAM Tamaulipas, TLA Tlaxcala, VER Veracruz, ZAC Zacatecas; Guatemala: ALT Alta Verapaz, BAJ Baja Verapaz, CHIM Chimaltenango, CHIQ Chiquimula, ESC Escuintla, GUA Guatemala, HUE Huehuetenango, IZA Ízabal, JAL Jalapa, JUT Jutiapa, PET Petén, QUE Quetzaltenango, QUI Quiché, RET Retalhuleu, SAC Sacatepéquez, SAN San Marcos, SOL Solula, SUC Suchitepéquez, TOT Totonicapán, ZAC Zacapa; Belize: CAY Cayo, STA Stan Creek, TOL Toledo; El Salvador: AHU Ahuachapán, CHA Chalatenango, MOR Morazán, PAZ La Paz, SAN San Salvador, SON Sonsonete, USU Usulután; Honduras: COM Comayagua, PAR El Paraíso, FRA Francisco Morazán, INT Intibuca, PAZ La Paz, LEM Lempira, OCO Ocotepeque, YORO Yoro; Nicaragua: BOA Boaco, EST Estela, JIN Jinotega, LEO León, MAD Madriz, MAN Managua, MAT Matagalpa, NUE Nueva Segovia, ATL Región Autónoma del Atlántico; Costa Rica: ALA Alajuela, CAR Cartago, GUA Guanacaste, LIM Limón, PUN Puntarenas, JOS San José; and Panama: BOC Bocas del Toro, CHI Chiriquí, NGO Ngöbe-Buglé; (B) Floristic provinces used for red oaks based and modified from Rzedowski (1978), Takhtajan (1986) and Morrone (2001): (i) CALI California; (ii) LAGU Sierra La Laguna; (iii) ALTIN northern Altiplano Mexicano and (iv) ALTIS southern Altiplano Mexicano; (v) TAM Tamaulipas; (vi) SMOR Sierra Madre Oriental: (vi-a) SMORN northern, (vi-b) SMORC central, and (vi-c) southern; (vii) SMOC Sierra Madre Occidental: (vii-a) SMOCC north-central, and (vii-b) SMOCS southern; (viii) SM Serranías Meridionales: (viii-a) FVT Faja Volcánica Transmexicana, (viii-b) SMS Sierra Madre del Sur, (viii-c) SMJ Serranías Meridionales Jalisco, (viii-d) SMG Serranías Meridionales Guerrero, (viii-e) SMO Serranías Meridionales Oaxaca, and (viii-f) SMI Serranías Meridionales Istmo; (ix) VTC Valle de Tehuacán-Cuicatlán; (x) BAL Depresión del Balsas; (xi) TUX Sierra de los Tuxtlas; (xii) GOL Planicie Costera del Golfo; (xiii) PACI Planicie Costera del Pacífico; (xiv) STI Serranías Transístmicas; and (xv) TALA Sierra de Talamanca; and, (c) Grid-cells of 1° × 1° latitude × longitude.

subdivided three of the provinces of Rzedowski (1978) that are composed of portions with different origins (Luna et al., 1999; Morrone, 2005). The Sierra Madre Oriental was subdivided into three parts: (vi-a) northern or Sierra Plegada (N-SMOR), (vi-b) central (C-SMOR) and (vi-c) southern (S-SMOR). The Sierra Madre Occidental was divided into two parts: (vii-a) north-central (NC-SMOC) and (vii-b) southern (S-SMOC). The Serranías Meridionales were divided into six parts: (viii-a) Faja Volcánica Transmexicana (FVT), (viii-b) Sierra Madre del Sur (SMS), (viii-c) Serranías Meridionales of Jalisco (SMJ), (viii-d) Serranías Meridionales of Guerrero (SMG), (viii-e) Serranías Meridionales of Oaxaca (SMO), and (viii-f) Serranías Meridionales del Istmo (SMI). In total, 23 floristic units were considered (Fig. 1B). Floristic provinces represent natural regions with a common geological origin; those used in this study can be proposed as a biogeographic framework for future studies on the conservation biogeography of Mexican and Central American plant species.

Grid cells—We used 183 grid cells of 1° × 1° latitude × longitude to analyze the distribution of the 75 red oak species (Fig. 1C). The grid-cell units provided an equal size unit and have been extensively used in Mexican biogeographic studies (Kohlmann and Sánchez, 1984; Luna et al., 2004; Serrato et al., 2004; Contreras-Medina and Luna, 2007).

Richness and endemism analysis—Species richness was measured as the total count of species within each study unit, i.e., each political division, floristic province, or grid cell. A species richness index was calculated by dividing the number of species present in one area by the total number of species considered (in our case, 75 species). Richness indices near 0 represent localities with a smaller number of species, while values near 1 represent areas with high species richness.

Endemism was measured using the endemism index of Crisp et al. (2001). Weighted endemism was determined in relation to species richness. First, the occurrence of a species in a particular study unit was divided by the total number of study units in which that species occurs. If a species was restricted to a single unit, it was scored as 1 for that unit and as 0 for all other units; if one species was found in two units, its score was 0.5; if in three units, it was 0.33, and so on. Then, we summed all species' scores to obtain the value of each study unit. The weighted endemism index tends to diminish the importance of species with wide distributions, but this index is correlated more with richness than endemism because it counts every species in each study unit (Crisp et al., 2001). Because this index directly reflects species richness, a correction is necessary to emphasize the importance of species with restricted distributions (corrected weighted endemism of Crisp et al. [2001]). To obtain the corrected weighted endemism index, we divided the weighted endemism index by the total count of species in each unit of analysis. The corrected weighted endemism removes the richness effect from the analysis, allowing the identification of areas containing species with restricted distributions. Units with the highest scores in weighted endemism are considered as centers of richness and those with corrected weighted endemism as centers of endemism.

Hotspots refer to areas containing the grid cells with the highest values, on average, of species richness, weighted endemism, and corrected weighted endemism indices following the criteria of Contreras-Medina and Luna (2007).

Complementarity analyses—Five methods based on complementarity algorithms were used to prioritize each political division, floristic province, or grid cell in the conservation of red oaks, identifying the minimum number of areas where each species was found at least once. The first two methods were richness-based, in which the selection of areas was undertaken using criteria of species richness alone. The last three methods were rarity-based, in which selection of areas was undertaken using only irreplaceability criteria, selecting areas that contained species unique to one site or with restricted distribution (Margules et al., 1988, 2002; Vane-Wright et al., 1991; Csuti et al., 1997; Rodrigues and Gaston, 2002).

In the first method, areas were selected using only a species richness index. The area with the highest richness index was selected and subsequently deleted from the matrix, and the richness indices were recalculated. The next area selected was that with the highest richness after the species that had been removed in the first area were deleted and the richness recalculated (i.e., the area with the highest number of complementary species). This procedure was repeated until all 75 species were found in the selected areas.

The second method was similar in process to the first, but it was based on the weighted endemism index. The first priority area selected was the one with the highest weighted endemism value. The species represented in that area were then deleted, and the index was iteratively recalculated with the remainder of the areas and species. The second area selected was that with the highest weighted endemism value recalculated and so on.

The third method gave priority to those areas with species that were restricted to a single site, and then to two areas, to three areas, and so on. If there was more than one area with species restricted to a single region, the areas with more single region species or those that included a high number of complementary species were prioritized.

The fourth method also prioritized those areas with species restricted to a single site, and then to two areas, and so on. This differs from the third method in that the highest weighted endemism index was used to prioritize when more than one area had the same number of species restricted to a single region. The fifth method prioritized areas based on the highest corrected weighted endemism index for the selection of the first area. After the corrected weighted endemism indices were recalculated, the highest score of this index was used for the selection of the second area until all the species were saved.

Reserve networks (simulated annealing)—Only grid cells previously identified as priorities in the complementarity analyses were used in this analysis. The grid cells determined as important for conservation were redrawn into smaller units of 5 × 5 km, which were considered as planning units. To determine the importance value (as an estimator of conservation cost) of each planning unit, we used three criteria associated with conservation targets:

(1) The vegetation types considered for Mexico (CONABIO, 1999) and Central America (CCAD-BM, 2004). A value of 0, 1, or 2 was assigned to each vegetation type, depending on the importance of each ecosystem to red oak conservation. In the case of Mexico, the ecosystems with higher values were oak and cloud forests, and in the countries of Central America, evergreen and semievergreen forests were given higher values. The importance value for each vegetation unit was defined with the following formula: (value assigned to each vegetation type) × 0.25 × (total area of each vegetation type). Each vegetation type located in a planning unit contributes its own value to the total cost (i.e., obtained by summing each of the values) when two or more vegetation types occur in a planning unit.

(2) The units already under conservation were identified with maps of the system of Mexican protected areas in the Comisión Nacional de Áreas Naturales Protegidas (CONANP, http://www.conanp.gob.mx/sig/) and the system of Central American protected areas in the Sistema de Información Ambiental Mesoamericano (SIAM) from the Comisión Centroamericana de Ambiente y Desarrollo (CCAD, http://www.ccad.ws/mapas/mapoteca.htm). These areas were not included in the simulated annealing analysis, following the scheme of systematic conservation planning, because all these identified priority areas must be excluded from it; this way we can propose the expansion or the creation of new areas for conservation. In this step, the intersection of the distribution of each species and the natural protected areas (NPA) was calculated to identify the species with some degree of protection.

(3) A range value was assigned on a scale of 1 through 6 to each species, where 6 represents species registered in one to three 1° × 1° grid cells, 5 for species registered in four to six grid cells, 4 for species recorded in seven to nine grid cells, 3 for species present in 10 to 15 grid cells, 2 for species registered in 16 to 29 grid cells, and 1 for species present in more than 30 grid cells. Also, a conservation value was assigned from 0 to 1, where 1 represents those species with all their records found outside the NPA network such that they have more priority for conservation; a value of 0 indicates species with all of their records included in the NPA network. Species with >50% of records inside the NPA network were automatically assigned a value of 0. A priority value for each species was obtained with: (range value of each species) × (conservation value of each species) expressed in integers.

The importance value of each species was obtained with the formula: (the range value of each species × the conservation value of each species) × (500/total number of records of each species). The highest values represent those species with restricted distributions whose records were not included in the NPA systems.

Simulated annealing analysis was implemented in MARXAN v. 1.8.2 (Ball and Possingham, 2000; Possingham et al., 2000). MARXAN works by selecting groups of areas (planning units) that meet a set of conservation targets with minimal total cost of the reserve network. The program runs iteratively and produces a range of near-optimal conservation solutions, which increases the chances of finding the best solution. In all the cases, the criteria were unweighted. The program CLUZ v. 1.6 (Smith, 2005) is the interface with GIS ArcView 3.2 (ESRI, 1999) and was used to enter data and map the results.

