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ANÁLISIS BIOGEOGRÁFICO DE LOS ENCINOS ROJOS (GÉNERO *QUERCUS*, SECCIÓN *LOBATAE*) EN MÉXICO, CON COMENTARIOS SOBRE SU TAXONOMÍA

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1) Organic evolution is function of *space*, *time* and *form*. 2) Of these three essential factors, *space* might be said to be the one with which biogeography (=panbiogeography, in my sense [Croizat´s]) is primarily concerned. However, *space* necessarily interplays with *time* and *form*, therefore three factors are as one of immediate biogeographic concern.

Croizat, 1964

Añadió que Odiseo se hallaba en Dodona para saber por la alta encina la voluntad de Zeus sobre si convendría que volviese manifiesta o encubiertamente al rico país de Ítaca, del cual se había ausentado hacía mucho tiempo.

Hómero, S. VIII a. C.

Y, si no ellos, serán sus hijos los que en su lugar se salven, porque la luz que has derramado no perecerá ni aun después de tu muerte; el justo desaparece, pero perdura su luz, y es necesaria la muerte del Salvador para que nos salvemos. La humanidad rechaza a sus profetas y los inmola, pero acaba venerando a los mismos a quienes sacrificó.

Dostoiesvki, 1880

Fue aquélla una época singular para Raskolnikov, se hubiera dicho que una especie de bruma caída sobre él lo mantenía una soledad agobiadora y desesperante, cuyo fin no podría preverse. Cuando mucho tiempo después recordó esos días, adivinó que su conciencia habíase eclipsado a veces, y que eso debió haber sucedido, salvo raros intervalos de lucidez, hasta que se produjo la catástrofe final.

Dostoiesvki, 1866

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RESUMEN

Se presenta un análisis de la distribución de las especies de encinos rojos (género *Quercus*, sección *Lobatae*) de México y América Central. En primer lugar, se realizó un análisis para identificar patrones biogeográficos y detectar áreas de endemismo utilizando cuatro técnicas diferentes: Análisis de Parsimonia de Endemismos (PAE), Análisis de Agrupamientos no ponderados (UPGMA), Análisis de Neighbor-Joining (NJ) y un Análisis de Redes, con dos unidades de análisis: unidades florísticas y gradillas de 1° latitud x 1° longitud. Cuando las unidades de estudio son áreas definidas a priori (criterios florísticos), los resultados del PAE y UPGMA son similares, pero cuando se utilizan las gradillas, el PAE permite identificar patrones tras el análisis de sus clados, pero resulta ineficaz para resolver las relaciones entre áreas y para identificar áreas de endemismo. Para intentar resolver estas relaciones se utiliza el UPGMA y NJ. Transformando una matriz binaria de presencia/ausencia en una matriz de inversos distribucionales para cada especie, el NJ permite visualizar un sistema de clasificación de áreas congruente con el primer análisis del PAE con unidades florísticas, y que es apoyado por el análisis de redes, y tras la identificación de ramas largas es posible identificar aquellas zonas con especies de distribución restringida. De esta forma se identifican un Componente Neártico Occidental, un Componente Neártico Oriental y una Zona de Transición que abarca la mayoría de los sistemas montanos mexicanos y de América Central, pero a la vez formada por un Componente Mexicano de Montaña y un Componente Mesoamericano. Se analiza la naturalidad de los principales sistemas montañosos de México, notando que las Sierras Madres Oriental, Occidental, del Sur y la Faja Volcánica Transmexicana no son unidades naturales. El análisis de redes muestra ser el método más efectivo para detectar áreas de endemismo, tras la eliminación progresiva de especies alelopátridas (intermediarias), y la sucesiva identificación de especies simpátridas mediante cliqués; con este método se detectaron nueve áreas de endemismo. En segundo lugar, se realizó un análisis corológico con la distribución puntual de 75 especies de encinos rojos presentes en México y América Central, para detectar áreas importantes de riqueza y endemismo. Se utilizaron tres unidades de análisis: divisiones políticas, provincias florísticas y gradillas de 1° latitud x 1° longitud. Se calcularon tres índices: riqueza, endemismo ponderado y endemismo ponderado corregido para todas las unidades de análisis. Con el objetivo de identificar las áreas prioritarias de conservación para este grupo, se realizaron cinco análisis de complementariedad (el objetivo es conservar el mayor número de especies con el menor número de áreas). La complementariedad se hizo siguiendo dos enfoques distintos, prioridad basada en riqueza (utilizando índice de riqueza y endemismo ponderado) y prioridad basada en rareza (utilizando endemismo ponderado, especies de distribución restringida y endemismo ponderado corregido). Se identificaron trece áreas prioritarias para la conservación en México y América Central. Siguiendo los lineamientos de la Planeación Sistemática de la Conservación, se propone la creación de nuevas áreas naturales con protección gubernamental, ya que algunas de estas regiones han sido consideradas como centros de riqueza y/o endemismo para otros grupos. Lo anterior es una propuesta en el desarrollo de la biogeografía de la conservación.

INTRODUCCIÓN

Familia Fagaceae

El orden Fagales incluye a nivel mundial 1054 especies, aproximadamente 33 géneros y ocho familias (Nothofagaceae, Fagaceae, Myricaceae, Juglandaceae, Rhoipteleaceae, Casuarinaceae, Ticodendraceae y Betulaceae), dentro del clado de las Eurosids I (APG II 2003).

La familia Fagaceae incluye siete géneros: *Castanea*, *Castanopsis*, *Chrysolepis*, *Fagus*, *Lithocarpus*, *Quercus* y *Trigonobalanus*, y 670 especies, ocupando el 82° sitio de las familias de mayor diversidad a nivel mundial (APG II 2003). El género *Quercus* es el más diversificado, con 400 a 500 especies (40 - 50% del total de especies de la familia), distribuidas en las regiones templadas del hemisferio norte.

La familia Fagaceae se caracteriza por la presencia de estructuras leñosas protectoras que rodean la base de una o varias flores imperfectas, las denominadas cúpulas. Las cúpulas son el resultado de la fusión de ramillas estériles de las inflorescencias postiladas (Manos et al. 2001). Las flores son unisexuales y monoicas, presentan tres carpelos con dos óvulos cada uno. El ovario se desarrolla en un fruto indehiscente, unilocular y con una sola semilla denominada nuez. En conjunto, la nuez y la cúpula constituyen el fruto que se denomina bellota, que es el carácter que define al grupo (Nixon 1989, 1997; Borgardt y Pigg 1999). Presentan además yemas escamosas, axilares y apicales, hojas 1-30 cm de largo, polen tricolpado y su dispersión es anemófila (Nixon 1997).

La división primaria entre la familia atiende a los síndromes de polinización de las especies: anemófila (*Quercus* y *Fagus*) y entomófila

(*Castanea*) (Figura 1). La variación del fruto es más compleja, pero proporciona uno de los caracteres diagnósticos más importantes dentro de la familia. Existen dos tipos de cúpulas principales: (a) dicasio cupular: en que las flores pistiladas se encuentran sobre una estructura valvada, encerrando a la nuez en diferentes grados, y las cuales se han reducido atendiendo a la reducción de flores (en *Quercus* existe el mejor ejemplo de reducción de valvas); y (b) flor cupular: en que cada flor pistilada está sostenida y envuelta por una valva (Manos et al. 2001) (Figura 2).

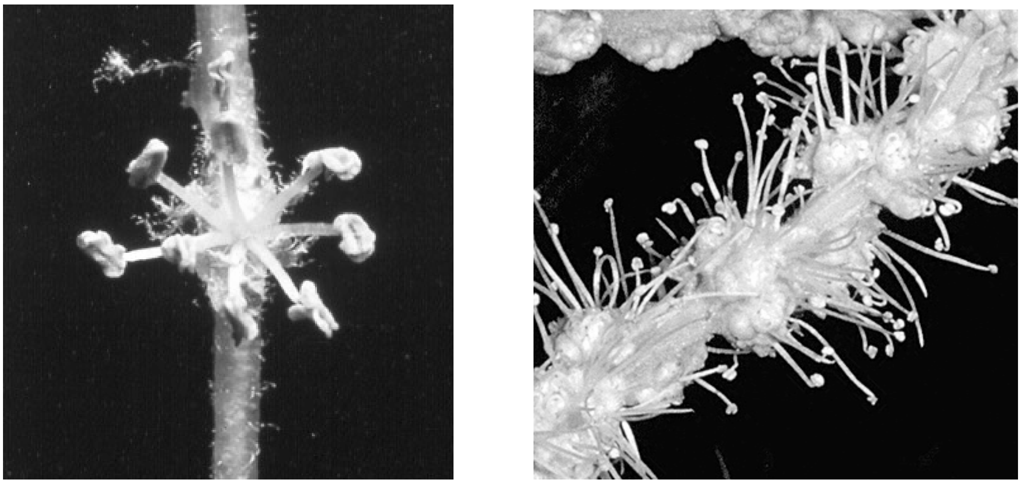

Figura 1. Flores estaminadas de *Quercus* (con síndrome de polinización anemófila) y de *Castanea* (con síndrome de polinización entomófila).

Figura 2. Diferentes arreglos cupulares en las fagáceas: *Castanea*, *Fagus*, *Quercus* (con dicasios cupulares) y *Lithocarpus* (con flores cupulares).

El género Quercus

El género *Quercus* es un grupo de árboles o arbustos, con yemas terminales prominentes; escamas de las yemas imbricadas y estípulas generalmente persistentes; hojas con arreglo espiralado, generalmente con venas secundarias paralelas, dientes marginales (si están presentes) simples, aristados, mucronados u oblicuos; inflorescencias estaminadas a partir de un eje (amentos); flores estaminadas solitarias o en grupos de 1-3 a lo largo del raquis, cada flor con 6 (2-12) estambres largos; polen tricolpado; las inflorescencias femeninas forman espigas o cabezuelas, nacen en axilas de hojas de ramas jóvenes sostenidas en una cúpula; perianto pistilado 5-6 lobado, basalmente adnado al ovario; 3 ovarios carpelados ínferos, con 3 estilos, lineares o subsésiles; bellotas como frutos, con una nuez única sostenida y envuelta en una cúpula; cúpulas con escamas externas imbricadas o concéntricas; maduración del fruto anual o bianual; y óvulos apicales abortivos, lateral o basal (Nixon 1993a).

El género *Quercus* se divide a nivel mundial en dos subgéneros: (a) *Cyclobalanopsis* (encinos con bellotas en racimos), con bellotas agrupadas y las escamas de la cúpula en anillos concrescentes, que habitan en zonas montanas y tierras bajas tropicales del este de Asia y Malasia; y (b) *Quercus*, con bellotas solitarias o en grupos de 1-3, con escamas de la cúpula arregladas en espiral, que habitan en las zonas templadas de Eurasia y América (desde América del Norte hasta Colombia). Dentro de este último, se reconocen cuatro secciones: *Cerris* (de las regiones templadas de Eurasia), *Lobatae* (encinos rojos exclusivos de América), *Quercus* (encinos blancos de América y Eurasia) y *Protobalanus* (encinos dorados endémicos de la región Californiana de América del Norte) (Manos y Standford 2001) (Figura 3). Estudios preliminares de Nixon (1993a) y Manos et al. (1999) proponen la inclusión de la sección *Cerris* dentro de la sección *Quercus*.

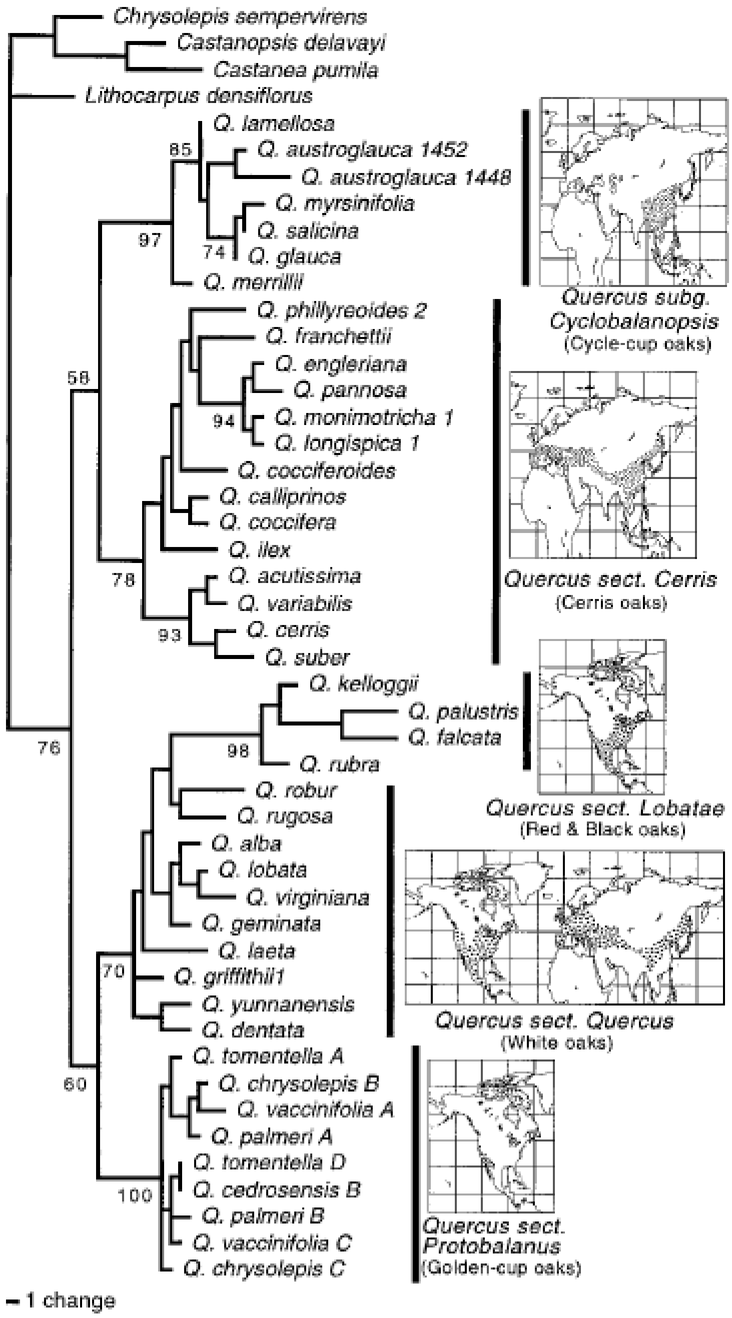

Figura 3. Relaciones filogenéticas y distribución de los principales subgéneros y secciones del género *Quercus* (Manos et al. 2001).

Los caracteres de frutos y semillas son de gran importancia en la clasificación de los encinos, pudiendo diferenciarse las tres subsecciones americanas con base en ellos. La sección *Lobatae* se caracteriza por la presencia de óvulos abortivos apicales (en raros casos sub-basales) sumados a la consistencia lanosa de la capa interna de la nuez; escamas de la cúpula aplanadas y delgadas, nunca aquilladas; cotiledones libres (raramente conados); una maduración anual o bianual del fruto; entre otros (Martínez 1951; Nixon 1993a; Manos et al. 1999, 2001).

Estado actual en la sistemática de los encinos

Hasta el siglo XVIII, los encinos eran poco conocidos y estudiados, con tan sólo nueve especies nombradas (cuatro de ellas americanas) en *Species Plantarum* en 1753 por Linneo. Es en el siglo XIX, cuando aparecen las primeras publicaciones relativas al género *Quercus*, siendo la primera la de André Michaux "*Les Chênes de l'Amérique Septentrionale*", en 1801, donde se describen 20 especies de Estados Unidos.

En 1802 aparecen los trabajos de Louis Née con 16 especies de encinos de México y California; entre 1808-1806, Alexander Humboldt y Aimé Bonpland nombran 17 especies en "*Plantes Aequinoxiales*"; en 1830 Schiede, Schlechtendal y Chamiso publicaron cinco nuevas especies; en 1835-1840, Henry Galeotti publicó 10 nuevas especies; en 1839-1857, Bentham describió 10 nuevas especies utilizando las colectas de Hartweg; en 1864, de Candolle publicó la mejor contribución del siglo XIX en su obra "*Prodromus Systematis Naturales Regni Vegetabilis*"; en 1869, Frederik Michael Liebmann publicó "*Les Chênes de l'Amérique Tropicale*" que publicó Oersted tres años después de su muerte, donde se describen 52 especies; Liebmann además publicó "Les Chênes du Mexique" basado en los ejemplares de Née; en 1889, Kellog y Green publican "Illustrations of West American oaks"; en 1895, Sargent publicó un estudio completo de los encinos de Estados Unidos “*Silva of North America*” (tomado de Martínez 1951).

Los dos trabajos más trascendentes del género *Quercus* fueron publicados en el siglo XX. El primero de ellos, publicado en 1924 por William Trelease, titulado “*The American oaks*”, agrupa en 131 series las 632 entidades que describe (entre especies y variedades), con 253 especies en total y 128 especies de encinos rojos (denominados Erythrobalanus) para México y alrededor de 50 especies en total y 34 especies de encinos rojos para América Central. Trelease hizo el primer intento de clasificar a las especies del género en categorías infragenéricas (Muller 1942) (Figura 4). Posteriormente se publicó la obra más completa del género *Quercus* para todo el mundo, publicada por Aimée Camus entre 1934 y 1954, compuesto por tres volúmenes y titulado “*Les Chênes monographie du Genre Quercus*”.

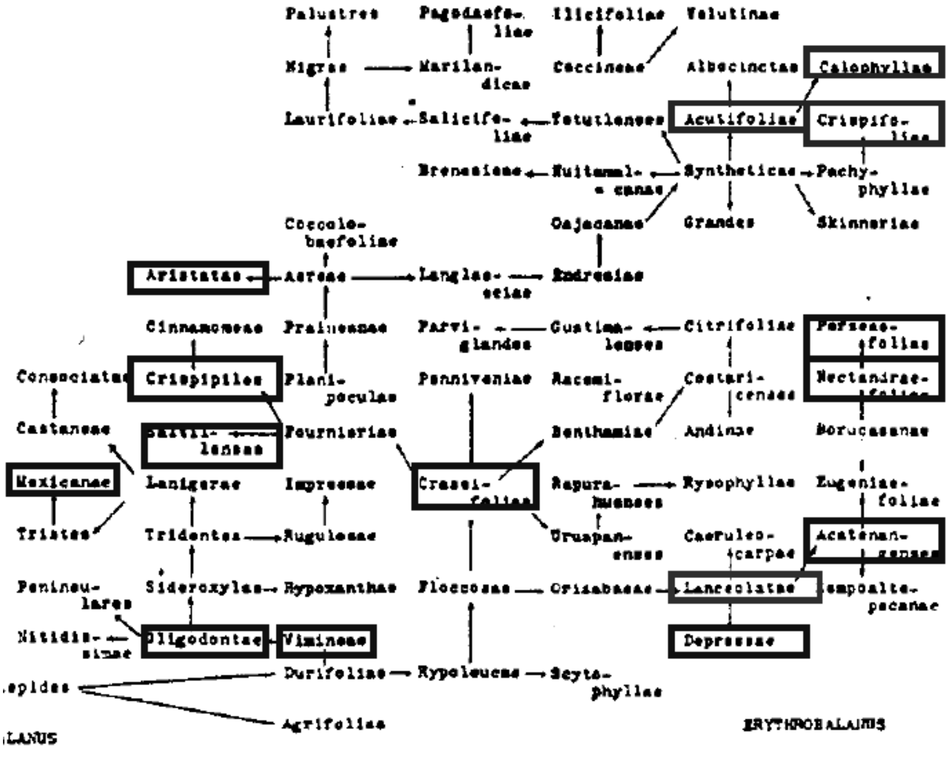

Figura 4. Relaciones de las series descritas por Trelease (1924) para los encinos rojos.

En los últimos años el interés por el estudio de los encinos mexicanos se ha incrementado. Los estudios taxonómicos del grupo se han centrado en tres aspectos: (a) estimaciones y revisiones monográficas (globales y regionales) del género y/o publicación de nuevas especies, (b) análisis filogenéticos a nivel genérico y de grupos o secciones específicas, y (c) análisis de la estructura genética e hibridación de encinos. Martínez (1951-1974) inició una revisión exhaustiva de las especies de encinos mexicanos, haciendo énfasis en descripciones y caracteres diagnósticos en el reconocimiento de especies. McVaugh (1974) realizó un estudio florístico para el territorio de Nueva Galicia (que incluye partes de Jalisco, Nayarit, Aguascalientes, Colima y Zacatecas). Espinosa (1979) publicó las especies de encinos para el Valle de México. Gónzalez-Villarreal (1986) realizó la aportación más importante para los encinos de Jalisco. Bello y Labat (1987) publicaron los encinos de Michoacán. De la Cerda (1989) publicó los encinos de Aguascalientes. Para el estado de Nuevo León, pese a no tener una monografía exhaustiva, existen al menos tres contribuciones importantes: Banda (1974) para el estado, Valdez y Aguilar (1983) para el municipio de Santiago, y Marroquín (1985) para el noroeste del estado. Vázquez (1992) realizó un estudio sobre los encinos de Puebla. Zavala (1995) publicó los encinos hidalguenses, aunque el estudio se centra en la región de El Chico, Hidalgo. Valencia (1995) realizó una contribución al conocimiento de los encinos de Guerrero, el cual fue posteriormente corregido (Valencia et al. 2002). Romero et al. (2002) publicaron los encinos del estado de México. Encina y Villarreal (2002) realizaron un estudio sobre los encinos de Coahuila. Santacruz y Espejel (2004) publicaron los encinos de Tlaxcala. Valencia y Nixon (2004) publicaron un listado preliminar de los encinos de

Oaxaca. Asimismo, han comenzado los estudios monográficos del género atendiendo la delimitación de las zonas basados en criterios biológicos y/o geológicos más que políticos, v.gr. el estudio de Vázquez (2000) para el Valle de Tehuacán-Cuicatlán y el de Valencia (2007) para la Faja Volcánica Transmexicana, además de los estudios en curso para Mesoamérica por Nixon y para la región del Bajío por Romero.

En América Central, el trabajo más importante es el realizado por Muller (1942), quien hizo la revisión de las especies centroamericanas que habitan en Guatemala, Belice, El Salvador, Honduras, Nicaragua, Costa Rica y Panamá, así como en el estado de Chiapas en México. En 1951, el mismo autor publicó los encinos de Panamá. Standley y Steyermark (1952) publicaron una revisión de las especies de encinos presentes en Guatemala. Burger (1977) describió las especies de encinos dentro de la *Flora Costaricensis*. El último trabajo publicado fue el realizado por Breedlove (2001) para la *Flora de Nicaragua*.

Asimismo se han descrito nuevas especies y realizado delimitación de especies dentro de series y complejos. Entre las especies descritas se encuentran *Q. macvaughii* (Spellenberg 1992), *Q. hintonorum*, *Q. coahuilensis* y *Q. miquihuanensis* (Nixon y Muller 1993), *Q. tuitensis* (Gónzalez-Villarreal 2003a), *Q. cualensis* y *Q. iltisii* (González-Villarreal 2003b), *Q. nixoniana* (Valencia y Lozada 2003) y Q. hirtifolia (Vázquez et al. 2004). Además, se han hecho redescripciones de especies poco estudiadas como *Q. rubramenta* (Valencia y Jiménez 1995), *Q. hintonii* (Romero et al. 2000), *Q. pinnativenulosa* (Valencia y Cartujano 2002) y *Q. depressa* (Vázquez et al. 2004).

Los problemas en la delimitación de especies en series y complejos comenzaron a abordarse desde el estudio de Nixon y Muller (1993) sobre el complejo *hypoxantha* (*Q. hintonorum*, *Q. hypoxantha*, *Q. miquihuanensis* y *Q. coahuilensis*), Valencia (1994) con *Q. affinis*, *Q. laurina* y *Q. acatenangensis*, y el estudio de Aguilar y Romero (1995) con cuatro especies que resultaron ser sinónimos de *Q. hintonii*. Spellenberg y Bacon (1996) estudiaron el complejo Racemiflorae (*Q. conzattii – Q. tarahumara – Q. radiata – Q. urbanii*), complejo retomado por MacCuley con herramientas moleculares. Romero et al. (2006) llevaron a cabo una delimitación fenética entre *Q*. *acutifolia* – *Q*. *conspersa*. Romero (2006) realizó un trabajo de delimitación taxonómica para la serie *Acutifoliae*. Pero aún existen problemas en ciertos grupos, como el complejo *Q. seemannii* en América Central (Nixon 2006) y el posible complejo *Q. salicifolia* (Breedlove 2001).

La variación foliar, estudiada morfológicamente por Herrera (2005) para *Q. conzattii*, *Q. urbanii* y *Q. eduardii* y por Mora (2006) para *Q. crassifolia*, ha cobrado importancia gracias a las herramientas moleculares, lo que ha permitido también el estudio de complejos de especies, así como de procesos de hibridación entre ellos. Bacon y Spellenberg (1996) iniciaron este tipo de estudios con el caso de *Q. conzattii x Q. eduardii*. González-Rodríguez et al. (2004a, 2004b, 2005) y González-Rodríguez y Oyama (2005) realizaron un estudio sobre las zonas de hibridación entre *Q. affinis x Q. laurina*. Tovar-Sánchez y Oyama (2004, 2006) y Tovar-Sánchez et al. (2008) realizaron estudios de hibridación entre *Q. crassipes x Q. crassifolia* y McCuley et al. (2007) con el complejo *Racemiflorae*.

Nuevas perspectivas para la delimitación y estudio de especies de encinos se han realizado con estudio de tricomas, v. gr. Valencia y Delgado

(2003) y Vázquez (2004), así como estudios de arquitectura foliar (Rodríguez y Romero 2007).

Aún hay pocos estudios filogenéticos dentro del género. Los primeros estudios filogenéticos fueron los realizados por Nixon (1993), Manos et al. (1999) y Manos y Stanford (2001) para todas las especies del género. A nivel de series se ha efectuado la filogenia de la Serie *Lanceolatae* con caracteres morfológicos (Valencia 2005), la cual ha sido retomada con marcadores moleculares por Ramos (2007).

Importancia del género Quercus en México

El género *Quercus* constituye uno de los elementos más importantes en la flora del Hemisferio Norte (Nixon 2006), debido a que su presencia es característica de las zonas montanas de Eurasia, América Central y del Norte. El género está ampliamente diversificado y cuenta con aproximadamente 500 especies diferentes. Se ha sugerido que la diversificación del género se llevó a cabo en el Eoceno medio, época en la que se postula que terminó el intercambio entre los encinos de Eurasia y América (Axelrod 1983; Manos y Standford 2001). Se considera que los dos centros principales de diversificación del género *Quercus* se encuentran en el sureste de Asia y en la parte central de América (los territorios de México y América Central) (Manos et al. 1999; Valencia 2003).

La importancia de este género radica en que los encinos son elementos dominantes de varios tipos de vegetación templada del hemisferio boreal, entre los que destacan los bosques de encino, bosques de pino-encino y bosques mesófilos de montaña, los cuales ocupan en conjunto más del 15% de la cubierta vegetal presente en el territorio mexicano (Rzedowski 1978; Challenger 2001).

Varios trabajos han considerado que la diversidad de especies de encinos para México es alta. Martínez (1951-1974), en sus trabajos pioneros, estimó la existencia de más de 200 especies, Rzedowski (1978) calculó que existen entre 150 y 200, cifra que coincide con la estimación de 170 a 213 especies hecha por González-Rivera (1993). Nixon (1993b) mencionó que el número de especies en México es de 135 a 150 especies, debido a una gran cantidad de sinonimias, lo que coincide con las 140 especies reportadas por Zavala (1998). El estudio más reciente hecho por Valencia (2004), menciona que existen alrededor de 161 especies válidas para México, de las cuales cuatro especies son encinos dorados, 81 especies son encinos blancos (sección *Quercus*) y 76 especies de encinos rojos (sección *Lobatae*). De las especies anteriores, Valencia (2004) mencionó que 31 especies de encinos (23 blancos, cinco rojos y tres dorados) se distribuyen también en Estados Unidos, 17 especies (ocho blancos y nueve rojos) amplían su área de distribución hacia América Central, y solamente una especie de encino blanco está presente desde Estados Unidos hasta Guatemala (Nixon 2006).

Los encinos rojos son más abundantes en zonas templado húmedas y sub-húmedas de los sistemas montanos de México y América Central, a diferencia de los encinos blancos, que a pesar de estar presentes en zonas húmedas, pueden tolerar condiciones más áridas y secas, por lo que su área de distribución es más amplia (González-Rivera 1993; Nixon 1993b; Zavala 1998; Valencia 2004). Nixon (1993b) y Zavala (1998) mencionan que los encinos rojos son más abundantes en la región occidental, sur y sureste del país, es decir, en las regiones más húmedas del país.

De las 76 especies estimadas de encinos rojos para México (Valencia 2004), cinco de ellas extienden su área de distribución hacia América del Norte y 10 hacia América Central, por lo que el 80% de los encinos rojos es endémico a México, aunque las 76 especies de encinos rojos presentes en México son endémicas a Megaméxico 3 sensu Rzedowski (1991a, b). Si además, se considera el planteamiento de Nixon (1993b) que menciona que los encinos rojos están restringidos ecológicamente a zonas húmedas, los encinos rojos son considerados un modelo idóneo en el análisis biogeográfico de los sistemas montanos de México y América Central.

OBJETIVOS

Analizar los patrones de vicarianza de los encinos rojos como modelo en la reconstrucción histórica de los elementos templados de montaña de México y América Central.

Como parte del trabajo se desprenden lo siguientes objetivos particulares:

a) Obtención de la información taxonómica y geográfica de las especies de encinos rojos, para su incorporación en una base de datos que permita la sistematización de la información.

b) Identificar áreas de riqueza y endemismo del grupo, no sólo para abordar las relaciones históricas de las áreas y sus biotas, sino además como una herramienta en la Biogeografía de la Conservación.

c) Contribuir a la elaboración de un Atlas Biogeográfico Mexicano, que aborde las relaciones con América Central y, en etapas posteriores con América del Norte.

d) Proponer nuevos métodos de análisis en biogeografía.

MATERIAL Y MÉTODOS

Se realizó una consulta de especímenes de herbario para obtener los datos de distribución de las especies de encinos rojos de México y América Central. Se capturaron cerca de 13,588 registros de encinos con localidades de colecta, además de que se conjuntó una base de datos que incluye todos los campos de las etiquetas de los ejemplares y un respaldo fotográfico de los mismos.

En este estudio se registraron 70 especies de encinos rojos para México, 69 de las reportadas por Valencia (2004) e incluyendo a *Q. acatenangensis* (sensu Nixon, 2006) como una especie diferente a *Q. ocoteifolia* de Valencia (2004), el área de distribución de esta última especie se concentra en la Sierra Madre Oriental y en las Serranías Meridionales de Oaxaca, mientras que *Q. acatenangensis* se encuentra desde Chiapas hasta Nicaragua. En el caso de *Q. salicifolia* la descripción hecha por Breedlove (2006) se ajusta más a la descripción de *Q. hondurensis* de Muller (1942), por lo que los registros de la primera se incluyeron como parte de la última.