We used an adaptive annealing schedule with 10 000 steps and 1 million iterations per run and finished each run with normal iterative improvement, a MARXAN procedure that removes nonessential sampling units and ensures solutions close to a global optimum (Ball and Possingham, 2000). We ran each simulation 50 times and saved the best (lowest cost) solution in each case. We recorded the number of times (of 50) that each planning unit was included in a MARXAN-identified conservation network. This measure describes the irreplaceability of planning units in the sense that the locations that were more irreplaceable were those that showed up in the majority of the simulations; thus, they should be given the highest priority. Irreplaceability was mapped in ArcView 3.2 (ESRI, 1999).

RESULTS

Species richness and endemism—*Political division analysis*—The richest Mexican states with respect to red oak species were Jalisco (26 species); Oaxaca (22); Veracruz and Hidalgo (19); Chiapas, Nuevo León and Puebla (17); and Chihuahua and Durango (16). Mexican states with fewer species were Baja

California Sur (1 species) and Baja California Norte (2). Red oaks were absent from the states of Tabasco, Campeche, Quintana Roo, and Yucatán. In Central America, Guatemala was the richest country with 13 species, followed by El Salvador, Honduras, and Nicaragua with six species each. The Francisco Morazán department of Honduras was the richest region with six species followed by San José province in Costa Rica with five species and La Paz department in Honduras, Matagalpa department in Nicaragua, Alajuela province in Costa Rica, and Chicomula province in Panamá with four species each (Fig. 2A).

From the 75 species of red oaks considered in this study, 58 (77.3%) were endemic to Mexico and the following five (6.6%) to Central America: *Q. costaricensis*, *Q. gulielmi-trealeasi*, *Q. hondurensis*, *Q. rapurahuensis*, and *Q. seemanni*.

The weighted endemism and corrected weighted endemism indices produced different results. The weighted endemism values showed the highest scores for Jalisco (6.59) followed by Nuevo León (6.04) states. Other groups of states with high values were Coahuila, Chihuahua, Tamaulipas, and Durango in the north; Guerrero, Oaxaca, and Chiapas in the south; and Hidalgo in the central part of Mexico. For Central American countries, San José and Alajuela provinces in Costa Rica, the Chimaltenango department in Guatemala, and the Francisco Morazán department in Honduras showed the highest values of weighted endemism (Fig. 2B). On the other hand, the Mexican states with higher corrected endemism index values were Baja California and Baja California Sur. A second important group was formed by Nuevo León with two exclusive species and six semi-restricted species (shared species with a neighbor state), and Coahuila with one exclusive species and four semi-restricted species. A third group was formed by the state of Jalisco with two endemic species and three semi-restricted species. In Central America, Costa Rica had two endemic species and one semi-restricted (see Table 1 for a complete list of endemic species), while the department of Huehuetenango in Guatemala and the province of Cartago in Costa Rica had the highest values of corrected weighted endemism (Fig. 2C).

Floristic province analysis—The species richness analysis of the Mexican floristic provinces showed that the highest red oak diversity was concentrated in the Sierras of Jalisco (24 species), the southern Sierra Madre Oriental (21), and the Sierra Madre del Sur (20) (Fig. 3A).

The weighted endemism index showed the highest values in the northern Sierra Madre Oriental, followed by the Serranías Transístmicas, and the north-central Sierra Madre Occidental. The Sierras of Jalisco, the southern Sierra Madre Occidental, the Sierra Madre del Sur, and the southern Sierra Madre Oriental were found to be of secondary importance (Fig. 3B). The highest corrected weighted indices were in California Peninsula, the Sierra La Laguna, and the Sierra de Talamanca in Central America. Other important areas were located in the northern Sierra Madre Oriental, the north-central Sierra Madre Occidental, and the Serranías Transístmicas (Fig. 3C).

In Mexico, seven species were endemic to the northern Sierra Madre Oriental, and two were semi-restricted. Five species were endemic to the Serranías Transístmicas, and another one was a semi-restricted species. Five species were endemic to the northern Sierra Madre Occidental. Three species were endemic to the Sierras of Jalisco and two species to the California. The Sierra Madre del Sur also had two endemic species. In the southern Sierra Madre Oriental, only one species was endemic, and one was semi-restricted. One endemic species was found in the Sierra La Laguna and one in the Depresión del Balsas. For Central America, three species were found to be endemic to the Sierra de Talamanca (see Table 1 for a complete list of endemic species).

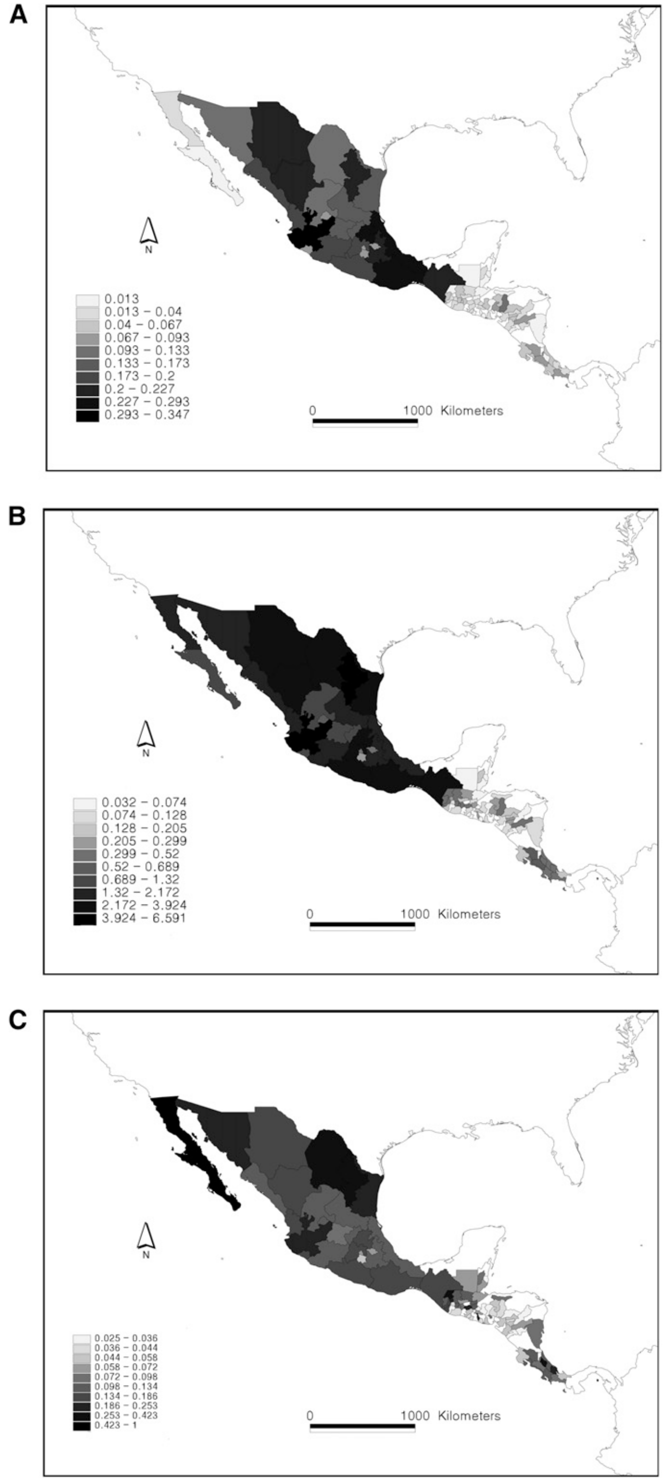

Fig. 2. Biogeographic analysis using political division: (A) with richness index in each states/districts/departments/provinces of Mexico and Central America; (B) with weighted endemism index; (c) with corrected weighted endemism index in each political division. Each graduate color represents a boundary decile of data.

Table 1. Endemic and semi-endemic *Quercus* species according to political divisions and floristic units.

Division	Endemic species
Political	
Baja California Norte (Mexican state)	*Q. agrifolia*, *Q. peninsularis*
Baja California Sur (Mexican state)	*Q. devia*
Nuevo León (Mexican state)	*Q. canbyi**, *Q. flocculenta**, *Q. galeanensis**, *Q. graciliramis*, *Q. hintonorum**, *Q. miquihuanensis**, *Q. saltillensis**, *Q. tenuiloba*
Coahuila (Mexican state)	*Q. coahuilensis*, *Q. flocculenta**, *Q. gravesii**, *Q. hintonorum**, *Q. saltillensis**
Jalisco (Mexican state)	*Q. cualensis*, *Q. iltisii**, *Q. radiata*, *Q. tuitensis**, *Q. urbanii*
Costa Rica (country)	*Q. costaricensis*, *Q. gulielmi-treleasi*, *Q. seemannii*
Floristic units	
Northern Sierra Madre Oriental	*Q. canbyi**, *Q. coahuilensis**, *Q. flocculenta*, *Q. galeanensis*, *Q. graciliramis*, *Q. hintonorum*, *Q. miquihuanensis*, *Q. saltillensis*, *Q. tenuiloba*
Altiplano Norte	*Q. gravesii**
Southern Sierra Madre Oriental	*Q. acherdophylla**, *Q. hirtifolia*
Serranías Transístmicas	*Q. acatenangensis*, *Q. benthamii**, *Q. crispipilis*, *Q. duratifolia*, *Q. hondurensis*, *Q. paxtalensis*
Central Sierra Madre Occidental	*Q. albocincta*, *Q. durifolia*, *Q. macvaughii*, *Q. radiata*, *Q. tarahumara.*
Serrranías Meridionales de Jalisco	*Q. cualensis*, *Q. iltisii*, *Q. tuitensis*
Sierra Madre del Sur	*Q. grahamii*, *Q. rubramenta*
California	*Q. agrifolia*, *Q. peninsularis*
Sierra La Laguna	*Q. devia*
Depresión del Balsas	*Q. hintonii*
Sierra de Talamanca	*Q. costaricensis*, *Q. gulielmi-treleasi*, *Q. seemannii*

Notes: Endemic and semi-endemic (*) species of *Quercus* in each political division and floristic unit.