Del resto de lo reportado por Valencia (2004), las áreas de distribución identificadas en este análisis son congruentes con lo que esta autora propone en la mayoría de los casos, con pequeñas adecuaciones que en general no afectan el área de distribución teórica con los registros puntuales. Sin embargo, en el caso de *Q. elliptica* que es reportada por Valencia (2004) con un área de distribución desde México hasta Nicaragua, en este estudio se considera que esta especie habita en México y regiones adyacentes de Guatemala donde se marca una discontinuidad, y considerando los registros de esta especie en el extremo oriental de Guatemala hasta Nicaragua como *Q. hondurensis*, de esta forma *Q. elliptica* en México se encuentra en zonas montanas bajas (ca. 1000 msnm) y *Q. hondurensis* se encuentra en general a altitudes superiores a 1000 msnm en América Central. En el caso de *Q. cortesii*, Valencia (2004) la reporta como exclusiva de México, pero siguiendo a Breedlove (2006) consideramos que *Q. cortesii* se distribuye hasta Panamá, manejando como sinónimo *Q. brenessi* reportado por Muller (1942) y Romero (2006) como especies diferentes. En el caso de la serie *Racemiflorae*, las incongruencias en la distribución de las cuatro especies que lo conforman se solucionó con lo reportado por Spellenberg y Bacon (1996).

Otro problema que surgió fue la delimitación taxonómica de las especies centroamericanas. En el caso de *Q. benthamii*, que ha sido reportado por Valencia (2004) desde Chiapas hasta Nicaragua, Breedlove (2006) mencionó que esta especie es válida y algunos de sus sinónimos son *Q. seemannii* y *Q. rapurahuensis*. La descripción de estas especies es similar, por lo que en este estudio se determinó a los registros de *Q. benthamii* para Costa Rica y Panamá como *Q. seemannii* siguiendo a Nixon (2006), además de reconocer como especie válida a *Q. rapurahuensis*, quedando restringida a Chiapas y zonas adyacentes de Guatemala *Q. benthamii*.

Tal como lo señala Nixon (2006), el problema taxonómico más importante en los encinos rojos de América Central se encuentra en el complejo *Q. seemannii*. Él menciona de manera directa que *Q. seemannii*, *Q. rapurahuensis* y *Q. eugeniefolia* son entidades diferentes dentro de este complejo y de manera indirecta señala el mismo caso para *Q. gulielmi-trealeasi*, criterio que fue utilizado en este estudio (aunque no se pudieron identificar ejemplares para *Q. eugeniefolia*) lo que concuerda con lo escrito por

Muller (1942, 1960) y Burger (1977). Por último, en el caso de *Q. xalapensis* reportada por Breedlove (2006) para Nicaragua, se determinó que esta especie es sinónimo de *Q. skinneri*, alcanzando en Nicaragua el límite sur de su distribución.

Después de lo anterior podemos mencionar que se tienen registradas 70 especies para México, de ellas 58 especies endémicas de su territorio (82.85% de las especies registradas para este país). En los países centroamericanos el de mayor riqueza de especies es Guatemala con 13 especies (con tres especies semi-restringidas a su territorio (*Q*. *benthamii*, *Q*. *crispipilis* y *Q*. *crispifolia*), seguido por El Salvador, Honduras y Nicaragua con seis especies cada uno. Costa Rica y Panamá en este estudio tienen registradas cinco especies, pero hay que mencionar que no se consideró en este estudio a *Q. panamandinaea* y tampoco a *Q. humboldtii* que está presente en el extremo oriental de Panamá y Colombia. El número de especies puede aumentar o disminuir en estos países conforme se solucionen algunos problemas taxonómicos del género.

Capítulo I

Torres-Miranda, A., Luna, I. & Oyama, K. 2009. Identifying biogeographic patterns and endemism areas of red oaks (*Quercus* L., section *Lobatae*) in the Mexican Transition Zone. (por enviarse a *Journal of Biogeography*).

Identifying biogeographic patterns and areas of endemism of red oaks (*Quercus* L., section *Lobatae*) in the Mexican Transition Zone and Central America

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Abstract.

Aim. Patterns of distribution of red oaks of the Mexican montane systems of Mexico and Central America were analysed to postulate a general hypothesis about the Mexican Transition Zone and nearest montane areas in Central America and to identify the areas of endemism.

Location. 22 floristic provinces and 158 grid-cells of Mexico (except the peninsula of Baja California) and Central America were analyzed.

Methods. A parsimony analysis of endemicity (PAE) for a presence/absence matrix was undertaken for the floristic provinces and the grid-cells, obtaining with the resultant cladograms the areas of endemism. Also it was applied an Unweighted Pair-Group Method with Arithmetic Average Algorithm (UPGMA) and a neighbor-joining analysis for the binary matrix of grids, and a matrix with the inverse of the distributions of each species. A matrix of sympatry was constructed to make a network analysis through the iterative elimination of intermediary species and the identification of cliqués.

Results. The strict consensus cladograms and the phenogram of floristic provinces, as well as the grid analysis with NJ and Network analysis let recognize the following patterns: an eastern Nearctic, a western Nearctic, and a Mexican Transition Zone integrated by a Mexican Montane Component and a Mesoamerican Component. From the analysis of grid-cells, PAE only identifies two areas of endemism, NJ eight possible areas of endemism, and the Network analysis nine confirmed areas of endemism, the last method being the more efficient.

Main conclusions. The pattern of distribution analysis showed that the provinces used as natural units in earlier works are not monophyletic. The Sierra Madre Occidental, Sierra Madre Oriental, Faja Volcánica Transmexicana and Sierra Madre del Sur are complex areas constituted at least by two different units. The identified areas of endemism by the network analysis are congruent with earlier works. Diversification of genus *Quercus* in the Miocene coincides with the tectonic and distentional activity, as well as climatic fluctuations that affected the spatial configuration of the Mexican and Central American montane systems.

Keywords: biogeography, Central America, endemism, cluster analysis, Mexican Transition Zone, network analysis, *Quercus*

INTRODUCTION

The genus *Quercus* is one of the most important woody floristic elements in the Northern Hemisphere (Nixon 2006), with many species in Asia, Europe, Northern and Central America, reaching marginally northern South America (Colombian Andes). This genus is about 500 species included in two subgenera, *Cyclobalanopsis* and

Quercus (Manos et al. 2001); the last one is divided in four subsections (Nixon 1993; Manos and Stanford 2001): *Cerris, Lobatae* (red or black oaks) *Quercus s.s.* (white oaks) and *Protobalanus* (intermediate or golden oaks), the first subsection only represented in Eurasia and North Africa. It has been suggested that the diversification of the genus occurred in the Middle Eocene, when the interchange of oaks of Eurasia and America finished (Axelrod 1983; Manos and Standford 2001). Manos et al. (1999) and Valencia (2004) suggested that the two main centres of diversification of the genus are found in southeastern Asia and the central part of America (Mexico and Central America); for the New World, Nixon (2006) considered that there are two centers of diversity: the mountains of southern Mexico and southeastern United States. Hooghiemstra (2006) suggested that during Miocene times, oaks dispersed from North to Central America, reaching their recent distribution and diversity.

In the Americas, oaks are dominant in many temperate and relatively dry vegetation types, i.e. 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, small or large trees. In Mexican temperate forests they are generally large, dominant overstorey trees, forming vegetation types that occupy more than the 15% of the plant cover of this country (Rzedowski 1978; Challenger 1998).

Section Lobatae (red oaks) is endemic to the New World; members of this section are more abundant in the mountains of Mexico and Central America. Section *Quercus* (white oaks) are represented both in humid and dry-arid areas, with a wider distribution (González-Rivera 1993; Nixon 1993; Zavala 1998; Valencia 2004). Nixon (1993) and Zavala (1998) suggested that red oaks are mainly distributed in the west, south and southeastern portions of Mexico, considered those the humid areas of the country. Following these authors, we considered that red oaks are a suitable model to study the biogeography of the mountainous systems of Mexico and Central America, in the Mexican Transition Zone (ZTM: Halffter 1976, 1978, 1987; Marshall and Liebherr 2000; Morrone and Márquez 2001; Escalante et al. 2004; Contreras-Medina et al. 2007a).

The ZTM was originally proposed by Halffter (1976, 1978, 1987) as a complex zone where Nearctic and Neotropical faunas superimpose including the montane areas of the southwestern United States, Mexico and almost all Central America, reaching the lowlands of central Nicaragua. Latter works mention that the ZTM is basically restricted to the montane areas of Mexico and only include the main physiographic features of the country: the Sierra Madre Occidental, Sierra Madre Oriental, Faja Volcánica Transmexicana and the Sierra Madre del Sur. Notwithstanding, a controversy exist about the inclusion of the Depresión del Balsas and the Sierra Madre de Chiapas-Guatemala in the ZTM (see Liebherr 1994; Marshall and Liebherr 2000; Morrone and Márquez 2001; Escalante et al. 2004; Morrone 2006; and Contreras-Medina et al. 2007a).

Halffter's proposal (1976, 1978, 1987) is based on generalizations done on analyses about the congruence in the areas of distribution of beetles related and their relation with other factors, as the geology of the areas. With this data, Halffter determined basic patterns of distributions of the taxa. The recognition of patterns in biogeography have been of fundamental interest and have been done with different approaches, i.e. cluster analysis through similitude indices (Jardine 1972; Hennig and Hausdorf 2004) and parsimony algorithms that, as other quantitative methods, have been severely criticized and questioned (Brooks and Van Veller 2003; Santos 2005; Nihei 2006).

The use of methods of parsimony led for the first time the recognition of patterns in the biotas, as well as a methodological tool to identify congruence zones in the distribution of different taxa, the so call areas of endemism (Morrone 1994), that were used until that time in a rigorous way (Maldonado and Uriz 1995; Luna et al. 1999, 2001; Morrone et al. 1999; Trejo-Torres and Ackerman 2001, 2002; Morrone and Escalante 2002; Rojas-Soto et al. 2003; Escalante et al. 2004; García-Trejo and Navarro 2004; Katinas et al. 2004; Espinosa et al. 2006; Contreras-Medina et al. 2007b; Vázquez-Miranda et al. 2007; Gutiérrez-Blando et al. 2008; Sánchez-González et al. 2008). The recognition of areas of endemism have been one of the main goals of historical biogeography, because they are the basic units of analysis in cladistic biogeography, which ultimate goal is to recognize the relation among areas (Linder 2001); under different approaches, the recognition of areas of endemism have been a problem undertaken in many studies (Axelius 1991; Henderson 1991; Anderson 1994; Harold and Mooi 1994; Morrone 1994; Linder 2001; Hausdorf 2002; Szumik et al. 2002; Hausdorf and Hennig 2003; Mast and Nyffeler 2003; Hennig and Hausdorf 2004; Szumik and Goloboff 2004; dos Santos et al. 2008).

The goal of this work is to recognize and contrast the areas of endemism and biogeographic patterns of red oaks that inhabits the ZTM sensu Halffter (1976), using different methods of analysis: cluster unweighted analysis and neighbor-joining, parsimony, and network analysis. The objective was to obtain congruence among these different methods, to analyze their advantages and disadvantages to establish a regionalization system, and to analyze their capabilities to recognize areas of endemism.

MATERIAL AND METHODS

Distributional Data

Distributional data of 72 red oak species from Mexico and Central America were obtained from the revision of herbarium specimens deposited in the following collections: MEXU, ENCB, IEB, XAL, UANL, CHAP, LL-TEX, and MO. In addition, revisionary, monographic, and floristic published studies were reviewed (Muller 1942, 1951; Martínez 1951, 1953, 1954, 1959, 1965, 1966, 1974; Standley and Steyermark 1952; Banda 1974; McVaugh 1974; Burger 1977; Espinosa 1979; Valdez and Aguilar 1983; Marroquín 1985; González-Villarreal 1986, 2003ab; Bello and Labat 1987; de la Cerda 1989; Spellenberg 1992; Vázquez 1992, 2000, 2006; Nixon and Muller 1993; Zavala 1995; 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; Romero 2006; Valencia and Lozada 2003; Santacruz and Espejel 2004; Valencia and Nixon 2004; Vázquez et al. 2004). With this information, a database that includes 13,454 georeferenciated records was constructed, and the distributional maps of each of the 72 species were obtained using the GIS ArcView ver. 3.2 (ESRI 1999).

Study area

Study area included the following countries: Mexico, Guatemala, Belize, El Salvador, Honduras, Nicaragua, Costa Rica and Panama, that includes de Mexican Transition Zone (ZTM, Halffter 1976, 1978, 1987) and the Sierra de Talamanca. The biogeographic analysis was performed using two different analysis units:

a) The first unit used was an adaptation to the regionalization system proposed by Rzedowski (1978) for Mexico and the floristic provinces of Takhtajan (1986) for

Central America integrated by 22 provinces (Figure 1a). We decided to use these provinces because to establish them, the vegetation type and the physiographic attributes were essential elements, and it is important to use them a priori to establish general patterns in the red oaks, because they are characteristics species of the temperate forests of the boreal hemisphere. Differently to Rzedowski (1978), we divided some Mexican floristic provinces as follows: the Altiplano in two parts, north and south; the Sierra Madre Occidental in two parts, nor-central and south; the Sierra Madre Oriental in three parts, north, central and south; the Serranías Meridionales in six parts: Faja Volcánica Transmexicana, Guerrero, Oaxaca, Jalisco, Depresión del Balsas and Sierra Madre del Sur. The Sierra de Talamanca was considered as an independent province. In this way, we considered the following provinces (i) northern Altiplano ALTIN, (ii) southern Altiplano ALTIS, (iii) Depresión del Balsas BAL, (iv) Planicie Costera del Golfo GOLF, (v) Planicie Costera del Pacífico PACI, (vi) Faja Volcánica Transmexicana FVT, (vii) Serranías Meridionales of Guerrero SMG, (viii) Serranías Meridionales del Istmo SMI, (ix) Serranías Meridionales of Jalisco SMJ, (x) Serranías Meridionales of Oaxaca SMO, (xi) Sierra Madre del Sur SMS, (xii) nor-central Sierra Madre Occidental SMOCC, (xiii) southern Sierra Madre Occidental SMOCS, (xiv) northern Sierra Madre Oriental (specifically Sierra Plegada) SMORN, (xv) central Sierra Madre Oriental SMORC (Potosian), (xvi) southern Sierra Madre Oriental SMORS (Hidalgo-Veracruz), (xvii) Tamaulipas TAM, (xviii) Sierra de los Tuxtlas TUX, (xix) Serranías Transístmicas STI, (xx) Valle de Tehuacán-Cuicatlán VTC, (xxi) Soconusco SOCO, and (xxii) Sierra de Talamanca TALA (Figure 1a).

b) The second unit of analysis was a system of 158 grid-cells of 1° x 1° of latitude/longitude that include all ZTM and Central America, and that have the advantage to use homogeneous in size areas without a priori determination (Figure 1b).

Parsimony analysis of endemicity

We used 72 species (columns) to construct two data matrices of presence (1) / absence (0) of species per area for both analyses units. A parsimony algorithm was applied to two matrices, one with 22 (provinces) x 72 (species) and other with 158 (grid-cells) x 72 (species). In both cases an area coded with all 0 were used to root the cladogram. A parsimony analysis of endemicity (PAE) following Morrone (1994) was undertaken using Nona (Goloboff, 1999) through WinClada ver. 1.00.24 (Nixon, 2002) was performed. Data were submitted to multiple TBR, searching on 100 initial trees (mult*100), holding 20 trees per replication (h/10). When we obtained more than two cladograms, we obtained the strict consense cladogram. Those areas with two or more shared species were identified as areas of endemism.

Cluster analysis

With the generated matrices in the above analysis, clustering unweighted analysis was undertaken (UPGMA, unweighted pair group with arithmetic mean) for the two units involved, using the Jaccard similarity coefficient with NTSYSpc 2.11 (Rohlf 2000). The UPGMA is a method that throws a unique tree (phenogram) through the iterative calcule of similitude matrices with a rooted topology; it can also be used distance matrices to obtain the phenograms.

The UPGMA is not the only method that use distance matrices to obtain unique trees. The neighbor-joining (NJ) is a clustering method that use distance matrices in an iterative was to construct trees of minimal evolution finding neighbors sequentially that minimize the total longitude of the tree. In this way, a different topology of a tree can be found. The presence/absence matrix of species per grid-cells was used and with the

Manhattan distance was obtained the NJ tree. This NJ tree has significant differences in the longitude of its branches. When the total length of the tree is minimized, in those localities with species with restricted distribution, the length of the branches is larger, so larger branches could indicate zones where species with restricted distribution can live in sympatry.

Species with wide distributions tends to difficult the recognition of patterns, because the possible role of dispersion through time. One option to minimize the effect of these species of wide distribution is to substitute in the original matrix of presence (1)/ absence (0), the inverse of the distribution of each taxa by unit of area (i.e. if one taxa is found in three grid-cells, the value 1 of presence in these three grid-cells will be substitute by its inverse 0.33). With these values, another time the Manhattan distances are calculated iteratively to obtain a new NJ tree. Differences in the longitudes of the branches identify those areas with species with restricted distribution and minimize the effect of organisms with wide distributions (i.e. using the inverse of the distribution). With this method, one different tree from grids-cells was obtained using the NJ method with NTSYSpc 2.11 (Rohlf 2000).

Sympatry inference and Network analysis

Finally, we applied the new approach to find patterns of sympatry based on network analysis based in Dos Santos et al. (2008). An adaptation was made to the method to obtain a sympatry matrix. Then, the distribution of the 72 species of red oaks was visualized in ArcView 3.2 (ESRI 1999) and the localities were united by the minimal distance, calculating the distance of the 72 trees and dividing that distance among the number of unique localities of each species and obtaining the mean for each species ($\overline{X}$). The sample mean of the 72 species was obtained, and the standard deviation (*s*) was calculated. To the population mean ($\mu = 24.28$ km) was subtracted the population standard deviation ($\sigma = 17.77$ km) and the value obtained was used to draw propinquity circles for all the taxa (6.5 km). With ArcView were intersected the 72 areas among themselves to obtain a sympatry matrix. We obtained a Boolean matrix of 72 (species) x 72 (species), with values by intersection among their species, where values near to 1 represents total homopatry, and values of 0 represents total alopatry.

The matrix is a graph G = (V,E) formed by V= 72 nodes (species) and E = edges that represent the relations of sympatry between the species, that is a directed multigraph. The matrix was analyzed with the program Pajek 1.24 (Batagelj and Mrvar 1999), obtaining the betweness value for each species (nodes) and iteratively eliminating those species with the higher betweness value. The betweness value is the frequency in which a node appears in the geodesic distances (shorter) that unites two pairs of vertexes. The clustering coefficient (CC1) was calculated; in theory, a CC1 of 1 denotes that the nodes that form a cluster or cliqué are intimately associated among them and differentiated from others, that is, there are not intermediate species among both cliqués. Also, it was calculated the clustering performed coefficient (CC2) to analyze iteratively the clustering performance. In theory, the elimination of species stops when the nodes has a CC1=1, or when CC1=0, because in the last case existed isolated nodes that do not formed cliqués. Once determined the cliqués that are formed with the iterative elimination of nodes (species), the areas that formed each cliqué were visualized in ArcView 3.2 (ESRI 1999) to determine the cliqués in a spatial context.

RESULTS

Parsimony Analysis of Endemicity

The floristic provinces analysis resulted in two cladograms of 141 length, consistency index of 51 and retention index of 60. The strict consensus cladogram had a length of 154, Ci = 46 and a Ri = 53 (Figure 2a). The TALA separates completely from the rest of the units. There are two main clades: the first (1) essentially Nearctic is composed by the Sierra Madre Oriental (SMORC and SMORN portions) and TAM; on the other hand is the Sierra Madre Occidental and the ALTIN. A second clade (2), essentially Neotropical, is the ZTM which relates the STI with the SMI, SOCO and the GOLF (Mesoamerica Component, CMA *sensu* Morrone and Márquez 2003), meanwhile another largest clade corresponds to the largest part of the Mexican Montane Component, CMM sensu Morrone and Márquez 2003) formed by a polytomy of (SMORS + VTC) + SMS, SMS, SMJ, FVT, PACI, BAL, maintaining the SMG, SMO and TUX out from the polytomy.

The analysis of the 158 grid-cells resulted in 50,000 cladograms of 341 length, consistency index of 21 and retention index of 71. The strict consensus cladogram had a length of 497, Ci = 14 and Ri = 55 (Figure 3). A polytomy of 48 grid-cells in the consensus was obtained. There are 11 defined clades as following: 1) to part of Mesetas Coahuilenses; 2) to Sierra Tarahumara in SMOCN; 3) to part of Mesetas Coahuilenses; 4) and 5) to part of to Planicie Chihuahuense; 6) to part of Mesetas Coahuilenses; 7) to the Meseta Central (ALTIS) + central FVT; 8) to the SMJ and SMOCS; 9) to SMORN and SMORC, with an internal clade corresponding to the Sierra Plegada; 10) to Mesoamerica Component with TALA + STI (Sierras de Comayagua and Sierra Madre de Chiapas-Guatemala); and 11) to the Sierra Tuito and Sierra Cuale + Highlands of BAL, SMS (highlands of Oaxaca and its occidental region), to the FVT (Campos Volcánicos and Cuencas Centrales) and SMORS, mainly the Hidalguense region (Figure 5a).

Cluster Analysis with UPGMA

Results obtained with the cluster analysis are, in general, congruent with the results of PAE. Using floristic provinces, the phenogram obtained has an r = 0.85969, and two main groups are formed (Figure 2b). The first group is essentially Neartic (1), and is formed by the SMOCC and ALTIN (western section), and in the other hand by the SMORN + SMORC and TAM (eastern section). A second group is essentially Neotropical (2), and is formed by three subgroups, the first one is formed by GOLF, SOCO, SMI and TUX. The second subgroup is formed by SMO and STI (Mesoamerica Component in strict sense). The third subgroup (Mexican Mountain Component) is divided in two component: ALTIS, the SMJ, SMOCS and GOLF, and in other hand by BAL, FVT, SMG, SMS, SMORS and VTC. The TALA is an entity completely different from the rest of the areas.

Finally, the phenogram of grid-cells (r = 0.8374) led recognize five major groups (Figure 4): 1) Central American group with two subgroups: TALA and Sierra de Comayagua, 2) Nearctic eastern group with two subgroups: SMORN + SMORC and Mesetas Coahuilenses, 3) Central Systems with three groups: the first group is composed by costal regions, the second group is [FVT central + SMS + Highlands BAL] + SMJ + [SMORS + FVT eastern], and the last group is Sierra Madre de Chiapas-Guatemala, 4) Nearctic western group with three subgroups: Meseta Central northern, SMOCS + ALTIS southern, and SMOCN, 5) Planicie Chihuahuense (see Figure 5b).

Cluster Analysis with Neighbor-Joining

A tree with four main branches was obtained with the neighbor-joining analysis using the presence/absence matrix of grid-cells (Figure 6a): 1) ALTIS eastern and [SMJ + SMOCS + ALTIS western], 2) ALTIS northern, 3) the group largest divided in three branches: the first Nearctic eastern [Meseta Coahuilense and SMORN + SMORC], the second is the ZTM in strict sense with [TALA, STI and FVT central + SMS + SMORS], and the last are TUX and coastal of Golfo, 4) Nearctic western with Mesetas Coahuilenses and [Planicie Chihuahuense + SMOCN] (see Figure 7a).

The neighbor-joining tree using the inverse of the distributions results in a tree with a better resolution and the relationships of its branches are more congruent with physiographic aspects. In this tree, four main branches can be identified: 1) SMJ + SMOCS + ALTIS western, 2) ALTIS nor eastern, 3) the branch largest including three principal groups: the first is Mesoamerican Component [TALA + Comayagua + Sierra Madre de Chiapas-Guatemala], the second group is the Mexican Mountain Component [TUX and Golfo coasts + Pacifico coasts + SMS western + [SMS eastern + FVT central + SMORS] + ALTIS southeastern, the last group is Nearctic eastern [Meseta Coahuilense + [SMORN + SMORC] + Mesetas Coahuilenses], 4) Nearctic western SMOCN and Planicie Chihuahuense (Figure 6b and Figure 7b).

Network Analysis

This analysis led identifies those species with wide distribution that are related with species with restricted distribution, and that can hide those patterns of restricted distribution, because these species have higher betweness values. The progressive elimination of these species led recognizes subnets defined in the main network. In this way, after iteratively eliminating eight species (*Q. crassifolia*, *Q. castanea*, *Q. cortesii*, *Q. sapotifolia*, *Q. candicans*, *Q. elliptica*, *Q. conspersa* and *Q. crispifolia*), two networks were obtained: 1) Montane Mexican Component (CMM) and 2) Mesoamerican Component (CM). After the elimination of 12 species in an iteratively, the CMM was divided in (1.1) the eastern montane systems that include the Sierra Madre Oriental, from Nuevo León to Veracruz-Hidalgo, reaching to the Sierras of Oaxaca-Puebla, and also including the northern part of the ALTIN, and (1.2) the western montane systems that include the SMOCC, the western FVT and the SMS. After the elimination of four species (*Q. gentryi*, *Q. scytophylla*, *Q. rysophylla* and *Q. canbyi*), the eastern systems were divided in (1.1.1) ALTIN + SMORN and (1.1.2) SMORC + SMORS (San Luis Potosí-Hidalgo-Veracruz) until the Sierras of Oaxaca-Puebla. The elimination of five more species (*Q. viminea*, *Q. fulva*, *Q. praineana, Q. conzattii* and *Q. uxoris*) separated the western systems in (1.2.1) SMS + western FVT and (1.2.2) SMOCC + Highlands of BAL. The elimination of *Q. rapurahuensis* divided the Mesoamerican Component in (2.1) STI and (2.2) TALA. The elimination of *Q. hypoxantha* and *Q. saltillensis* separated (1.1.1.1) SMORN of (1.1.1.2) ALTIN. The elimination of *Q. durifolia* separated the SMOCC in (1.2.2.1) Sierra Tarahumara and (1.2.2.2) the SMOCS + Highlands of BAL. With the elimination of *Q. uxoris* and *Q. nixoniana* were separated (1.2.1.1) the western FVT and (1.2.1.2) the SMS. With iterative eliminations were maintained the above relations, but some nodes maintained isolated; only can be separated the Sierra Madre de Chiapas component after successive eliminations, but with many nodes isolated. The succession of networks is shown in Figure 8.

Endemism areas

The strict consensus cladogram obtained with the floristic provinces (Figure 2a) let recognize six areas of endemism: a) SMORN with seven species (*Q. flocculenta*, *Q,* *galeanensis*, *Q. graciliramis*, *Q. hintonorum*, *Q. miquihuanensis*, *Q. saltillensis*, *Q. tenuiloba*), b) SMOCC with five species (*Q. albocincta*, *Q. durifolia*, *Q. macvaughii*, *Q. radiata*, *Q. tarahumara*), c) STI with five species (*Q. acatenangensis*, *Q. crispipilis*, *Q. crispifolia*, *Q. hondurensis*, *Q. paxtalensis*), d) SMJ with three species (*Q. cualensis*, *Q. iltisii*, *Q. tuitensis*), e) SMS with two species (*Q. grahamii*, *Q. rubramenta*), f) TALA with three species (*Q. costaricensis*, *Q. gulielmi-trealeasi*, *Q. seemannii*). Finally, there is an area constituted by SMG, ALTIS, BAL, PACI, FVT, SMJ, SMS, and SMORS + VTC (Montane Mexican Component) with four species: *Q. acutifolia*, *Q. crassipes*, *Q. laurina* and *Q. sapotifolia*.

The strict consensus cladogram obtained with grid-cells by PAE (Figure 3) resulted in only one area of endemism located in TALA and defined by the presence of two species (*Q. costaricensis* and *Q. gulielmi-trealeasi*, within group 10 in cladogram). With the PAE analyzes some areas resulted with at least one endemic species, but they do not qualify as areas of endemism sensu Morrone (1994).

The neighbor-joining analysis led recognize those zones that contains species with restricted distribution, because it is an algorithm that minimize the distances between areas, and those zones with species with restricted distribution will have larger branches. In this way, the presence/absence matrix showed seven larger branches that indicated species restricted to seven areas. They are: a) Sierra Plegada, b) Sierra de Cuale, c) SMORS, d) Sierras de Puebla-Oaxaca, e) SMOCS, h) SMG, and g) Sierra Madre de Chiapas. Also, it can be used the inverse of the distribution of the species, identifying eight large branches that corresponds to the following areas: a) Sierra Plegada, b) ALTIN, c) Sierras de Oaxaca-Puebla + SMORS, d) Highlands of BAL, e) SMG, f) SMJ, g) SMOCS, h) Sierra Madre de Chiapas.

Finally, with the network analysis was obtained nine groups of sympatric species. Each group of species in the space represent an area of endemism, so with the network analysis are detected the following areas of endemism: a) SMORS, SMORC reaching the Sierras of Oaxaca and Puebla, b) ALTIN, c) Sierra Plegada, d) Sierra Tarahumara, e) southern SMOCS + Highlands of BAL, f) western FVT, g) SMG, h) Sierra Madre de Chiapas-Guatemala, and i) TALA. Table 1 offers the sympatric species to each network obtained.

DISCUSSION

Biogeographic patterns

The results obtained with the analyses with PAE and UPGMA with floristic provinces are shown in Table 2. The TALA with UPGMA is the most different province, meanwhile with PAE this province and the TUX have unresolved relationships. Halffter (1976, 1978, 1986) and Rzedowski (1991a) mentioned that the Nicaragua Depression was a barrier that prevent the distribution of Nearctic taxa to Southern America, and thus being the limit of Megaméxico 2 (Rzedowski 1991b). In the case of red oaks, the Nicaragua Depression was an effective barrier for the species of the genus, and the diversity of species decreases towards Costa Rica (Torres-Miranda et al. en prep). Notwithstanding, the TALA is a zone with a high humidity and precipitation, and also with rough topography originated in the Tertiary and that have been explained partially by Plio-Pleistocenic glaciations (Kappelle et al. 1992).

In both analyses exist a Nearctic component, divided in an eastern and in a western parts, corresponding to the generalized tracks obtained by Contreras-Medina and Eliosa-León (2001), that mentioned the existence of fragmented ancentral biotas. The Sierra Madre Oriental (from Nuevo León to San Luis Potosí) and the Sierra Madre

Occidental define basically the Nearctic component. Notwithstanding, the SMORS belong to a third component, the ZTM.

The ZTM comprises the FVT and the southern SMORS, that reaches the karst Huasteco in the north and the Nicaragua Depression in the south. The Tehuantepec Isthmus has been acting as a barrier dividing the ZTM in two components, the Mexican montane and the Mesoamerican, that corresponds to the homonym domains identified by Morrone and Márquez (2003) and Gutiérrez et al. (2008) for terrestrial mammals, with slight differences. The Mexican montane component identified by Escalante et al. (2005) is considered by some authors as the ZTM in strict sense (Morrone 2004, 2006; Escalante et al. 2004).

The results obtained with PAE, UPGMA and NJ with the presence/absence matrix and NJ with the inverse distributional matrix are present in Table 3.