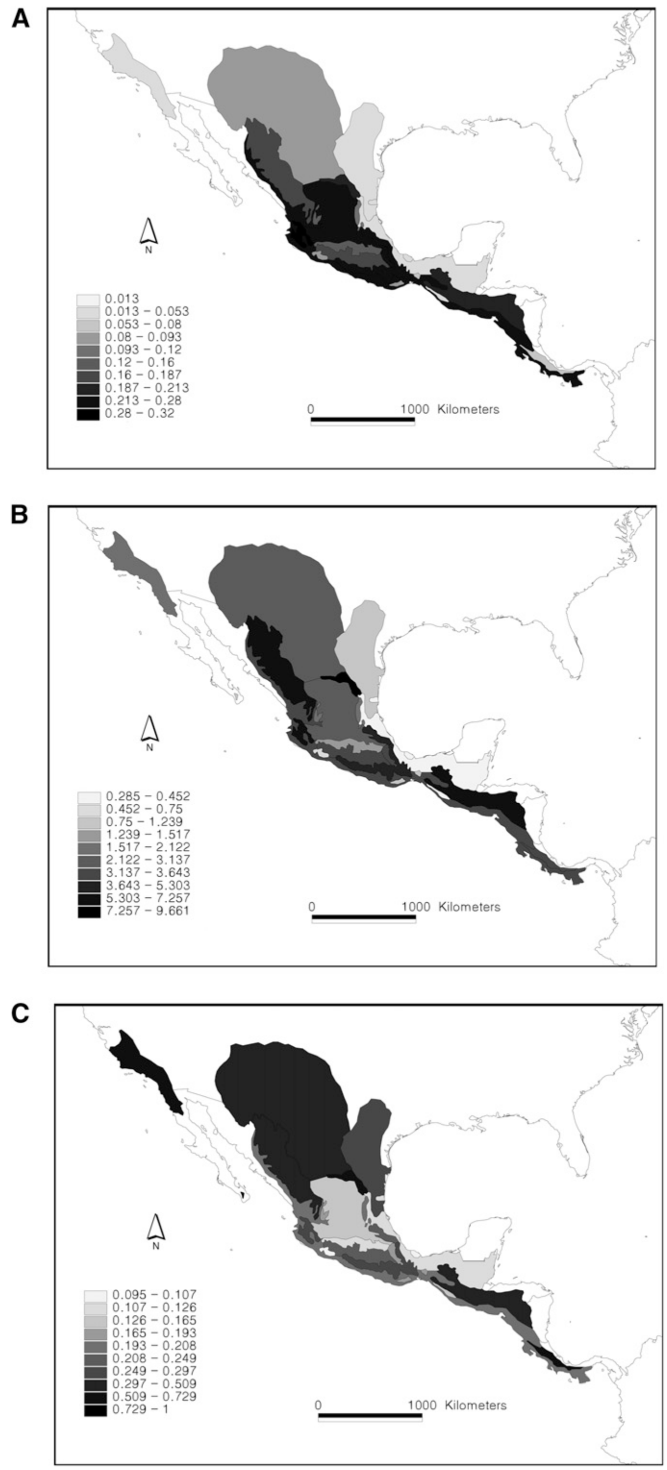

Fig. 3. Biogeographic analysis using floristic provinces: (A) with richness index in each floristic province; (B) with weighted endemism index value of each floristic province; (C) with corrected endemism index value of each floristic province. Each graduate color represents a boundary decile of data.

Grid-cell analysis—Grid-cell analysis showed two centers of species richness: one was located in the west in the Sierras of Jalisco (23 species), and the other was in the east where the southern Sierra Madre Oriental converges with the Sierras of Oaxaca (20) (Fig. 4A).

The northern Sierra Madre Oriental and the Sierras of Jalisco had the highest weighted endemism indices, followed by the southern Sierra Madre Oriental at its border with the northern Sierras of Oaxaca, the Sierra Madre del Sur, the Sierra Madre de Chiapas, the volcanic chains of Guatemala (included in the Serranías Transístmicas), and a smaller part of the southern Sierra Madre Occidental (Fig. 4B).

Corrected weighted endemism index values showed that the Sierra La Laguna was the area with the most restricted species distribution followed by the northern Sierra Madre Oriental (Sierra Plegada) (Fig. 4C). In Central America, the most important area was found in Sierra de Talamanca, with the highest values of corrected weighted endemism due to the presence of three endemic species: *Quercus costaricensis*, *Q. gulielmi-treleasi*, and *Q. seemanii*. Other important areas were found in northwestern Honduras, in the central Chortis plateau, and in the western part of the Sierra de Comayagua.

Complementarity analyses—Complementarity analyses supported 14 priority areas for red oak conservation; some of these areas included two or more political divisions of Mexico or Central America (Fig. 5A). Considering the results of the

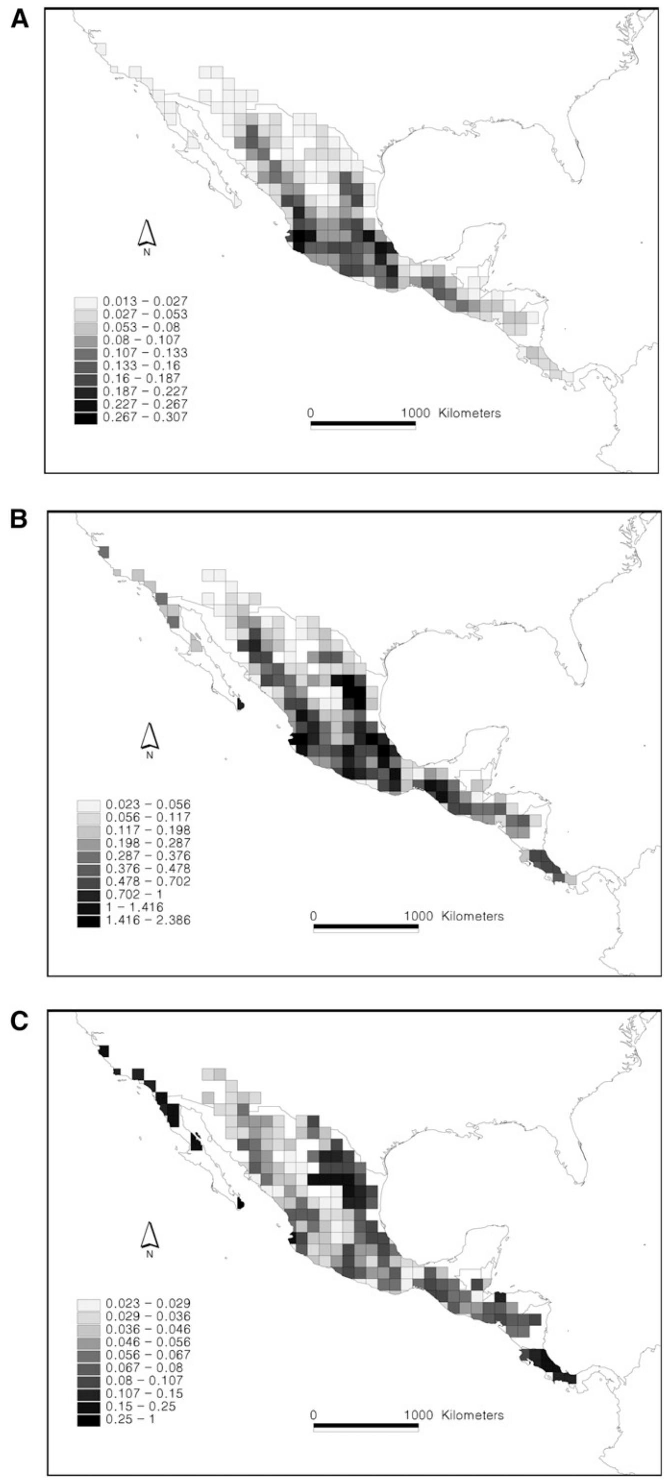

Fig. 4. Biogeographic analysis using grid-cells of 1° × 1° latitude/longitude: (A) with richness index in each grid-cell; (B) with weighted endemism index value in each grid-cell; (c) with corrected weighted endemism index value of each grid cell. Each graduate color represents a boundary decile of data.

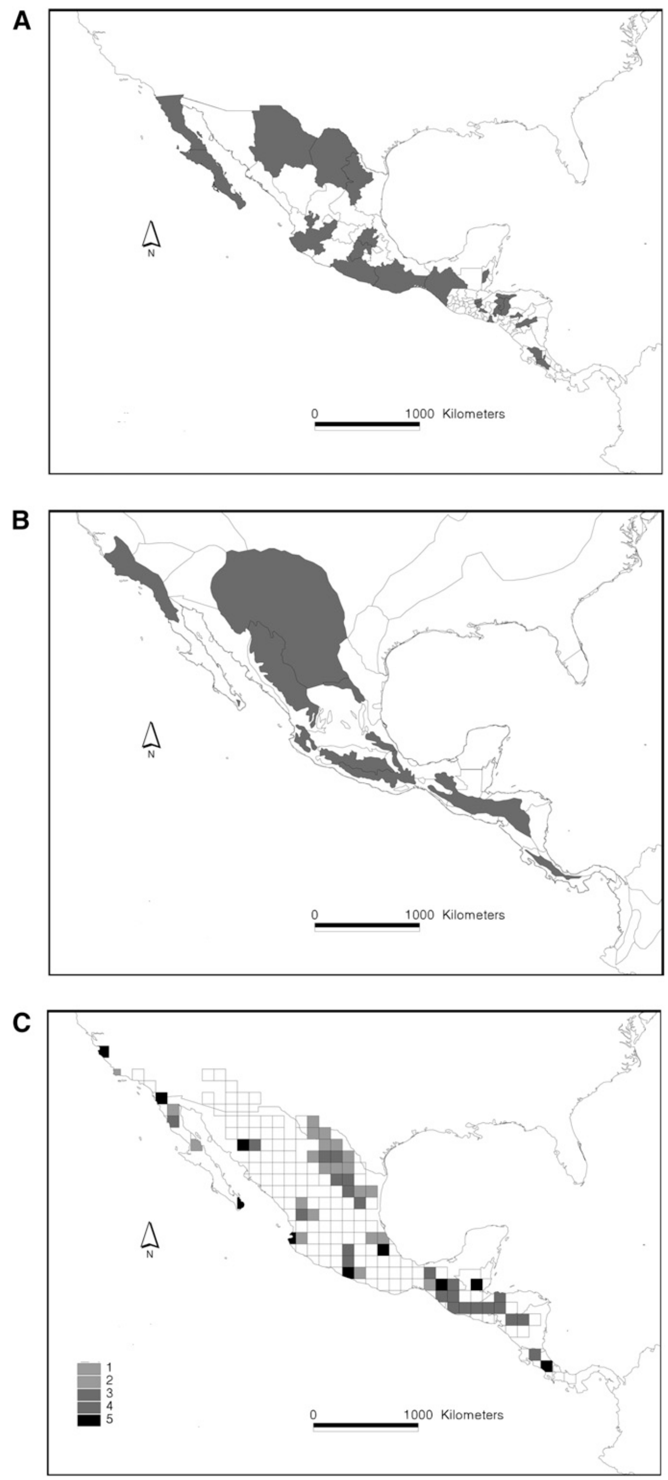

Fig. 5. Complementarity-based priority areas: (A) Political division; (B) Floristic units; (C) grid-cells 1° × 1° latitude × longitude.

five methods used, 13 Mexican states were defined as high priority for red oak conservation in at least one method: Jalisco, Nuevo León, Chiapas, Hidalgo, Coahuila, Chihuahua, Sonora, Baja California, Baja California Sur, Guerrero, Oaxaca, Estado de México, and Puebla. Methods 1, 2, and 4 identified 11 states as priorities. With method 5, only 10 states were priorities, while method 3 indicated 13 states to protect all of the species.

The complementarity analyses based on methods 1 to 4 prioritized the states of Jalisco, Nuevo León, and Chiapas, followed by the states of Baja California, Chihuahua, Coahuila, Estado de México, and Hidalgo. According to method 5, the more important states for conservation were Baja California, Baja California Sur, Coahuila, Nuevo León, Jalisco, and Estado de México, followed by Chiapas, Guerrero, Hidalgo, and Sonora (Table 2). The provinces that were found to be the most important in each region in Central America were as follows: San José and Alajuela in Costa Rica, the region including the departments Chiquimula and Zacatepequez in Guatemala; Comayagua, Francisco Morazán, La Paz, and Yoro in Honduras; Chalatenango, Morazán, and Usulatán in El Salvador; Nueva Segovia and Matagalpa in Nicaragua; and the district of Cayo in Belize (Table 2).

The complementarity analysis based on floristic provinces as units showed nine important areas for conservation of red oaks: Sierra Madre Oriental, Serranías Meridionales, Serranías Transístmicas, Sierra Madre Occidental, Sierra de Talamanca, California, Depresión del Balsas, Sierra La Laguna, and northern Altiplano Mexicano, in decreasing order of importance. All analyses gave similar results, with the exception of the analysis based on rarity using the corrected weighted index, which gave a different order of importance: Sierra La Laguna, Sierra de Talamanca, and California, followed by Depresión del Balsas, Sierra Madre Occidental, and Serranías Meridionales.

When we analyzed the different sections of the Sierra Madre Oriental, Sierra Madre Occidental, and Serranías Meridionales, the analyses showed 11 units for red oak conservation: northern Sierra Madre Oriental (Sierra Plegada), Serranías Transístmicas, north-central Sierra Madre Occidental, Serranías Meridionales de Jalisco, southern Sierra Madre Oriental (Hidalgo-Oaxaca), Sierra de Talamanca, California, Sierra Madre del Sur, Depresión del Balsas, Sierra La Laguna, and northern Altiplano Mexicano (Fig. 5B). Importance values varied depending on the algorithm used, but it was evident that, for four of the five algorithms, the most important units were the northern Sierra Madre Oriental, Serranías Transístmicas, and north-central Sierra Madre Occidental; for the fifth algorithm, the three priority areas were Sierra La Laguna, California, and Sierra de Talamanca (Table 3).

The number of priority grid-cells identified by the complementarity-based methods varied from 24 with method 5 to 42 with method 2 (Table 4). In total, 57 priority grid-cells were identified with at least one method of the five complementarity-based analyses (Table 4; Fig. 5C), which form 14 continuous areas of importance for conservation of red oaks (Fig. 6). Priority varied depending on the algorithm used, but the three areas that appeared as priorities in the majority of the cases were the northern Sierra Madre Oriental (Sierra Plegada), Serranías Meridionales of Jalisco, and southern Sierra Madre Occidental, with the exception of the fifth algorithm that added Sierra La Laguna and California as priority areas.

We identified seven hotspots for red oaks based on areas with the highest average of richness, weighted endemism, and corrected weighted endemism species indices. These hotspots were in decreasing order of importance: Serranías Meridionales of Jalisco, northern Sierra Madre Oriental (Sierra Plegada), southern Sierra Madre Oriental plus Serranías Meridionales of Oaxaca, southern Sierra Madre Occidental, Depresión del Balsas, Serranías Meridionales of Guerrero, and Sierra Madre de Chiapas plus Guatemala.

Reserves networks—The current Mexican and Central American Natural Protected Areas protect 31 species of red

TABLE 2. Importance values for areas when prioritizing by political entities

Political entity	Importance value				
	Method 1	Method 2	Method 3	Method 4	Method 5
Mexico					
Baja California	8	4	4	4	1
Baja California Sur	11	9	7	7	2
Chiapas	3	3	3	3	7
Chihuahua	5	5	10	10	
Coahuila	9	7	5	5	3
Estado de México	10	8	6	6	6
Guerrero	7	11	8		8
Hidalgo	4	6	9	9	9
Jalisco	1	1	1	1	5
Nuevo León	2	2	2	2	4
Oaxaca	7	11	8	8	
Puebla			9		
Sonora			10	10	10
Guatemala					
Chiquimula	12	12	12	12	
Zacapa	12	12	12	12	
Belize					
Cayo	12	12	12	12	12
El Salvador					
Chalatenango	12	12	12	12	
Morazán	12	12	12	12	
Usulatán	12	12	12	12	
Honduras					
Comayagua	12	12	12	12	
Francisco Morazán	12	12	12	12	
La Paz	12	12	12	12	
Yoro	12	12	12	12	
Nicaragua					
Matagalpa	12	12	12	12	
Nueva Segovia	12	12	12	12	
Costa Rica					
Alajuela	6	10	11	11	11
San José	6	10	11	11	

Notes: Priority political entities for conservation according to the five complementarity-based analyses. The numbers represent the importance of each area according to each method with 1 being the most important.

TABLE 3. Importance values for conservation areas when prioritizing by floristic units according to the five complementarity-based methods, with 1 being the most important.

Floristic unit areas	Importance value				
	Method 1	Method 2	Method 3	Method 4	Method 5
Altiplano Norte	10	10	9	9	7
California	9	8	7	8	3
Central Sierra Madre Occidental	5	4	3	4	5
Depresión del Balsas	8	9	10	10	10
Northern Sierra Madre Oriental	2	1	1	1	4
Serranías Meridionales de Jalisco	1	3	4	3	8
Serranías Transístmicas	3	2	2	2	6
Sierra de Talamanca	6	6	5	6	2
Sierra La Laguna	11	11	11	11	1
Sierra Madre del Sur	7	7	6	7	9
Southern Sierra Madre Oriental	4	5	8	5	11

TABLE 4. Importance values for areas when prioritizing by grid cells.

		Minimal designation of areas to conserve all the species				
Floristic region	Grid	Method 1	Method 2	Method 3	Method 4	Method 5
California						
	A	X	X	X	X	X
	B		X			
	H	X	X	X	X	X
	N					X
	R	X	X		X	X
	Z					X
	AI					X
Northern Sierra Madre Occidental (Tarahumara)						
	AJ	X	X	X	X	X
	AK	X	X	X	X	
Altiplano Norte						
	Y		X			
	AG		X			
	AH		X			
	AO		X			
	AP		X			
	AT		X			
	AU	X	X	X		
	AV	X	X	X		
	AW		X			
	BD		X			
	BE		X			
	BF		X			X
Northern Sierra Madre Oriental (Sierra Plegada)						
	BP	X		X		X
	BO		X		X	X
	BW		X	X	X	X
	BX			X		X
	BY			X		
	CH	X	X		X	
Sierra La Laguna						
	BZ	X	X	X	X	X
Southern Sierra Madre Occidental						
	CC	X				
	CK	X	X	X	X	
	CL	X				X
Serranias Meridionales de Jalisco						
	CY	X	X	X	X	X
	CZ	X				X
Southern Sierra Madre Oriental						
	DF			X		
	DG					X
	DQ	X	X	X	X	X
Depresión del Balsas						
	DN	X		X	X	
	DV	X				X
Sierra Madre del Sur						
	ED	X	X	X	X	X
	EE	X		X		
Serranías Transístmicas						
	EK	X	X	X	X	
	ES					X
	ET	X	X	X	X	X
	EU	X	X	X	X	
	EV	X	X	X	X	X
	EZ	X	X	X	X	
	FA	X	X	X	X	
	FD	X	X	X	X	
	FF	X	X	X	X	
	FG	X	X	X	X	
	FH	X	X	X	X	
	FI	X	X	X	X	
	FJ	X	X	X	X	
	FO	X	X	X	X	
	FP	X	X	X	X	
Sierra de Talamanca						
	FU	X	X	X	X	
	FX	X	X	X	X	X
Total		**36**	**42**	**34**	**30**	**24**

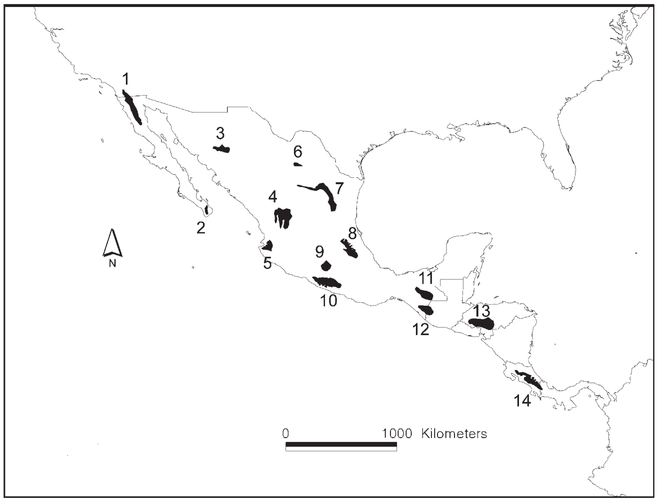

Fig. 6. Important areas in richness and endemism of red oaks: (1) Sierra San Pedro Mártir, (2) Sierra La Laguna, (3) Sierra Tarahumara, (4) southern Sierra Madre Occidental, (5) Serranías Meridionales de Jalisco, (6) Altiplano Norte in Coahuila, (7) northern Sierra Madre Oriental, (8) southern Sierra Madre Oriental, (9) Depresión del Balsas, (10) Sierra Madre del Sur, (11) Altos de Chiapas, (12) Sierra Madre de Chiapas, (13) Sierra de Comayagua, (14) Sierra de Talamanca.

oaks (41%) in 2 259 011 ha inhabited by these species; 63.2% belongs to Mexico, 1.9% to Guatemala, 6.3% to Honduras, and 28.6% to Costa Rica.