The strict consense cladogram identified 11 clades (Figure 3). Among these clades there are those which emphasize the close relationship existent within the central montane systems composed by the FVT, Highlands of Balsas and SMS + SMORS and Sierras of Oaxaca-Puebla, pattern repeated in the four analyses undertaken. Other patterns that repeats in our analysis are: 1) the relationship of the SMOCS and the SMJ; 2) in the north, the division of the Sierra Madre Oriental in two different areas, Sierra Plegada and Karst Huasteco; 3) the relationship between the Sierra Plegada and the Mesetas Coahuilenses; and, 4) the separation of the Sierra Madre Occidental in a northern and a southern part, in the limits of Durango and Chihuahua.

The relations among the 11 clades cannot be explained, because the great amount of homoplasies (analogous to dispersion) that collapse the majority of the areas in the analysis, creating artificial groups, as in the case of the coastal grid-cells. As Brooks and Van Veller (2003) argued, when species disperses after speciation or when they respond to all events of vicariance, as in this case, uncertain relations can be obtained.

Santos (2005) mentioned that the ideal organisms to run PAE are those with limited capacities to dispersal and with speciation almost exclusively by vicariance, characteristics that are not fulfilled by red oaks, because the fruits are dispersed by mammals, and hybridation has been assumed as a manner to extend their area of distribution, giving origin to new hybrid species as *Q. dysophylla* (Tovar-Sánchez and Oyama 2004).

For this reason, the results obtained with the other analyses were taken up again to identify the relations among the rest of the areas. With the UPGMA is possible to identify four main clusters: western Nearctic, the ZTM do not include the TALA and the Sierras de Comayagua-Isabella, forming a “Mesoamerican” cluster, separated from the ZTM by the fault system of Motagua in Guatemala, and finally an oriental Nearctic cluster. There is not similitude between both Nearctic clusters. This is the only analysis that shows that the southern limit of the ZTM is found in the fault system of Motagua, reason why the STI is divided in an eastern and western part.

In the first analysis with NJ, the STI are identified as a complex area composed by two main branches, separated by the fault system of Motagua in Guatemala: the Sierra Madre de Chiapas-Guatemala + Highlands of Chiapas and related with the TALA. Also is identified a relation among the Meseta Central (ALTIS) and SMOCS + SMJ (including Sierra de Cuale). In the second analysis with NJ, is established a system that do not contradict the results with PAE and represents a more coherent classification system that the obtained with UPGMA, inclusive with the Network Analysis. An eastern Nearctic component (Sierra Plegada + Mesetas Coahuilenses) and a western Nearctic component (SMOCC + Mesetas Chihuahuenses) are found, also identified by

Contreras-Medina et al. (2007), both being part of the Nearctic domain of Morrone (2004, 2006). In this study, the ZTM differently of Halffter (1987), comprises the rest of the montane systems of Mexico and Central America, including the TALA, proposal that is near to the results of Liebherr (1994), Marshall and Liebherr (2000), and Contreras-Medina et al. (2007).

The network analysis is congruent with the results of NJ. First, it separates the Mesoamerican component cliqué from the rest of the montane systems of Mexico, identifying an eastern and a western cliqués. Inside the eastern cliqué exists a Nearctic branch that includes the Sierra Plegada + Mesetas Coahuilenses and a transitional one comprising the Sierra Madre Oriental (Karst Huasteco) + Sierras de Oaxaca-Puebla. The western cliqué is defined by the northern and SMOCS, the SMJ and SMG.

In summary, in this study the Mexican Transition Zone comprises: [SMOCS + SMJ, central FVT + SMS, SMORS + Sierras Oaxaca-Puebla] + [STI + TALA].

The Mesoamerican component (STI + TALA) has been recognized in other studies as the southern track by Morrone and Márquez (2003), Mesoamerican Montane Component (Cabrera and Willink 1973; Contreras-Medina et al. 2007) and Central America “core” (Gutiérrez et al. 2008). This component also coincides, in part, with the North-American caribbean and the Sud-American caribbean of Rosen (1976) or Sudamérica of Contreras-Medina and Eliosa-León (2001), and in this study is considered as part of the ZTM. As mentioned by Kappelle et al. (1992), the TALA was a zone that facilitated the interchange of Nearctic elements to South America.

The formation of the STI dates from the Cretacic-Paleogene (Marshall 2008), including formations inclusive Precambric (Ferrusquía-Villafranca 1993). The Serranías were not colonized until the global cooling during the Late Eocene-Miocene (Graham 1993), epoch that coincides with the time of diversification of the genus

Quercus (Axelrod 1983, Valencia 2004). The Serranías are divided by the fault system of Motagua that forms fluvial valleys in central Guatemala and delimits the North American plate of the Caribbean plate (Marshall 2008). In the western part is formed by the Chiapas system-Guatemala + Highlands of Chiapas + Sierra de Cuchumatanes + Volcanic Arch of El Salvador, and in the eastern part by the Sierras de Comayagua in Honduras + Sierra Isabella + Sierra Chontaleña, the last two in Nicaragua.

The Mexican montane component was recognized by Escalante et al. (2005) and by Morrone and Márquez (2003), but in their delimitation both recognized the Sierra Madre Occidental and the Sierra Madre Oriental as natural units. In later studies, Morrone (2004, 2006) named this component as ZTM in strict sense. The main conflict is found in the delimitation of both Sierras Madres.

The Sierra Madre Occidental is a Tertiary volcanic province that includes the Meseta Central and the eastern part of Chihuahua (Ferrari et al. 2005). It was formed in the Cretacic-Tertiary with a Tertiary ignimbritic cover of ~300,000 km^2. The northern zone is cover with Oligocene ignimbrits and the southern zone with Earlier Miocene ignimbrits (Ferrari et al. 2005), coinciding with the division of the province of this study. The northern part is related with the Mesetas Chihuahuenses and the southern part with the Meseta Central.

Eguiluz et al. (2000) mentioned that the Sierra Madre Oriental is a montane massif product of the raising and deformation of Mesozoic rocks, with a faulting and folding due to an inversion in the Earlier Tertiary, which extends from Nuevo León to Cuicatlán, with an interruption in the FVT. The Sierra in the region of San Luis Potosí presents a minor topographic relief, that acts as a barrier dividing the Sierra Madre Oriental in two parts (Luna et al. 1999, González-Zamora et al. 2007): a northern part that is related with the Mesetas Coahuilenses, and a southern part, from the karst hidalguenses to Cuicatlán (Sierras Oaxaca-Puebla), also found by Luna et al. (1999).

The FVT is a magmatic arch that crosses the central part of Mexico, from the coasts of the Pacific Ocean to the Gulf of Mexico, and its formation dates from the Middle Miocene (Gómez-Tuena et al. 2005). In this study, the western part corresponds to the SMJ, the eastern part is related with the Sierra Madre Oriental, and the central part has a greater relationship with the SMS. The subdivision of the FVT proposed by Torres-Miranda y Luna (2007) is congruent with Luna et al. (1999).

The SMS is a marginal montane system whose origin is difficult to precise, because it owes Proterozoic (in Oaxaca), Jurassic and Cenozoic rocks. Since the Early and Middle Tertiary this system had important volcanic activity (Ferrusquía-Villafranca 1993). In this study, this province is separated in two parts, a western part (Serranías of Guerrero) and an eastern part (Oaxaca massif).

The FVT and the SMS have been identified as sister provinces in the analyses of Liebherr (1992), Marshall and Liebherr (2000), Flores-Villela and Goyenechea (2001) and Gutiérrez et al. (2008). In the PAE and NJ analyses is identified a relationship between the central FVT and the SMS, meanwhile the western FVT (SMJ) is more related with the SMOCS, but in the network analysis the SMJ is related with the SMS, result that is congruent with Luna et al. (1999) and Gutiérrez et al. (2008). Following this idea, is confirmed the theory of Halas et al. (2005) that the FVT placed an important role in the colonization and interchange of species, because all the species present in the FVT have high betweness values.

Following Escalante et al. (2004, 2005), we included the BAL as part of the ZTM, because the species that are considered as endemic to this province are restricted to the Highlands of the Balsas, in the southern part of the Nevado de Toluca.

Endemism areas

The recognition of areas of endemism, that is, those areas that shares the distributional congruence of two or more species, is the first step to make a cladistic biogeography analysis, whose objective is to find the relation of the areas and to reconstruct the fragmentation events of these areas (Morrone 2001).

In this study, the strict consense cladograms of PAE have been used to identify areas of endemism. With the floristic provinces analysis was identified seven areas of endemism, three of them included in a more inclusive area of endemism, which basically corresponds to the Mexican montane component of this study. Notwithstanding, when using a biotic regionalization system implicitly implies the tendency to validate the areas previously used to obtain *ad hoc* results. Because these inconvenient, we decided to used as units of analysis a system without a priori delimitation, a system of grid-cells.

The grid-cell analysis with PAE led identify only one area of endemism: the Sierra of Talamanca. The rest of the areas were not defined by at least two synapomorphies; an alternative to increase the number of synapomorphies to identify the areas of endemism is to increase the size of the grid-cells (Morrone y Escalante 2002), but this increment has the inconvenient to loose spatial resolution.

The NJ analysis using a presence/absence matrix let identify six potential areas of endemism, meanwhile for the matrix of the inverse of the distribution were identified eight possible areas of endemism. The corroboration of the possible areas must be realized identifying the present species in those zones. The NJ led maximize the relationships of areas that owe species with restricted distributions. The problem lies in that the length of the branch is increased with the single presence of a species of restricted distribution (i.e. if a single species is distributed in two grid-cells, the length of both branches in the tree will increase even if there is not any other species in sympatry). Other inconvenient of the NJ is that the length of the branches is not increased in areas that even having sympatric species, their distributional ranges are a little wider (i.e. present in five grid-cells); that is why the TALA was not identified as an area of endemism, because it only have three endemic species of red oaks.

Notwithstanding the inconvenient of the NJ to identify areas of endemism, this method is convenient to identify areas with species with restricted distribution, that at the same time are considered as possible areas of endemism; with this method, it is possible to identify efficiently and quickly areas of importance for the conservation of species. Also, the NJ offers a useful tool in the identification of relations among areas, information that is loose in the PAE analyses, and can offer efficient hierarchical system that the obtained with PAE and UPGMA.

The network analysis resulted to be the more efficient method to identify areas of endemism. This method led identify areas of endemism following the approach of Nelson and Platnick (1984), that is, the total congruence of the areas of distribution of at least two species (homopatry). It not possible to define an area of endemism based on the distribution of a single species with restricted distribution (Axelius 1991). The PAE also let identify areas of endemism following this approach, but as Linder (2001) mentioned, one of the main problems of the parsimony analysis are the large matrices, because it is not possible to obtain all the possible solutions and many of them have low resolution, as in this study.

The iterative elimination of intermediary species resolves the controversy of Harold y Mooi (1994) and Hausdford (2002) concerning the hidden patterns of homopatry between two areas due to the presence of one species with alelopatry between both areas. Species with higher betweness are removed, so the effect of alelopatry is minimized and is maximized the total homopatry, and is reflected when the CC1 tend to 1 for all the nodes (species).

The identified cliqués through iterative removal of species can be directly seen in the geographic space without using *a priori* units (*i.e.* regionalization systems), or units than subtract resolution to the analysis (grid-cells), and that can cause artificial or uncertain results.

The network analysis proposed in this work let elucidate the relations of endemism among groups of nets of sympatric species, whose inclusion relation is mutually inclusive, i.e. large cliqués can be broken in smaller cliqués. In this way, nine areas of endemism were obtained located in the geographic space (Figure 8).

In the Mesomerican component, the areas of endemism identified are the TALA in Costa Rica and Panama, and the Sierra Madre de Chiapas and Highlands of Guatemala (without including the Highlands of Chiapas and Sierra de Cuchumatanes in Guatemala). These areas are supported by the studies of Cabrera and Willink (1971), Savage (1982) and Halas et al. (2005). Raven and Axelrod (1966) mentioned that the endemic elements of Central America are relatively independent of North America and South America. Raven and Axelrod (1966) and Graham (1993) also mentioned that the dispersal of plant species from North America to South America occurred in the Pliocene, when the global cooling caused the expansion of the temperate zones to low altitudes, in the same period in which Axelrod (1983) estimated that the diversification of the American oaks occurred.

In the Oriental systems are identified three areas of endemism, two of them (Sierra Plegada and Mesetas Coahuilenses) included in the Nearctic component, and the other (SMORS + SMORC + Sierras Oaxaca-Puebla) belongs to the Mexican Montane Component.

In the Occidental systems are identified four areas of endemism: the SMOCC, belonging to the Nearctic component; and eastern SMS, SMJ (western FVT) and southern SMOCS + highlands of Balsas, the last three belonging to the Mexican Montane Component. The last area of endemism is defined by the distribution of the bicentric species *Q. urbanii*, that is find in both regions, and that is sympatric with *Q. hintonii* in the Highlands of Balsas and with *Q. radiata* in the SMOCS.

None of the areas of endemism is found in the central FVT, because this region has a recent geologic origin and did not promote the *in situ* speciation of oaks, with the exception of *Q. dysophylla*, hybrid species between *Q. crassipes* and *Q. crassifolia,* intimately related with the contact zone of the eastern FVT with the Sierra Madre Oriental.

The origin of the montane systems is in some cases Mesozoic (Sierra Madre Oriental and Sierra Madre Occidental) or inclusive earlier (STI or certain regions of Oaxaca); some of these systems have suffered vulcanism processes, of folding and/or faulting in the Tertiary, mainly in the Miocene-Pliocene (Neogene). Despite that tectonic forces do not act in the STI, also in the Neogene occurred coolings that expanded the temperate vegetation and the temperature fluctuations promote *in situ* speciation.

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Table 1. Cliqués obtained and species that support them, through the iterative elimination of intermediary species.