Nine of the 14 important areas derived from our grid-cell analysis for red oak conservation are entirely within or in the periphery of zones with some type of protection. However, careful analysis of the localities of these red oaks reveals that they are not necessarily found within the protected areas but rather in the vicinity. In Mexico, there are 11 officially protected areas that include 31 species of red oaks (Table 5).

The simulated annealing analysis indicated that the coverage of 12 current Natural Protected Areas (NPAs) can be expanded by at least 120 000 ha (Table 5). Of these NPAs, six are in Mexico (with a suggested increment of 65 000 ha), two in Guatemala (20 000 ha), two in Honduras (25 000 ha), and two in Nicaragua (10 000 ha). The analysis also indicated the need to create 26 new areas composed of at least 512 500 ha for the conservation of red oaks (Table 5) in sites that are not presently officially protected, all of which are located in Mexico (Fig. 7). With this proposal, the 75 species of red oaks of Mexico and Central America could be conserved, including those with restricted distributions, as well as 632 500 ha of temperate forests that include mixed forests, oak forests, pine–oak forests, coniferous forests, and cloud forests.

DISCUSSION

Species richness and endemism—Most of the species diversification of red oaks occurred in Mexico with a lesser amount in Central America and only one species, *Q. humboldtii*, reaching South America. In Mexico, climatic changes during the Pleistocene have been proposed as the main causes of several episodes of species migration and colonization both in terms of altitude and latitude (Axelrod, 1975; Hooghiemstra, 2006).

Three areas with the highest species richness were detected with the different units of analyses: (1) Serranías Meridionales of Jalisco, (2) southern Sierra Madre Oriental plus the Sierras north of Oaxaca, and (3) Sierra Plegada in the northern Sierra Madre Oriental. The first two areas are congruent with two of the centers of high biological and geological complexity proposed for Mexico (Contreras-Medina and Eliosa-León, 2001). The Sierra Plegada in the northern Sierra Madre Oriental is an important area rich in mammals (Ceballos et al., 2002) and gymnosperms (Contreras-Medina and Luna, 2007). We noted that the Faja Volcánica Transmexicana is not a rich area for red oaks as earlier workers had suggested for other groups of organisms (e.g., Rzedowski [1978]; Fa and Morales [1993]).

Eight floristic provinces were detected as important for red oak endemicity across all the analyses: the northern Sierra Madre Oriental (Sierra Plegada), southern Sierra Madre Oriental, Serranías Meridionales of Jalisco, Sierra Madre Occidental, Serranías Transístmicas, Sierra La Laguna, California, and Sierra of Talamanca. Three of them, the southern Sierra Madre Oriental, the Serranías Meridionales of Jalisco, and the southern Sierra Madre Occidental have also been identified as important centers of endemicity for birds (Escalante-Pliego et al., 1993) and mammals (Ceballos et al., 2002).

Despite the decrease in species richness and endemism in Central America as compared to Mexico, the ecological role and dominance of the genus in the montane forests of Central America is crucial for Sierra de Talamanca (Kappelle et al., 1992), Guatemala (Islebe, 1996), and Honduras (Mejía and Hawkins, 1995). Particularly, Sierra de Talamanca has three of the five endemic species reported in Central America.

Complementarity analyses—We obtained a similar number of areas with the five different complementarity-based analyses that were used, but the order of prioritization changed. Prioritization of areas using complementarity-based methods is sensitive to the size of the units of analysis; when using large units as floristic provinces, the number of areas obtained is the same with the five complementarity methods (14 areas in which all of the species are conserved). In this case, the areas of highest priority changed among the five methods: the northern Sierra Madre Oriental was the most important area based on methods 2, 3, and 4; the Sierra of Jalisco was for the method 1; and the Sierra La Laguna for the method 5. When we used medium-sized areas, such as political divisions, method 5, which used corrected weighted endemism indices, was able to conserve all species in only 12 political entities. All other complementarity-based methods needed almost 25 political entities to conserve all of the species, representing almost double the areas. Method 3 was the worst of the five methods and required 27 areas to include all the species.

Finally, when we used small-sized areas, such as the 1° × 1° grid cells, the complementarity-based methods were more efficient. In this case, method 5, which used the corrected weighted endemism index, was the most efficient, utilizing only 24 grid cells to conserve all the species. Methods 3 and 4 required 30–34 grid cells to conserve all of the species. Complementarity methods based on rarity were more efficient in maximizing conservation efforts in terms of conserving most of the species with the fewest areas. Complementarity methods based on richness (methods 1 and 2) required between 36 and 42 grid cells to include all the species to prioritize areas.

When combined, the species richness and endemism measures allowed us to recognize 12 priority conservation areas for

Table 5. Systematic conservation planning: areas that are already officially protected but that still need protection.

Suggested important floristic unit already protected	Site now protected: Name	Size (ha)	No. of species protected	Suggested increment in area (ha)	No. of species protected including the increased area	Suggested important areas to protect	Area (ha) to protect	No. of species that will be protected
1. California	PN San Pedro Mártir	72909	1	10000	2			
Totals		**72909**		**10000**				
2. Sierra La Laguna	RB Sierra La Laguna	112437	1					
Total		**112437**						
3. Northern Sierra Madre	APFF Tutuaca	363440	5	10000	7	Yécora	20000	6
Occidental	PN Cascada de Basseseachic	5911	4	10000	5	Álamos	20000	6
Totals		**721057**		**20000**			**40000**	
4. Southern Sierra Madre	RB La Michilía	9421	2			Guacamayita	15000	4
Occidental						Sierra Valparaíso	20000	6
						Sierra Los Huicholes	30000	8
Totals		**9421**					**65000**	
5. Serranías Meridionales de Jalisco						Sierra Zapotán	12500	6
						Sierra Cuale-Tuito	50000	10
						Sierra Cacoma	20000	6
							82 500	
6. Mesetas Coahuilenses						Sierra La Madera	25000	4
Total							**25 000**	
7. Northern Sierra Madre	PN Cumbres de Monterrey	177395	6	15000	8	Sierra La Concordia	15000	2
Oriental (Sierra Plegada)						Los Mimbres	15000	6
						Galeana	15000	5
						Puerto Purificación	10000	4
						Peña Nevada	25000	6
Totals		**177395**		**15000**			**80000**	
8. Southern Sierra Madre	RB Barranca de Metztitlán	96043	10	10000	11	Huayacocotla	15000	6
Oriental	APRN Cuenca Río Necaxa	41692	10			Epazoyucan	10000	6
	PN El Chico	2729	5			Tenango	10000	6
						Cuetzalán	10000	3
						Zoquiapan	20000	7
Totals		**140464**		**10000**			**65000**	
9. Depresión del Balsas						Sierra Nanchititla	30000	6
						Nevado de Toluca	20000	10
Total							**50000**	
10. Sierra Madre del Sur						Carrizal de Bravo	15000	5
						Heliodoro Castillo	15000	6
						Sierra Atoyac	25000	6
Totals							**55000**	
11. Sierra Norte de Chiapas	PN Lagunas de Montebello	6396	3			Huitepec	25000	5
Totals		**6396**					**25000**	
12. Sierra Madre de Chiapas	RB El Triunfo	119183	6			Mozotal	25000	4
volcanic arc Guatemala	RB/ZV Volcán Tacaná	8963	1	10000	2			
	ZV Volcán Tajomulco	12494	1	10000	4			
	ZV Volcán Lacandon	4313	0	10000	4			
Totals		**144953**		**30000**			**25000**	
13. Serranías de Comayagua	PN La Tigra	23821	2					
	PN Celaque	26640	3					
	PN Montaña Comayagua	18480	2	5000	4			
	RVS Corralitos	5730	0					
	RVS Mixcure	8060	0					
	RB Monserrat	2240	0	10000	4			
	RB Montecillos	13120	3					
	RB Hierbabuena	3510	1					
	RB Opalaca	14660	1					
	RB Guajiquiro	6700	1					
	RB Cerro El Uyuca	1138	3	10000	6			
	AUM Carias Bermúdez	4535	1					
	RB Mesas de Moropotente	7500	2	10000	5			
Totals		**128634**		**35000**				

TABLE 5. Continued.

Suggested important floristic unit already protected	Site now protected: Name	Site now protected: Size (ha)	Site now protected: No. of species protected	Suggested increment in area (ha)	No. of species protected including the increased area	Suggested important areas to protect	Area (ha) to protect	No. of species that will be protected
14. Sierra de Talamanca	PN La Amistad	193 477	3					
	RF Cordillera Volcánica	61 049	3					
	RF Los Santos	60 212	2					
	PN Tapanti	58 482	2					
	PN Chirripo	50 557	1					
	PN Braulio Carrillo	47 781	1					
	ZP Monteverde	26 790	2					
	RF Río Macho	22 110	1					
	ZP Las Tablas	19 998	2					
	PN Juan Castro Blanco	14 512	0					
	RB Alberto Manuel Brenes	7832	1					
	ZP Cerros de Escazu	7205	1					
	PN Volcán Poas	6533	1					
	ZP Río Navarro	6489	2					
	ZP Río Toro	4322	2					
	ZP Cuenca Río Tuis	4130	1					
	ZP Caraigres	3217	1					
	ZP Cerro La Carpintera	2395	1					
	RF Grecia	2312	2					
	PN Volcán Irazú	2008	1					
	RVS La Marta	1295	0					
	PN Volcán Turrialba	1261	0					
	Other areas (11)	3436	0					
		607 403						
Totals		**2 121 069**	**31**	**120 000**	**37**		**512 500**	**57**

Notes: The first column lists the important areas for red oaks that were suggested by the present analyses and are already included in protected areas (the names of these areas are the second column. The sixth column indicates the number of species that will be protected with the inclusion of the incremented area. Ninth column indicates the number of species that will be protected when the new areas are protected. RB: Biosphere Reserves, PN: National Parks, APFF: Flora and Fauna Protection Areas, APRN: Natural Resources Protection Areas, ZV: Close hunting zones, RVS: Wildlife Refuges, RF: Forestry Reserves, ZP: Protective.

Mexico and two for Central America (Fig. 6). This proposal coincides with the priority areas based on nonvolant mammals for Mexico (Arita et al., 1997). It is also important to note that oak and pine–oak forests in Mexico harbor the majority of endemic vertebrates (Flores-Villela and Gerez, 1994).

Reserves networks—In terms of implementation of systematic conservation planning (Margules and Pressey, 2000; Sarkar et al., 2006), we must conserve zones in addition to those already decreed as Natural Protected Areas. The zones identified as irreplaceable with the annealing simulated analysis coincide with the Priority Conservation Regions for Mexico (Arriaga et al., 2000), which are based on indices of species diversity and number and quality of different ecosystems. Our study supports the hypothesis that conservation of red oaks would indirectly allow the conservation and protection of the ecosystems associated with this genus, including mixed forests, oak forests, pine–oak forests, coniferous forests, and cloud forests (Challenger, 1998). Some of these ecosystems such as cloud forests harbor a high biodiversity and are considered to be one of the most fragile ecosystems in the Neotropics (Hamilton et al., 1994; Churchill et al., 1995; Luna et al., 2006).