CLIQUÉS	REGION	SPECIES
1	Mexican Region	*Q. acherdophylla, Q. acutifolia, Q. affinis, Q. albocincta, Q. aristata, Q. canbyi, Q. crassipes, Q. coahuilensis, Q. conzattii, Q. coccolobifolia, Q. cualensis, Q. depressa, Q. durifolia, Q. dysophylla, Q. eduardii, Q. emoryi, Q. flocculenta, Q. fulva, Q. galeanensis, Q. gentryi, Q. graciliriamis, Q. grahamii, Q. gravesii, Q. hintonii, Q. hintonorum, Q. hirtifolia, Q, hypoleucoides, Q. hypoxantha, Q. iltisii, Q. laurina, Q. macvaughii, Q. mexicana, Q. miquihuanensis, Q. nixoniana, Q. ocoteifolia, Q. planiocula, Q. pinnativenulosa, Q. praineana, Q. radiata, Q. rubramenta, Q. rysophylla, Q. salicifolia, Q. saltillensis, Q. sartorii, Q. scytophylla, Q. sideroxyla, Q. tarahumara, Q. tenuiloba, Q. tuitensis, Q. urbanii, Q. uxoris, Q. viminea, Q. xalapensis*
1.1	Eastern Nearctic	*Q. acherdophylla, Q. canbyi, Q. coahuilensis, Q. depressa, Q. flocculenta, Q. galeanensis, Q. graciliramis, Q. gravesii, Q. hintonorum, Q. hirtifolia, Q. hypoxantha, Q. miquihuanensis, Q. pinnativenulosa, Q. rysophylla, Q. saltillensis, Q. sartorii, Q. tenuiloba, Q. xalapensis*
1.1.1	Mesetas Coahuilenses + Northern Sierra Madre Oriental	*Q. coahuilensis, Q. flocculenta, Q. galeanensis, Q. graciliramis, Q. gravesii, Q. hintonorum, Q. hypoxantha, Q. miquihuanensis, Q. saltillensis, Q. tenuiloba*
1.1.1.1	Meseta Coahuilense	*Q. coahuilensis, Q. gravesii*
1.1.1.2	Sierra Plegada	*Q. flocculenta, Q. galeanensis Q. graciliramis, Q. hintonorum, Q. miquihuanensis, Q. tenuiloba,*
1.1.2	Central + southern Sierra Madre Oriental	*Q. acherdophylla, Q. depressa, Q. hirtifolia, Q. pinnativenulosa, Q. sartorii, Q. xalapensis*
1.2	Western Nearctic	*Q. albocincta, Q. aristata, Q. conzattii, Q. cualensis, Q. durifolia, Q. fulva, Q. gentryi, Q. grahamii, Q. hintonii, Q. iltisii, Q. macvaughii, Q. nixoniana, Q. planipocula, Q. praineana, Q. radiata, Q. rubramenta, Q. salicifolia, Q. scytophylla, Q. tarahumara, Q. tuitensis, Q. urbanii, Q. uxoris, Q. viminea*
1.2.1	Serranías Meridionales of Jalisco-Sierra Madre del Sur	*Q. aristata, Q. cualensis, Q. grahamii, Q. iltisii, Q. nxoniana, Q. planipocula, Q. rubramenta, Q. tuitensis, Q. uxoris*
1.2.1.1	Serranías Meridionales of Jalisco (western Faja Volcánica Transmexicana)	*Q. aristata, Q. cualensis, Q. iltisii, Q. planipocula, Q. tuitensis,*
1.2.1.2	Sierra Madre del Sur	*Q, grahamii, Q. rubramenta*
1.2.2	Sierra Madre Occidental	*Q. albocincta, Q. durifolia, Q. hintonii, Q. macvaughii, Q. radiata, Q. tarahumara, Q. urbanii*
1.2.2.1	Northern Sierra Madre Occidental	*Q. albocincta, Q. macvaughii, Q. tarahumara*
1.2.2.2	Southern Sierra Madre Occidental + Depresión del Balsas	*Q. hintonii, Q. radiata, Q. Urbanii*
2	Central America Region	*Q. acatenangensis, Q. benthamii, Q. costricensis, Q. crispipilis, Q. duratifolia, Q. gulielmi-trealeasi, Q. hondurensis, Q. paxtalensis, Q. rapurahuensis, Q. seemannii, Q. Skinneri*

2.1	Serranías Transístmicas	*Q. acatenangensis, Q. benthamii, Q. crispipilis, Q. duratifolia, Q. hondurensis, Q. paxtalensis, Q. skinneri*
2.1.1.1	Sierra Madre de Chiapas-Guatemala	*Q. bethamii, Q. crispipilis, Q. duratifolia, Q. paxtalensis*
2.2	Sierra de Talamanca	*Q. costaricensis, Q, gulielmi-trealeasi, Q. seemannii*

Table 2. Comparative table between the floristic provinces analyses with PAE and UPGMA.

PAE	UPGMA
Sierra de Talamanca	
Sierra de los Tuxtlas	Sierra de Salamanca
2. NEARCTIC	**2. NEARCTIC**
2.1 Eastern	2.1 Western
Tamaulipas	Northern Altiplano
Central Sierra Madre Oriental (San Luis Potosí)	Nor-central Sierra Madre Occidental
Northern Sierra Madre Oriental (Sierra Plegada)	2.2 Eastern
	Central Sierra Madre Oriental (San Luis Potosí)
2.2 Western	
	Northern Sierra Madre Oriental (Sierra Plegada)
Altiplano Norte	
Nor-central Sierra Madre Occidental	Tamaulipas
Southern Sierra Madre Occidental	
MEXICAN TRANSITION ZONE	**MEXICAN TRANSITION ZONE**
MESOAMERICAN COMPONENT	*MESO-AMERICAN COMPONENT*
Planicie Costera del Golfo	Sierra de los Tuxtlas
Soconusco	Serranías del Istmo
Serranías del Istmo	Soconusco
Serranías Transístmicas	Planicie Costera del Golfo
	Serranías Transístmicas + Serranías de Oaxaca
MEXICAN MONTANE COMPONENT	
Serranías de Oaxaca	*MEXICAN MONTANE COMPONENT*
Serranías de Guerrero	3.3.1 Occidental
Southern Altiplano (Meseta Central)	Planicie Costera del Pacífico
Depresión del Balsas	Southern Sierra Madre Occidental
Planicie Costera del Pacífico	Serranías de Jalisco
Faja Volcánica Transmexicana	Southern Altiplano (Meseta Central)
Serranías Meridionales of Jalisco	3.3.2 Central
3.2.1 Eastern systems	Depresión del Balsas
Sierra Madre del Sur	Faja Volcánica Transmexicana
Southern Sierra Madre Oriental	Serranías Meridionales of Guerrero
Valle de Tehuacán-Cuicatlán	3.3.3 Oriental
	Sierra Madre del Sur
	Southern Sierra Madre Oriental
	Valle de Tehuacán-Cuicatlán

Table 3. Identified areas with PAE, UPGMA and NJ (with presence/absence matrix and inverse distributional matrix) in the grid-cell analysis.

PAE	UPGMA
Sierra de Talamanca 1. Northern Sierra Madre Occidental 2. Coasts of Veracruz and Guatemala 3. Sierra Patuca (Honduras) + Volcanic Arch of El Salvador 4. Sierra Chontaleña of Nicaragua 5. Coasts of Jalisco, Nayarit and Guerrero including Sierra de Cuale in Jalisco 6. Sierra Comayagua-Isabella 7. Meseta Central, southern Altiplano 8. Sierra de Talamanca 9. Serranías Meridionales of Jalisco + southern Sierra Madre Occidental 10. Sierra Plegada + Altiplano Coahuilense 11. Faja Volcánica Transmexicana + Sierra Madre del Sur a) Highlands of Balsas b) Eastern Sierra Madre del Sur (Oaxaca) c) Campos Volcánicos de Michoacán d) Western Sierra Madre del Sur (Guerrero) e) Southern Sierra Madre Oriental (Karst Huasteco) + Sierras Oaxaca-Puebla	**NEARCTIC** 1. Grandes Planicies of North America 2. Northern + southern Sierra Madre Occidental **MEXICAN TRANSITION ZONE** 3. Meseta Central (southern Altiplano) 4. Central systems Eastern Faja Volcánica Transmexicana + southern Sierra Madre Oriental + Sierras de Oaxaca-Puebla Serranías Meridionales of Jalisco Central Faja Volcánica Transmexicana + Sierra Madre del Sur 5. Sierra Madre de Chiapas-Guatemala + Highlands of Chiapas **ORIENTAL SYSTEMS** 6. Mesetas Coahuilenses 7. Central + northern Sierra Madre Oriental **CENTRAL AMERICA SYSTEMS** 8. Sierras Comayagua-Isabella + Sierra Maya 9. Sierra Salamanca
NJ (with presence/absence matrix)	NJ (with inverse distributions matrix)
NEARCTIC 1. Grandes Planicies + Northern Sierra Madre Occidental **MEXICAN TRANSITION ZONE** 2. Coastal areas + Sierra Cuale 3. Central Systems Central Faja Volcánica Transmexicana + Sierra Madre del Sur + Depresión del Balsas Sierra Madre Oriental southern + Sierras Oaxaca-Puebla + Faja Volcanica eastern 4. Serranías Transístmicas Sierra Madre de Chiapas-Guatemala-Highlands of Chiapas Sierras de Comayagua-Isabella 5. Sierra de Talamanca	**WESTERN NEARCTIC** 1. Grandes Planicies (Meseta Chihuahuense) 2. Northern Sierra Madre Occidental **EASTERN NEARCTIC** 3. Mesetas Coahuilenses 4. Northern Sierra Madre Oriental (Sierra Plegada) **MEXICAN TRANSITION ZONE** *MEXICAN MONTANE COMPONENT* 5. Central systems Central Faja Volcánica Transmexicana + Sierra Madre del Sur + Balsas Southern Sierra Madre Oriental + Sierras Oaxaca-Puebla + Eastern Faja Volcánica Transmexicana *MESO-AMERICAN COMPONENT* 6. Sierra Madre de Chiapas-Guatemala-Highlands of Chiapas 7. Sierras de Comayagua-Isabella 8. Sierra de Salamanca

6. Northern Sierra Madre Oriental	
7. Mesetas Coahuilenses	*WESTERN COMPONENT*
8. Serranías Meridionales of Jalisco + southern Sierra Madre Occidental	9. Meseta Central
9. Eastern + western Meseta Central	10. Southern Sierra Madre Occidental + Serranías Meridionales of Jalisco

FIGURES

Figure 1. Units used in biogeographic analysis: (a) Floristic provinces used for red oaks based and modified from Rzedowski (1976) for Mexico and Takhtajan (1986) for Central America: (i) northern Altiplano ALTIN, (ii) southern Altiplano ALTIS, (iii) Depresión del Balsas BAL, (iv) Planicie Costera del Golfo GOLF, (v) Planicie Costera del Pacífico PACI, (vi) Faja Volcánica Transmexicana FVT, (vii) Serranías Meridionales of Guerrero SMG, (viii) Serranías Meridionales del Istmo SMI, (ix) Serranías Meridionales of Jalisco SMJ, (x) Serranías Meridionales of Oaxaca SMO, (xi) Sierra Madre del Sur SMS, (xii) nor-central Sierra Madre Occidental SMOCC, (xiii) southern Sierra Madre Occidental SMOCS, (xiv) northern Sierra Madre Oriental (specifically Sierra Plegada) SMORN, (xv) central Sierra Madre Oriental SMORC (Potosian), (xvi) southern Sierra Madre Oriental SMORS (Hidalgo-Veracruz), (xvii) Tamaulipas TAM, (xviii) Sierra de los Tuxtlas TUX, (xix) Serranías Transístmicas STI, (xx) Valle de Tehuacán-Cuicatlán VTC, (xxi) Soconusco SOCO, and (xxii) Sierra de Talamanca TALA; and, (b) Grid-cells of 1° x 1° latitude/longitude.

Figure 2. Comparative results obtained using floristic units with (a) Parsimony Analysis of Endemicity (strict consense cladogram of the floristic provinces units. L = 154, Ci = 46 and Ri = 53), and (b) Cluster Analysis with UPGMA (phenogram with Jaccard index. r = 0.85969).

Figure 3. Strict consense cladogram of the 158 grid-cells with PAE. L = 497, Ci = 14 and Ri = 55.

Figure 4. Phenogram obtained with UPGMA with the 158 grid-cells. r = 0.8374.

Figure 5. Patterns obtained of (a) strict consense cladogram in PAE, and (b) similitude in UPGMA.

Figure 6. Tree obtained with neighbor-joining: (a) with presence/absence matrix, and (b) with matrix using the inverse of the distributions of the species.

Figure 7. Patterns obtained in the NJ tree: (a) with distances in presence/absence matrix, and (b) with matrix using the inverse of the distributions of the species.

Figure 8. Networks obtained with the iterative elimination of intermediary species. Numbers inside each map refers to the subnets of each network. Numbers in the arrows refers to the number of species eliminated to obtain that subnet.

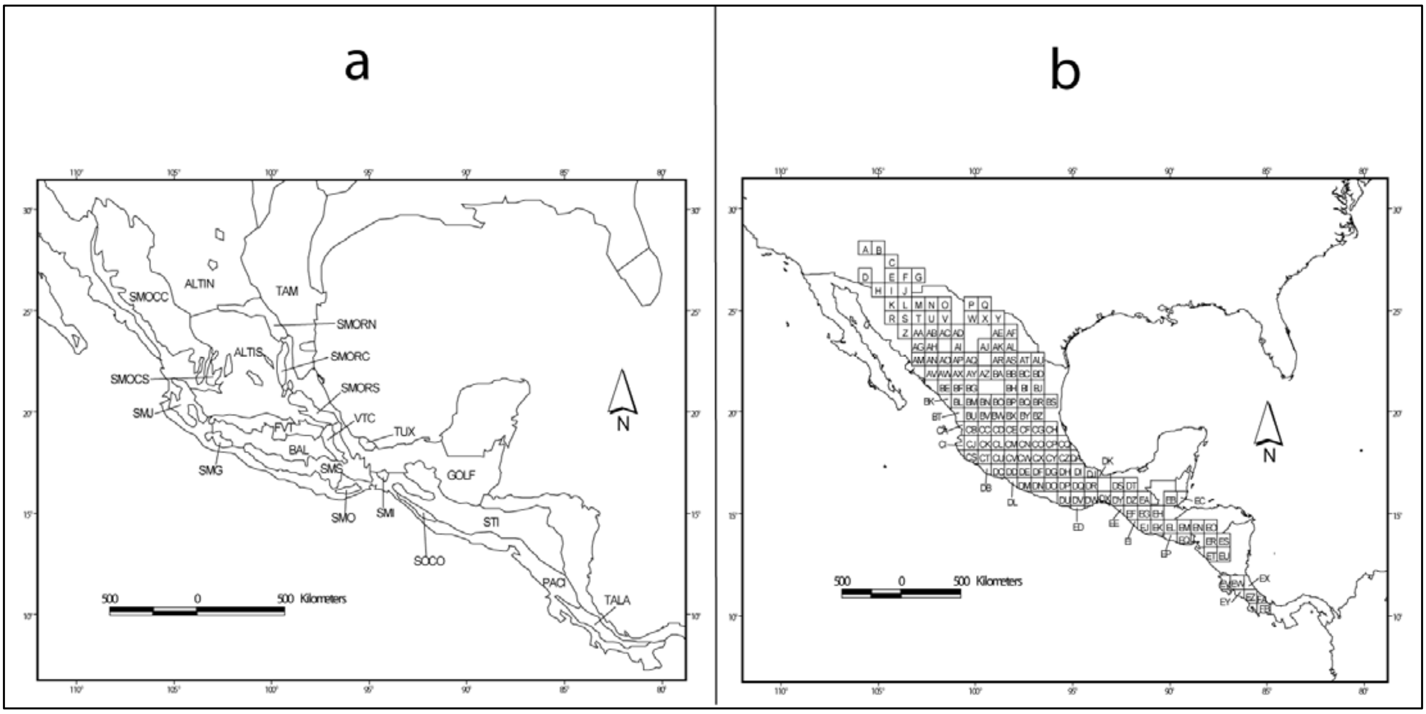


Figure 1

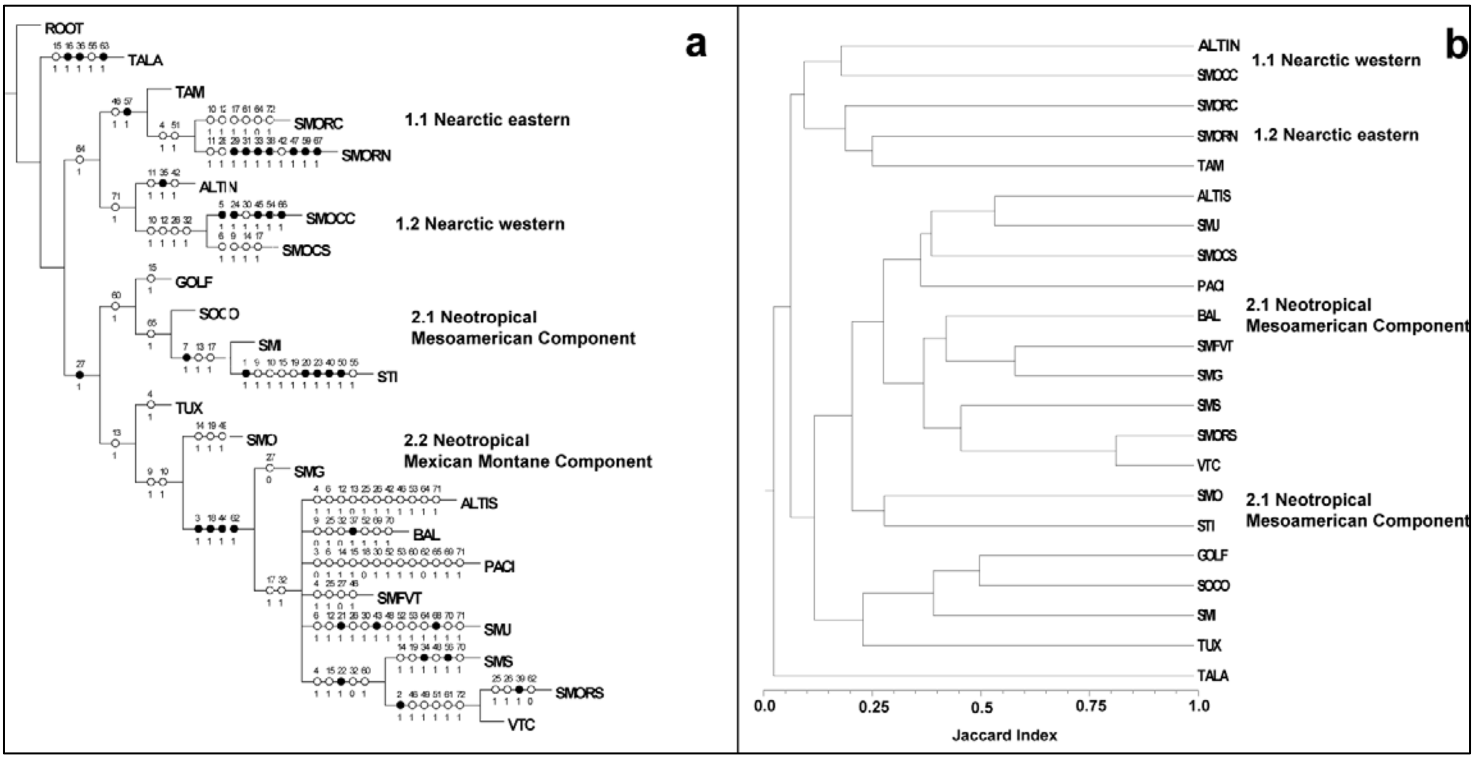
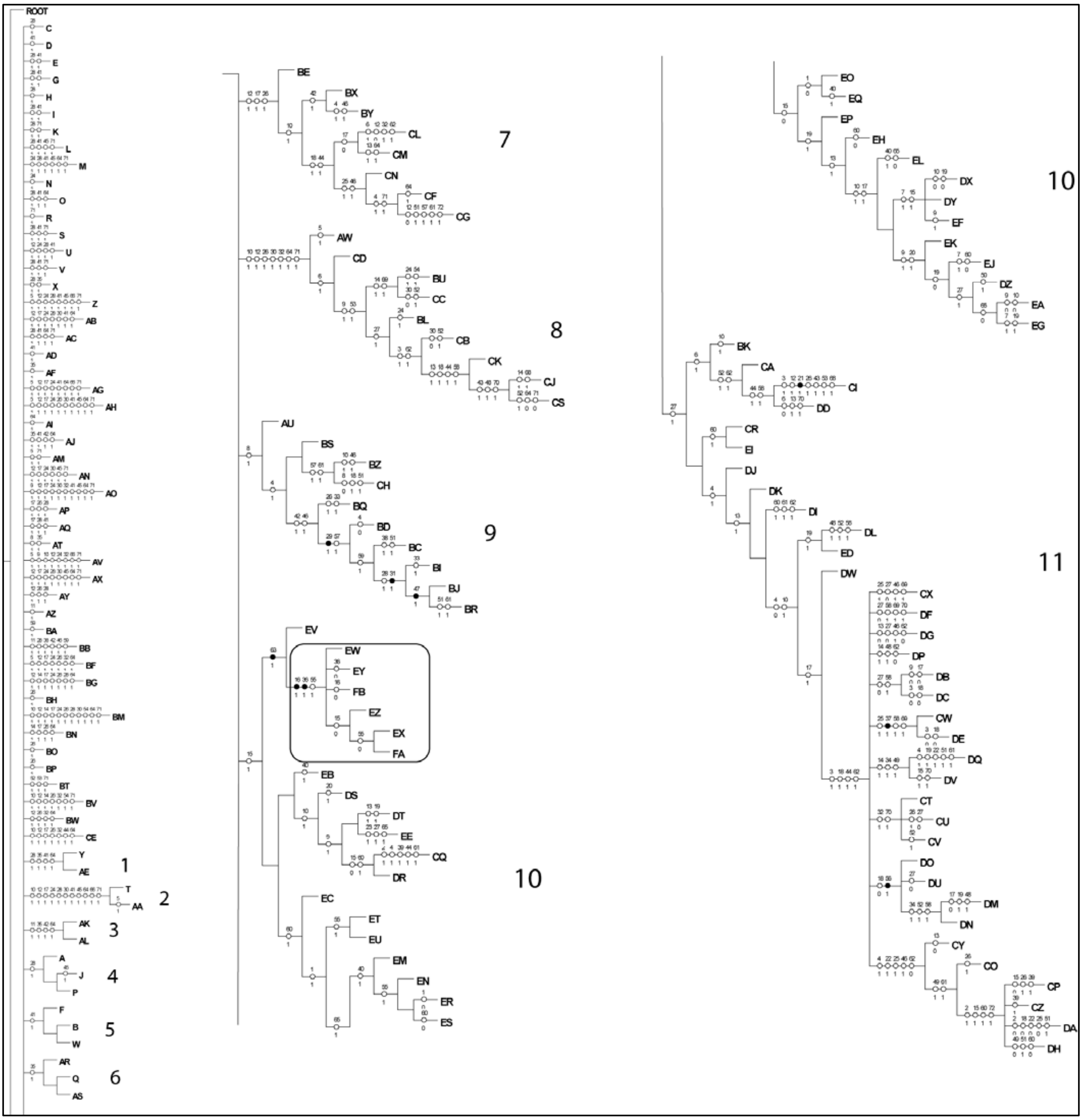


Figure 2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CG
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CJ
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9
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EK
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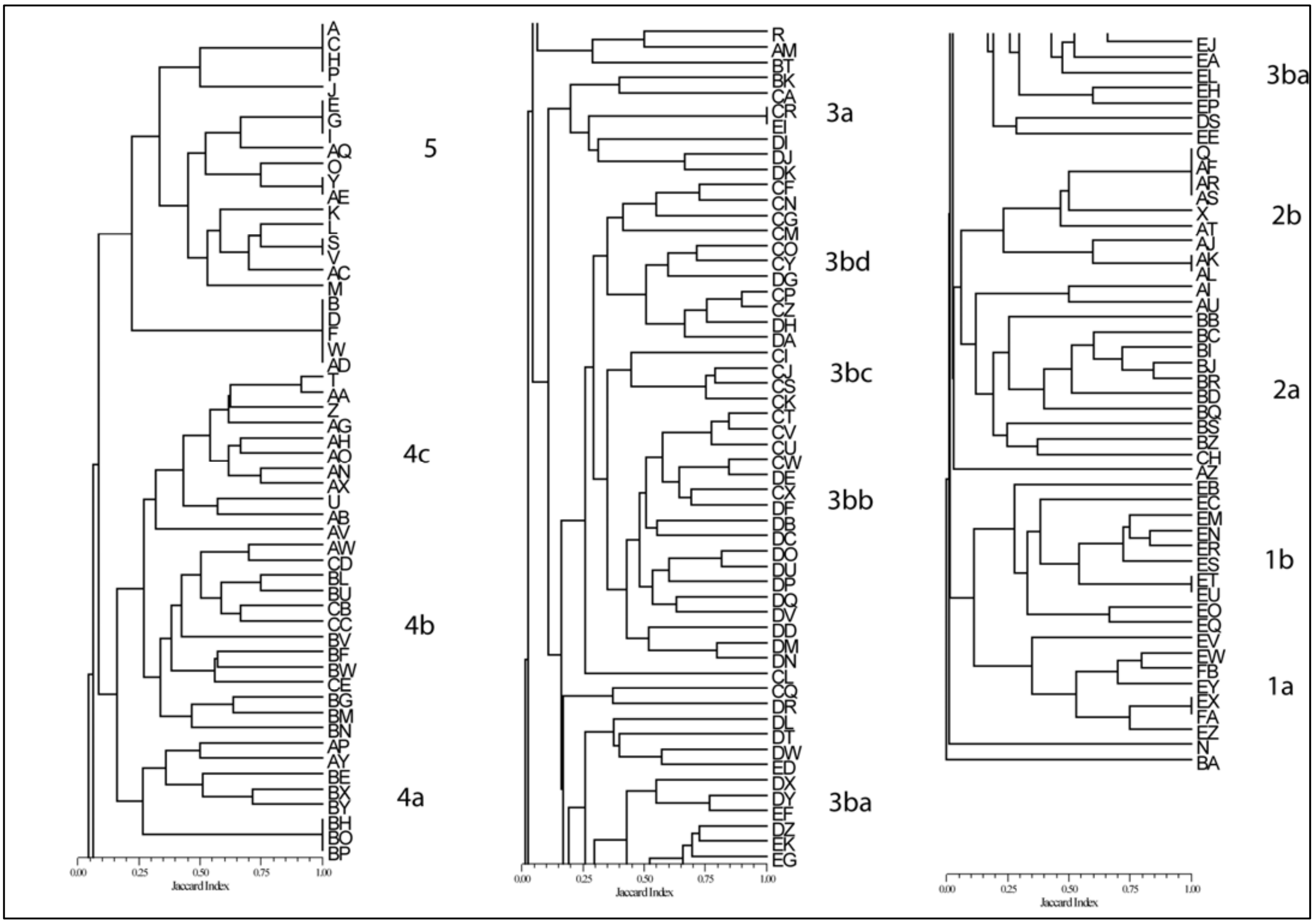
11

Figure 3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AW
CD
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BU
CB
CC
BV
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CE
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AP
AY
BE
BX
BY
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5
4c
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4a
0.00
0.25
0.50
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Jaccard Index
R
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CF
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CY
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CP
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CQ
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DT
DW
ED
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EF
DZ
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3a
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3bb
3ba
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0.75
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Jaccard Index
EJ
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EH
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DS
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Q
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AR
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X
AT
AJ
AK
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AI
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BJ
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BS
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CH
AZ
EB
EC
EM
EN
ER
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EO
EQ
EV
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FB
EY
EX
FA
EZ
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1a
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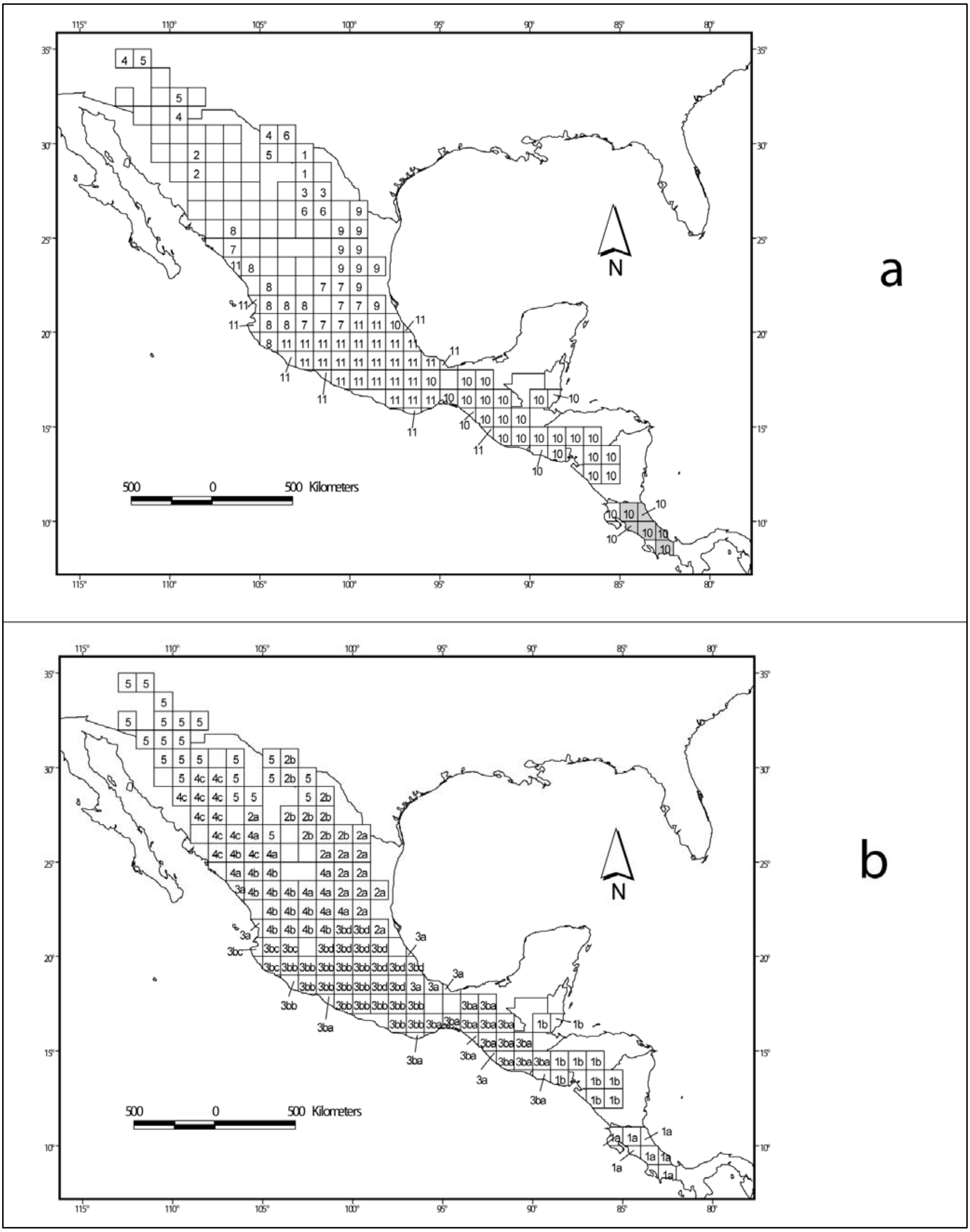
0.75
1.00
Jaccard Index