Conservation efforts in some countries of Central America, at least in the case of temperate forests, have been more efficiently planned than in Mexico. Costa Rica can be considered as the country with the largest system of Natural Protected Areas of all the countries studied herein, followed by Honduras and Nicaragua. In the case of Guatemala, there are still many gaps in the knowledge of red oak distribution, limiting the results of the annealing simulated analysis. In Mexico, the creation of at least 26 new Natural Protected Areas and the enlargement of at least six current areas can increase more than 25% of the total protected surface in the 14 zones identified as high priority in this study.

Deforestation rates of oak forests in Mexico ranged from 5000 to 30 000 ha per year (Masera et al., 1995). This alarming loss rate of oak forests urgently requires a strong effort to protect the richest areas of species and endemism. In the case of Mesoamerican red oaks, it is necessary to implement a general program of protection and conservation for the whole geographic range to preserve not only species richness and endemism but all biological processes that can occur at different spatial scales. The response of forest species to global threats such as climatic changes is considered as the most serious threat to plant biodiversity (Malcolm et al., 2006) and can be studied at the global scale by focusing, for example, on the genetic basis of physiological responses of tree species distributed in different local climates (e.g., Hamrick, 2004; Scotti-Saintagne et al., 2004; González-Martínez et al., 2006). On the other hand, evolutionary processes such as hybridization, introgression, genetic assimilation, interspecific gene flow, and pollen swamping frequently occur among oak species. Oaks are one of the most remarkable examples in the biological literature where the reproductive barriers between species are incomplete (Futuyma, 1998). The processes mentioned do not necessarily occur in the main centers of species richness or endemism but in other

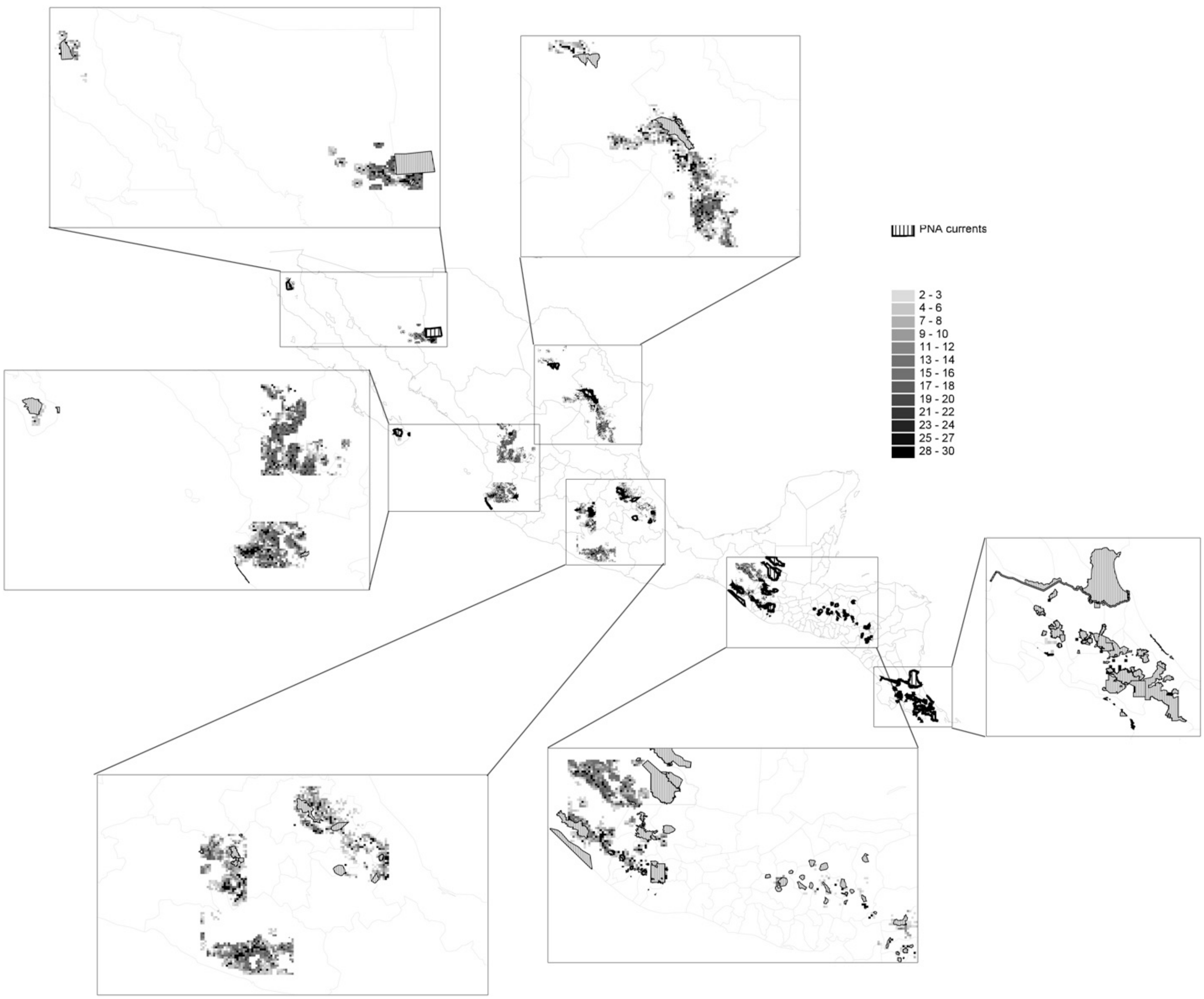

Fig. 7. Results of the MARXAN analysis. Map shows the single best solution. The scale of gray reflect irreplaceability values that indicate the number of times out of 50 that a unit was located in a MARXAN conservation network. Polygons represent the current Natural Protected Areas.

geographic regions where species meet, increasing genetic diversity by intensive gene flow (Tovar-Sánchez and Oyama, 2004; Tovar-Sánchez et al., 2008) and promoting other biological process such as plant–insect interactions (Tovar-Sánchez and Oyama, 2006a, b). In Mexico, an example of the previously mentioned assumptions are found in the Faja Volcánica Transmexicana, which has low richness and endemism values but acts as a gene flow corridor among species (González-Rodríguez et al., 2004; Tovar-Sánchez and Oyama, 2004).

Concluding remarks—Red oaks are a useful taxon as a model to prioritize conservation areas based on principles of conservation biogeography. This study indicates a necessity to protect large areas of temperate and subtropical forests to conserve red oaks and their associated ecosystems. Unfortunately, many temperate forests in Mexico and Central America are endangered by human activities. Fragmentation and degradation of habitats directly affect the genetic connectivity of species by interrupting the processes of gene flow and seed dispersal. Small and isolated populations are prone to local extinction; therefore, vulnerability assessments are also needed to fulfill the requirements of systematic conservation planning for protected areas. The proposal that emerged from this study is a first step to detect the minimum number of areas to be protected by local regulations. However, more connected areas are needed to protect species living in temperate forests and to maintain their basic biological processes and ecosystem functions in Mexico and Central America.

LITERATURE CITED

Arita, H. T., F. Figueroa, A. Frisch, P. Rodríguez, and K. Santos del Prado. 1997. Geographical range size and the conservation of Mexican mammals. *Conservation Biology* 11: 92–100.

Arriaga, L., J. M. Espinoza, C. Aguilar, E. Martínez, L. Gómez, and E. Loa. 2000. Regiones terrestres prioritarias de México.

Comisión para el Uso y Conocimiento de la Biodiversidad, Mexico City, Mexico.

Axelrod, D. I. 1975. Evolution and biogeography of the Madrean-Tethyan sclerophyll vegetation. *Annals of the Missouri Botanical Garden* 62: 280–334.

Ball, I. R., and H. P. Possingham. 2000. MARXAN (v. 1.8.2): Marine Reserve Design Using Spatially Explicit Annealing. A manual. Available from website http://www.ecology.uq.edu.au/index.html?page=27710 [accessed February 2010].

Ball, I. R., H. P. Possingham, and M. Watts. 2009. MARXAN and relatives: Software for spatial conservation prioritisation. In A. Moilanen, K. A. Wilson, and H. P. Possingham [eds.], Spatial conservation prioritisation: Quantitative methods and computational tools, 185–195. Oxford University Press, Oxford, UK.

Bello, M. A., and J. N. Labat. 1987. Los encinos (*Quercus*) del estado de Michoacán, México. Cuadernos de estudios mexicanos I. Centre d'Etudes Mexicaines et Centramericaines–Instituto Nacional de Investigaciones Forestales, Michoacán, Mexico.

Brawn, J. D. 2006. Effects of restoring oak savannas on bird communities and populations. *Conservation Biology* 20: 460–469.

Breedlove, D. E. 2001. Fagaceae. *In* W. D. Stevens, C. Ulloa, A. Pool, and O. M. Montiel [eds.], Flora de Nicaragua. Monographs in systematic botany from the Missouri Botanical Garden, vol. 85, 1076–1084. Missouri Botanical Garden Press, St. Louis, Missouri, USA.

Burger, W. 1977. Flora costaricensis: Fagaceae. *Fieldiana Botany* 40: 53–82.

CCAD-BM [Comisión Centroamericana del Ambiente y Desarrollo–Banco Mundial]. 2004. "Ecosistemas de Mesoamérica". Escala 1:250 000 [map]. CCAD-BM [location unknown].

Ceballos, G., J. Arroyo-Cabrales, and R. Medellín. 2002. *In* G. Ceballos and J. Simonetti [eds.], Diversidad y conservación de los mamíferos Neotropicales, 377–413. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad–Universidad Nacional Autónoma de México. Mexico City, Mexico.

Challenger, A. 1998. Utilización y conservación de los ecosistemas terrestres de México. CONABIO–Instituto de Biología, UNAM–Agrupación Sierra Madre, A.C., Mexico City, Mexico.

Churchill, S. P., H. Balslev, E. Forero, and J. L. Luteyn. 1995. Biodiversity and conservation of Neotropical montane forests. New York Botanical Garden, Bronx, New York, USA.

CONABIO [Comisión para el Uso y Conocimiento de la Biodiversidad]. 1999. "Uso de suelo y vegetación modificado por Conabio". Escala 1:1 000 000 [map]. Comisión Nacional para el Uso y Conocimiento de la Biodiversidad. Mexico City.

Contreras-Medina, R., and H. Eliosa-León. 2001. Una visión panbiogeográfica preliminar de México. *In* J. Llorente and J.J. Morrone [eds.], Introducción a la biogeografía en Latinoamérica: Teorías, conceptos, métodos y aplicaciones, 197–211. Facultad de Ciencias, Universidad Nacional Autónoma de México, Mexico City, Mexico.

Contreras-Medina, R., and I. Luna-Vega. 2007. Species richness, endemism and conservation of Mexican gymnosperms. *Biodiversity and Conservation* 16: 1803–1821.

Contreras-Medina, R., I. Luna-Vega, and J. J. Morrone. 2007. Gymnosperms and cladistic biogeography of the Mexican Transition Zone. *Taxon* 56: 905–915.

Cook, R. R., and P. J. Auster. 2005. Use of simulated annealing for identifying essential fish habitat in a multispecies context. *Conservation Biology* 19: 876–886.

Crisp, M. D., S. Laffan, H. P. Linder, and A. Monro. 2002. Endemism in the Australian flora. *Journal of Biogeography* 28: 183–198.

Csuti, B., S. Polasky, P. H. Williams, R. L. Pressey, J. D. Camm, M. Kershaw, A. R. Kiester, B. Downs, R. Hamilton, M. Huso, and K. Sahr. 1997. A comparison of reserve selection algorithms using data on terrestrial vertebrates in Oregon. *Biological Conservation* 80: 83–97.

Dávila-Aranda, P., R. Lira, and J. Valdés-Reyna. 2004. Endemic species of grasses in Mexico: A phytogeographic approach. *Biodiversity and Conservation* 13: 1101–1121.

De la Cerda, M. 1989. Encinos de Aguascalientes. Universidad Autónoma de Aguascalientes. Aguascalientes, Mexico.

Diniz-Filho, J. A. F., L. M. Bini, M. P. Pinto, T. F. L. Rangel, P. Carvalho, S. L. Vieira, and R. P. Bastos. 2007. Conservation biogeography of anurans in Brazilian Cerrado. *Biodiversity and Conservation* 16: 997–1008.

Encina, J. A., and J. A. Villarreal. 2002. Distribución y aspectos ecológicos del género *Quercus* (Fagaceae) en el estado de Coahuila, México. *Polibotánica* 13: 1–23.

Escalante-Pliego, P., A. G. Navarro-Sigüenza, and A. T. Peterson. 1993. A geographic, ecological, and historical analysis of land bird diversity. *In* T. P. Ramammoorthy, R. Bye, A. Lot, and J. Fa [eds.], Biological diversity of Mexico: Origins and distribution, 281–307. Oxford University Press, New York, New York, USA.

Espinosa, J. 1979. Fagaceae. *In* J. Rzedowski and G. C. de Rzedowski [compilers], Flora fanerogámica del Valle de México, vol. I, 81–91. Compañía Editorial Continental (CECSA), Mexico City, Mexico.

ESRI [Environmental Systems Research Institute]. 1999. ArcView GIS 3.2 [computer program]. ESRI, California. USA.

Fa, J. E., and L. M. Morales. 1993. Patterns of mammalian diversity in Mexico. *In* T. P. Ramammoorthy, R. Bye, A. Lot, and J. Fa [eds.], Biological diversity of Mexico: Origins and distribution, 319–361. Oxford University Press, New York, New York, USA.

Flores-Villela, O., and P. Gerez. 1994. Biodiversidad y conservación en México: Vertebrados, vegetación y uso de suelo. Universidad Nacional Autónoma de México, Mexico City, Mexico.

Futuyma, D. J. 1998. Evolutionary biology, 3rd ed. Sinauer, Sunderland, Massachusetts, USA.

González-Martínez, S. C., K. V. Krutovsky, and D. B. Neale. 2006. Forest tree population genomics and adaptive evolution. *New Phytologist* 170: 227–238.

González-Rodríguez, A., D. M. Arias, S. Valencia, and K. Oyama. 2004. Morphological and RAPD analysis of hibridization between *Quercus affinis* and *Q. laurina* (Fagaceae), two Mexican red oaks. *American Journal of Botany* 91: 401–409.

González-Villarreal, L. M. 1986. Contribución al conocimiento del género *Quercus* (Fagaceae) en el estado de Jalisco. Colección Flora de Jalisco, Instituto de Botánica, Universidad de Guadalajara. Jalisco, Mexico.

González-Villarreal, L. M. 2003a. *Quercus tuitensis* (Fagaceae, Quercus sect. Lobatae), a new deciduous oak from western Jalisco, Mexico. *Brittonia* 55: 42–48.

González-Villarreal, L. M. 2003b. Two new species of oak (Fagaceae, *Quercus* sect. *Lobatae*) from the Sierra Madre del Sur, Mexico. *Brittonia* 55: 49–60.

Halffter, G. 1987. Biogeography of the montane entomofauna of Mexico and Central America. *Annual Review of Entomology* 32: 95–114.

Hamilton, L. S., J. O. Juvik, and F. N. Scatena [eds.]. 1994. Tropical montane cloud forest. Springer Verlag, New York, New York, USA.

Hamrick, J. L. 2004. Response of forest trees to global environmental changes. *Forest Ecology and Management* 197: 323–335.

Holz, I., and S. R. Gradstein. 2005. Crytogamic epiphytes in primary and recovering upper montane oak forests of Costa Rica—Species richness, community composition and ecology. *Plant Ecology* 178: 89–109.

Hooghiemstra, H. 2006. Inmigration of oak into northern South America: A paleo-ecological document. *In* M. Kapelle [ed.], Ecology and conservation of Neotropical montane oak forests, ecological studies, vol. 185, 17–28. Springer, Berlin, Germany.

Islebe, G. A. 1996. Vegetation, phytogeography and paleoecology of the last 20,000 years of montane Central America. Ph.D. dissertation, University of Amsterdam, Amsterdam, Netherlands.

Kappelle, M., A. M. Cleef, and A. Chaverri. 1992. Phytogeography of Talamanca montane *Quercus* forests, Costa Rica. *Journal of Biogeography* 19: 299–315.

Kirkpatrick, J. B. 1983. An iterative method for establishing priorities for the selection of nature reserves: An example from Tasmania. *Biological Conservation* 25: 127–134.

Kohlmann, B., and S. Sánchez. 1984. Estudio areográfico del género *Bursera* Jacq. ex L. (Burseraceae) en México: Una síntesis de métodos.

In E. Ezcurra and B. Kohlmann [eds.], Métodos cuantitativos en biogeografía, 45–120. Instituto de Ecología A. C., Mexico City, Mexico.

Luna-Vega, I., O. Alcántara, and R. Contreras-Medina. 2004. Patterns of diversity, endemism and conservation: an example with Mexican species of Ternstroemiaceae Mirb. ex DC. (Tricolpates: Ericales). *Biodiversity and Conservation* 13: 2723–2739.

Luna-Vega, I., O. Alcántara, R. Contreras-Medina, and A. Ponce. 2006. Biogeography, current knowledge and conservation of threatened vascular plants characteristics of Mexican temperate forests. *Biodiversity and Conservation* 15: 3773–3799.

Luna-Vega, I., O. Alcántara, D. Espinosa, and J. J. Morrone. 1999. Historical relationships of the Mexican cloud forests: A preliminary vicariance model applying Parsimony Analysis of Endemicity to vascular plant taxa. *Journal of Biogeography* 20: 1299–1305.

Malcolm, J. R., C. Liu, R. P. Neilson, L. Hansen, and L. Hannah. 2006. Global warming and extinctions of endemic species from biodiversity hotspots. *Conservation Biology* 20: 538–548.

Manos, P. S., J. J. Doyle, and K. C. Nixon. 1999. Phylogeny, biogeography, and processes of molecular differentiation in *Quercus* subgenus *Quercus* (Fagaceae). *Molecular Phylogenetics and Evolution* 12: 333–349.

Manos, P. S., and A. M. Stanford. 2001. The historical biogeography of Fagaceae: Tracking the Tertiary history of temperate and subtropical forests of the northern hemisphere. *International Journal of Plant Sciences* 162 (supplement 6): 577–593.

Margules, C. R., A. O. Nicholls, and R. L. Pressey. 1988. Selecting networks of reserves to maximize biological diversity. *Biological Conservation* 43: 63–76.

Margules, C. R., and R. L. Pressey. 2000. Systematic conservation planning. *Nature* 405: 243–253.

Margules, C. R., R. L. Pressey, and P. H. Williams. 2002. Representing biodiversity: Data and procedures for identifying priority areas for conservation. *Journal of Biosciences* 27 (suppl. 2): 309–326.

Marshall, C. J., and J. K. Liebherr. 2000. Cladistic biogeography of the Mexican transition zone. *Journal of Biogeography* 27: 203–216.

Martínez, M. 1951. Los encinos de México y Centroamérica. *Anales del Instituto de Biología*, *Universidad Nacional Autónoma de México* 22: 351–368.

Martínez, M. 1953. Los encinos de México III. *Anales del Instituto de Biología*, *Universidad Nacional Autónoma de México* 24: 237–271.

Martínez, M. 1954. Los encinos de México IV. *Anales del Instituto de Biología*, *Universidad Nacional Autónoma de México* 25: 35–64.

Martínez, M. 1959. Los encinos de México XII. *Anales del Instituto de Biología*, *Universidad Nacional Autónoma de México* 30: 63–83.

Martínez, M. 1965. Los encinos de México XIII. *Anales del Instituto de Biología*, *Universidad Nacional Autónoma de México* 36: 119–140.

Martínez, M. 1966. Los encinos de México XIV. *Anales del Instituto de Biología*, *Universidad Nacional Autónoma de México* 37: 81–95.

Martínez, M. 1974. Los encinos de México XV. *Anales del Instituto de Biología*, *Serie Botánica* 1: 21–56.

Masera, O. R., T. Hernández, A. Ordóñez, and A. Guzmán. 1995. Land use change and forestry. Regional perspective. Preliminary national inventory of greenhouse gases: Mexico. UNEP PROJECT GF/4102-92-01. Instituto Nacional de Ecología, Programa de las Naciones Unidas para el Medio Ambiente, U. S. Country Studies Program, Mexico City, Mexico.

McVaugh, R. 1974. Flora novo-galiciana. *Contributions from the University of Michigan Herbarium* 12: 1–93.

Mejía, D., and T. Hawkins. 1995. Los bosques nublados de Honduras. Serie miscelánea CONSEFOR no. 42. Corporación Hondureña de Desarrollo Forestal – Overseas development agency – Escuela Nacional de Ciencias Forestales (COHDEFOR-ODA-ESNACIFOR), Tegucigalpa, Honduras.

Morrone, J. J. 2001. Biogeografía de América Latina y el Caribe. Manuales y Tesis SEA, Zaragoza, España.

Morrone, J. J. 2005. Hacia una síntesis biogeográfica de México. *Revista Mexicana de Biodiversidad* 76: 207–252.

Morrone, J. J., and J. Márquez. 2001. Halffter's Mexican Transition Zone, beetle generalized tracks, and geographical homology. *Journal of Biogeography* 28: 635–650.

Muller, C. H. 1942. The Central American species of *Quercus*. U.S. Department of Agriculture, Washington, D.C., USA.

Muller, C. H. 1951. Fagaceae. Flora of Panama. Part IV. Fascicle 2. *Annals of the Missouri Botanical Garden* 47: 95–104.

Nixon, K. C. 2006. Global and Neotropical distribution and diversity of oak (genus *Quercus*) and oak forests. *In* M. Kappelle [ed.] Ecology and conservation of Neotropical montane oak forests. Ecological studies, vol. 185, 3–13. Springer, Berlin, Germany.

Nixon, K. C., and C. H. Muller. 1993. The *Quercus hypoxantha* complex (Fagaceae) in northeastern Mexico. *Brittonia* 45: 146–153.

Pearce, J. L., D. A. Kirk, C. P. Lane, M. H. Mahr, J. Walmsley, D. Casey, J. E. Muir, S. Hannon, A. Hansen, and K. Jones. 2008. Prioritizing avian conservation areas for the Yellowstone to Yukon Region of North America. *Biological Conservation* 141: 908–924.

Pinto, M. P., and C. E. V. Grelle. 2009. Reserve selection and persistence: Complementing the existing Atlantic Forest reserve system. *Biodiversity and Conservation* 18: 957–968.

Possingham, H., I. Ball, and S. Andelman. 2000. Mathematical methods for identifying representative reserve networks. In S. Ferson and M. Burgman [eds.] Quantitative methods for conservation biology, 291–305. Springer-Verlag, New York, New York, USA.

Rodrigues, A. S., and K. J. Gaston. 2002. Rarity and conservation planning across geopolitical units. *Conservation Biology* 16: 674–682.

Romero, S. 2006. Revisión taxonómica del complejo Acutifoliae de *Quercus* (Fagaceae) con énfasis en su representación en México. *Acta Botánica Mexicana* 76: 1–45.

Romero, S., R. Lira, and P. Dávila. 2000a. A phenetic study of the taxonomic delimitation of *Quercus acutifolia* and *Q. conspersa* (Fagaceae). *Brittonia* 52: 177–187.

Romero, S., C. Rojas-Zenteno, and M. L. Aguilar. 2002. El género *Quercus* (Fagaceae) en el estado de México. *Annals of the Missouri Botanical Garden* 89: 551–593.

Romero, S., C. Rojas-Zenteno, and C. Almonte. 2000b. *Quercus hintonii* Warb. (Fagaceae), encino endémico de la Depresión del Balsas, México y su propagación. *Polibotánica* 11: 121–127.

Rzedowski, J. 1978. La vegetación de México. Limusa, Mexico City, Mexico.

Santacruz, N., and A. Espejel. 2004. Los encinos de Tlaxcala. Universidad Autónoma de Tlaxcala, Tlaxcala, Mexico.

Sarkar, S., R. L. Pressey, D. P. Faith, C. R. Margules, T. Fuller, D. M. Stoms, A. Moffett, K. A. Wilson, K. J. Williams, P. H. Williams, and S. Andelman. 2006. Biodiversity conservation planning tools: Present status and challenges for the future. *Annual Review of Environment and Resources* 31: 123–159.

Scotti-Saintagne, C., C. Bodénes, T. Barreneche, E. Bertocchi, C. Plomion, and A. Kremer. 2004. Detection of quantitative traits loci controlling bud burst and height growth in *Quercus robur* L. *Theoretical and Application Genetics* 109: 1648–1659.

Serrato, A., G. Ibarra-Manríquez, and K. Oyama. 2004. Biogeography and conservation of the genus *Ficus* (Moraceae) in Mexico. *Journal of Biogeography* 31: 475–485.

Shriner, S. A., K. R. Wilson, and C. H. Flather. 2006. Reserve networks based on richness hotspots and representation vary with scale. *Ecological Applications* 16: 1660–1673.

Smith, B. 2005. CLUZ guide v. 1.6 [computer program]. Available from http://www.kent.ac.uk/anthropology/dice/cluz/ [accessed February 2010].

Smith, S. E., and D. J. Read. 1997. Mycorrhizal symbioses. Academic Press, San Diego, California, USA.

Spellenberg, R. 1992. A new species of black oak (*Quercus*, subg. *Erythrobalanus*, Fagaceae) from the Sierra Madre Occidental, Mexico. *American Journal of Botany* 79: 1200–1206.

Spellenberg, R., and J. R. Bacon. 1996. Taxonomy and distribution of a natural group of black oaks of Mexico (*Quercus*, section *Lobatae*, subsection *Racemiflorae*). *Systematic Botany* 21: 85–99.

Standley, P. C., and I. Steyermark. 1952. Fagaceae. Flora of Guatemala. *Fieldiana Botany* 24: 369–396.

Takhtajan, A. 1986. Floristic regions of the world. University of California Press, Berkeley, California, USA.

Tovar-Sánchez, E., and K. Oyama. 2004. Natural hybridization and hybrid zones between *Quercus crassifolia* and *Quercus crassipes* (Fagaceae) in Mexico: Morphological and molecular evidence. *American Journal of Botany* 91: 1352–1363.

Tovar-Sánchez, E., and K. Oyama. 2006a. Community structure of canopy arthropods associated to *Quercus crassifolia* × *Quercus crassipes* species complex. *Oikos* 112: 370–381.

Tovar-Sánchez, E., and K. Oyama. 2006b. The role of hybridization of the *Quercus crassifolia* × *Quercus crassipes* species complex on the community structure of endophagous insects. *Oecologia* 147: 702–713.

Tovar-Sánchez, E., Z. Cano-Santana, and K. Oyama. 2004. Canopy arthropod communities on Mexican oaks at sites with different disturbances regimes. *Biological Conservation* 115: 79–87.

Tovar-Sánchez, E., P. Mussali-Galante, R. Esteban-Jiménez, D. Piñero, D. M. Arias, O. Dorado, and K. Oyama. 2008. Chloroplast DNA polymorphism reveals geographic structure and introgression in *Quercus crassifolia* × *Q. crassipes* complex in México. *Canadian Journal of Botany* 86: 228–239.

Valdéz, V., and M. L. Aguilar. 1983. El género *Quercus* en las unidades fisonómico-florísticas del municipio de Santiago, Nuevo León, México. *Boletín Técnico del Instituto de Investigaciones Forestales* 98: 1–99.

Valencia, S. 1995. Contribución al conocimiento del género *Quercus* (Fagaceae) en el estado de Guerrero, México. Contribuciones del Herbario de la Facultad de Ciencias No. 1. Universidad Nacional Autónoma de México, Mexico City, Mexico.

Valencia, S. 2004. La diversidad del género *Quercus* (Fagaceae) en México. *Boletín de la Sociedad Botánica de México* 75: 33–53.

Valencia, S. 2005. Análisis filogenético de la serie Lanceolatae Trel. del género *Quercus*, Fagaceae. Ph.D. dissertation, Universidad Nacional Autónoma de México, Mexico City, Mexico.

Valencia, S. 2007. Encinos. *In* I. Luna-Vega, J. J. Morrone, and D. Espinosa [eds.], Biodiversidad de la Faja Volcánica Transmexicana, 139–148. Las Prensas de Ciencias, Mexico City, Mexico.

Valencia, S., and S. L. Cartujano. 2002. *Quercus pinnativenulosa* (Fagaceae), un encino poco conocido de la Sierra Madre Oriental. *Anales del Instituto de Biología*, *Serie Botánica* 73: 87–92.

Valencia, S., and J. Jiménez. 1995. Redescripción de *Quercus rubramenta* Trel. *Anales del Instituto de Biología*, *Serie Botánica* 61: 5–10.

Valencia, S., and L. Lozada. 2003. *Quercus nixoniana* (Fagaceae), una nueva especie de la sección *Lobatae*, de la Sierra Madre del Sur, México. *Novon* 13: 261–264.

Valencia, S., and K. C. Nixon. 2004. Encinos. *In* A. García-Mendoza, M. J. Ordóñez, and M. Briones-Salas [eds.], Biodiversidad de Oaxaca, 219–225. Instituto de Biología, Universidad Nacional Autónoma de México–Fondo Oaxaqueño para la Conservación de la Naturaleza–World Wildlife Fund, Mexico City, Mexico.

Valencia, S., M. Gómez-Cárdenas, and F. Becerra-Luna. 2002. Catálogo de encinos del estado de Guerrero, México. Libro Técnico No. 1. Instituto Nacional de Investigaciones Forestales–Centro Nacional de Investigación Disciplinaria en Conservación y Mejoramiento de Ecosistemas Forestales (INIFAP-CENID-COMEF), Mexico City, Mexico.

Vander-Wall, S. B. 2001. The evolutionary ecology of nut dispersal. *Botanical Review* 67: 74–117.

Vane-Wright, R., C. Humphries, and P. Williams. 1991. What to protect? Systematics and the agony of choice. *Biological Conservation* 55: 235–254.

Vázquez, M. L. 1992. El género *Quercus* (Fagaceae) en el estado de Puebla, México. B.Sc. dissertation. Universidad Nacional Autónoma de México, Mexico City, Mexico.

Vázquez, M. L. 2000. Fagaceae. Flora del Valle de Tehuacán-Cuicatlán. Fascículo 28. Instituto de Biología, Universidad Nacional Autónoma de México, Mexico.

Vázquez, M. L. 2006. Trichome morphology in selected Mexican red oak species (*Quercus* section *Lobatae*). *Sida* 22: 1091–1110.

Vázquez, M. L., S. Valencia, and K. C. Nixon. 2004. Notes on red oaks (*Quercus* sect. *Lobatae*) in eastern Mexico, with description of a new species, *Quercus hirtiifolia. Brittonia* 56: 136–142.

Walker, P., S. R. Leather, and M. J. Crawley. 2002. Differential rates of invasion in three related alien oak gall wasps (Cynipidae: Hymenoptera). *Diversity & Distributions* 8: 335–349.

Whittaker, R. J., M. B. Araújo, P. Jepson, R. J. Ladle, J. E. M. Watson, and K. J. Willis. 2005. Conservation biogeography: Assessment and prospect. *Diversity & Distributions* 11: 3–23.