Figure 4


a
b
115°
110°
105°
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85°
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35°
30°
25°
20°
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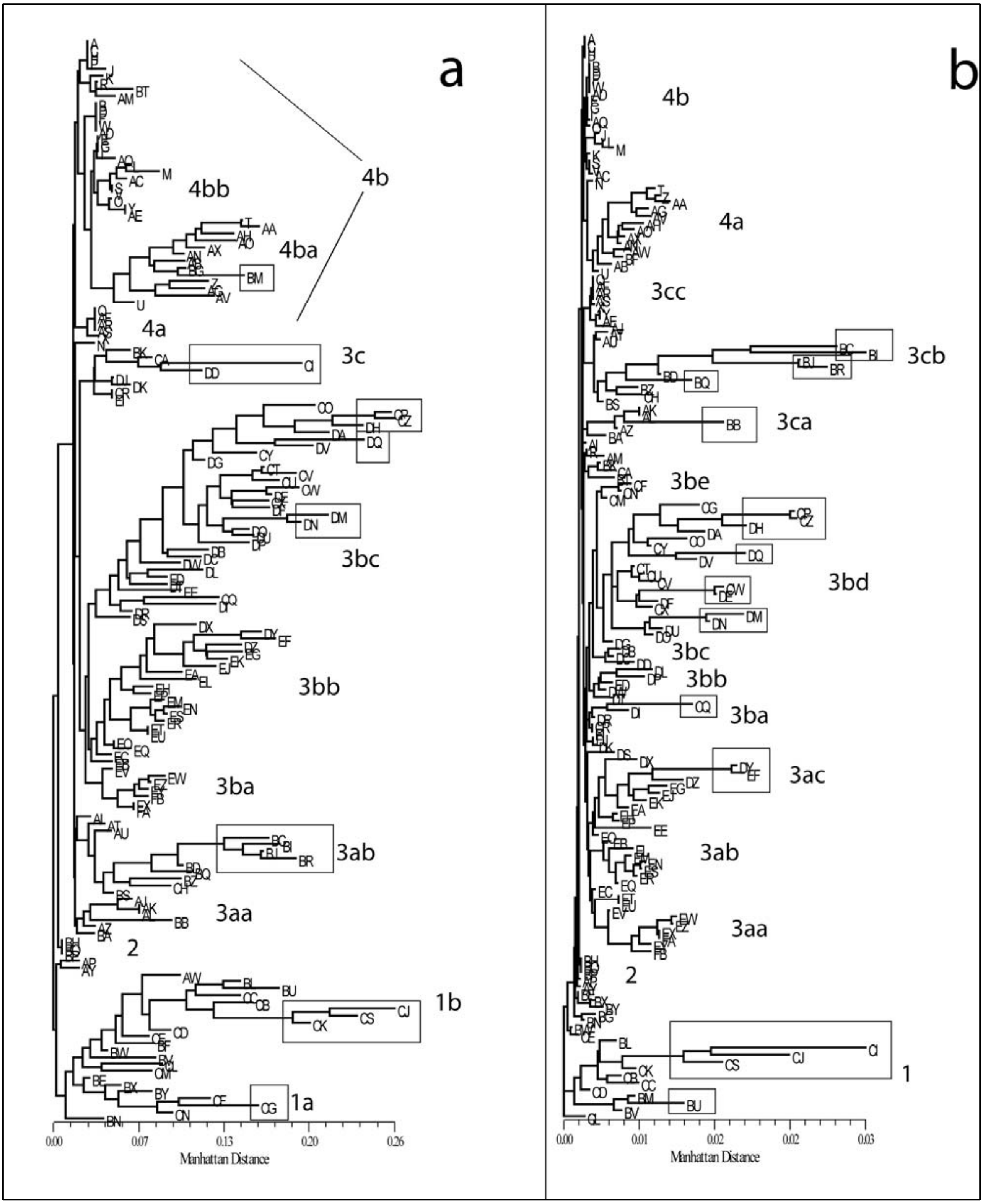
10°
N
500 0 500 Kilometers

Figure 5


a
4b
4bb
4ba
4a
3c
3bc
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3ba
3ab
3aa
2
1b
1a
0.00
0.07
0.13
0.20
0.26
Manhattan Distance
b
4b
4a
3cc
3cb
3ca
3be
3bd
3bc
3bb
3ba
3ac
3ab
3aa
2
1
0.00
0.01
0.01
0.02
0.02
0.03
Manhattan Distance

Figure 6

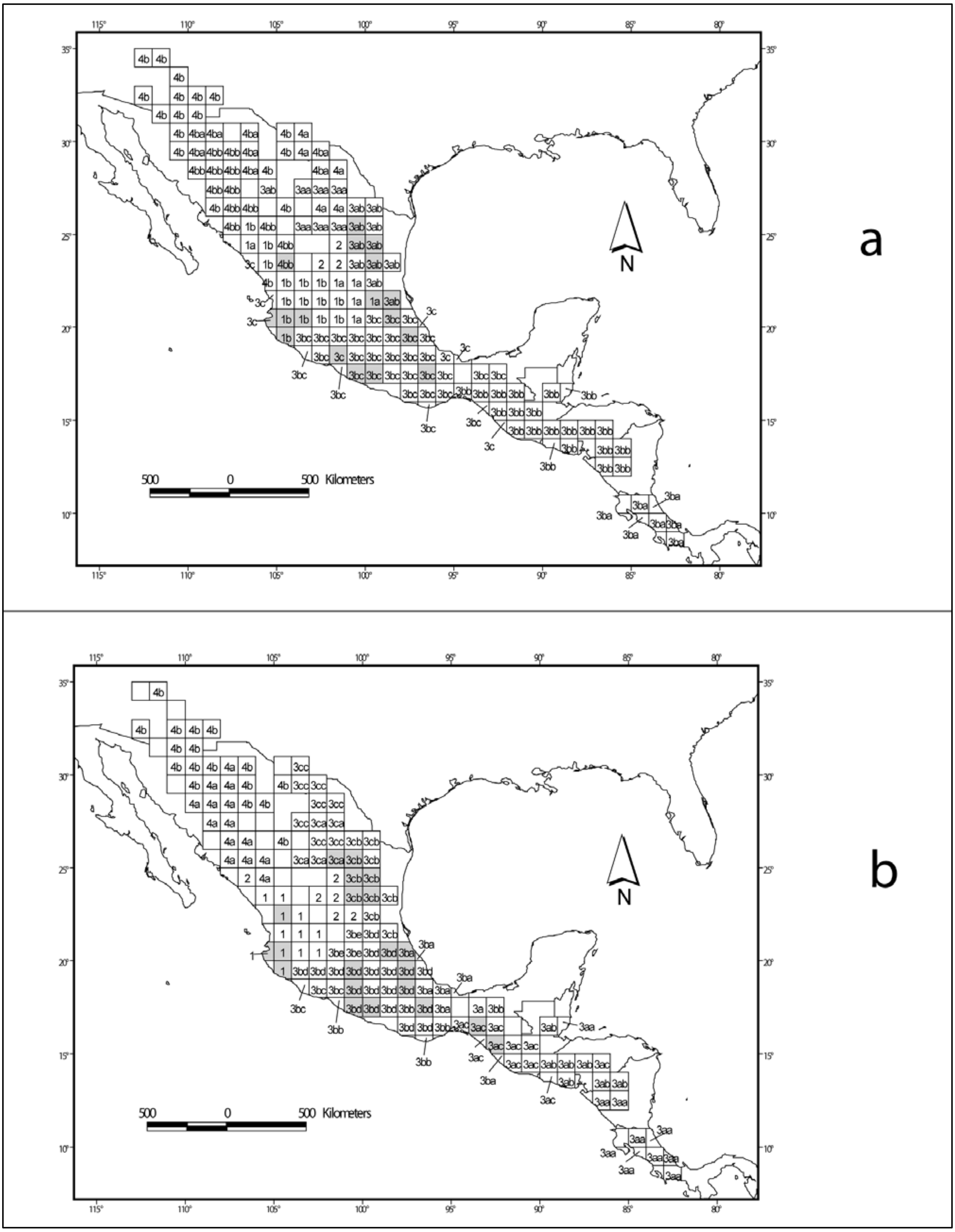
a
b
N
500 0 500 Kilometers
115°
110°
105°
100°
95°
90°
85°
80°
35°
30°
25°
20°
15°
10°

Figure 7

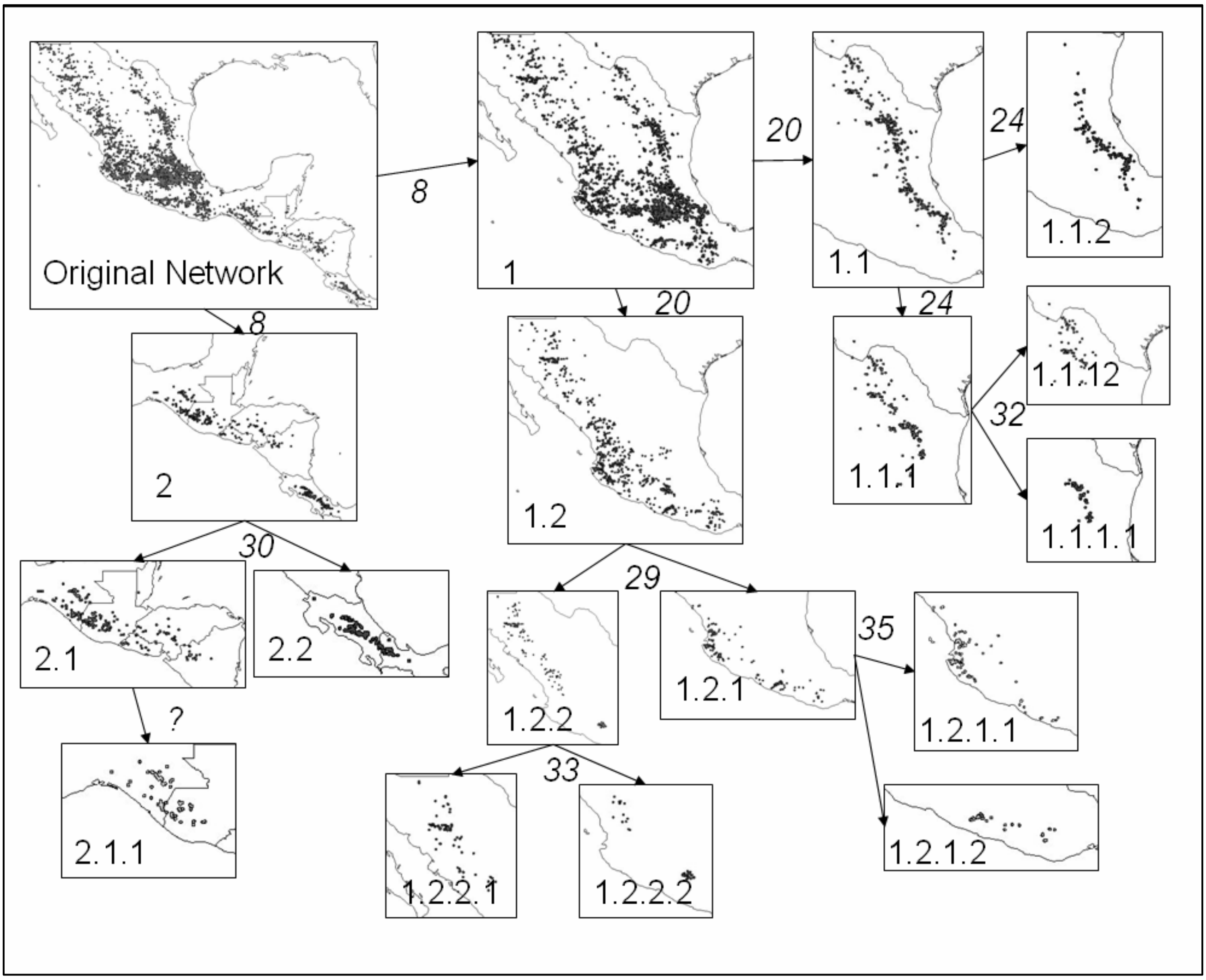
Original Network
8
1
20
1.1
24
1.1.2
8
2
20
1.2
24
1.1.12
32
1.1.1
1.1.1.1
30
2.1
2.2
29
1.2.2
1.2.1
35
1.2.1.1
?
2.1.1
33
1.2.2.1
1.2.2.2
1.2.1.2

Figure 8

Capítulo II

Torres-Miranda, A., Luna, I. & Oyama, K. 2009. Conservation biogeography of red oaks (Quercus L., section Lobatae) in Mexico and Central America. (por enviarse a *Biological Conservation*).

Conservation biogeography of red oaks (*Quercus* L., section *Lobatae*) in Mexico and Central America

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ABSTRACT

Patterns of richness and endemism of 75 red oak species (*Quercus* L., section *Lobatae*) were analyzed for Mexico and Central America. Patterns of distribution were analyzed using three different units: political divisions, floristic provinces, and grid-cells of 1° x 1° latitude/longitude. Two complementarity algorithms based on species richness and three algorithms based on species rarity were used to identify important areas for red oak conservation. Thirteen areas for red oak conservation were established using the aforementioned criteria, nine of them located within Natural Protected Areas (NPAs). We propose to extend the land coverage of the current NPAs and to create new ones based on the results of this study allowing *ca*. 2 million ha of cloud, oak, and pine-oak forests to be conserved.

Keywords: Conservation biogeography, areography, endemic species, Mesoamerica, oaks, *Quercus*, rarity, species diversity.

1. Introduction

The application of biogeographical principles to problems concerning the conservation of biodiversity has emerged as a new domain in the interface between biogeography and conservation biology (Whittaker et al., 2005). Conservation biology faces several challenges when identifying priority areas that incorporate biological and environmental patterns and process. Groups of species representative of some ecosystems could be useful as potential indicators for conservation assessments.

Areography is defined as the study of the distributional areas of taxa (Rapoport, 1975; Rapoport and Monjeau, 2001). These studies can offer information about areas of faunal and floristic richness and endemism in a country or continent, and may also contribute to the delimitation of biogeographic regions. With this approach, it is possible to generate useful information about several aspects of the geographical distribution of organisms in different areas, and to detect important areas for conservation.

The main goal of systematic conservation planning is the selection of areas that can act as reserves for species, populations, biological assemblages, and ecosystems. This objective has been reached using different tools designed to select areas that fulfill three fundamental criteria: complementarity, irreplaceability, and vulnerability (Kirkpatrick, 1983; Vane-Wright et al., 1991; Csuti et al., 1997; Margules et al., 2002; Margules and Pressey, 2000; Sarkar et al., 2006).

The genus *Quercus* is one of the most important woody floristic elements in the Northern Hemisphere, with 500-600 species in Asia, Europe, North and Central

America (Manos et al. 1999; Manos and Stanford 2001). The genus *Quercus* is divided in two subgenera, *Cyclobalanopsis* and *Quercus* (Manos et al., 1999, 2001). The subgenus *Quercus* is divided in four sections: *Quercus s.s.* (white oaks), *Lobatae* (red and black oaks), *Protobalanus* (intermediate or golden oaks), and *Cerris* (Nixon, 1993a; Manos and Stanford, 2001). The section *Quercus s.s.* has the widest geographic distribution occurring in Europe, Asia and the Americas. The sections *Lobatae* and *Protobalanus* are only present in the Americas, and the section *Cerris* is distributed throughout Europe, Asia and north of Africa. The recognized richness of extant species of the genus *Quercus* indicates the occurrence of two main centers of genus diversification in southeastern Asia and Mexico (Manos et al., 1999; Valencia, 2004).

In the Americas, oaks occur in many temperate and relatively dry 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, small or large trees. Oaks play a major ecological role as dominant species and diverse mutualistic associations involving 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) have been found. Oak forests are also involved in the maintenance of the diversity of other organisms including vertebrates (Brawn, 2006), arthropods (Tovar-Sánchez et al., 2003; Tovar-Sánchez and Oyama, 2006a), and epiphytes (Holz and Gradstein, 2005), among others.

Most estimates of Mexican *Quercus* have considered species diversity to be high, representing from 25 to 35% of the total species in the world (Table 1). In Mexican temperate forests, oaks form dense stands that account for more than 15% of the country’s plant cover (Rzedowski, 1978; Challenger, 1998). Recently, Valencia (2004) reported 161 species for Mexico: four golden (*Protobalanus*), 81 white

(*Quercus*) and 76 red (*Lobatae*) oaks. For Central America, Nixon (2006) cited nine species in Belize, 25-26 in Guatemala, 8-10 in El Salvador, 14-15 in Honduras, 14 in Nicaragua, 14 in Costa Rica, and 12 in Panama (Table 1).

Some Mexican oak species cause taxonomic problems due to their high morphological variability, which encompasses characteristics of more than one species (Romero et al., 2000a; Valencia, 2005; Mora, 2006; Nixon, 2006; Uribe-Salas et al., 2008). Oaks have a great ability to hybridize between species, yielding intermediate forms between those of the parental species (Whittemore and Schaal, 1991; Bacon and Spellenberg, 1996; Petit et al., 2003; Dodd and Afzal-Rafii, 2004). However, studies of Mexican oaks indicate that hybrids can be clearly differentiated from putative parental species by diagnostic morphological and molecular characteristics. This is the case for the *Q. laurina*-*Q. affinis* complex (González-Rodríguez et al., 2004a, b, 2005; González-Rodríguez and Oyama, 2005), the *Q. crassifolia*-*Q. crassipes* complex (Tovar-Sánchez and Oyama, 2004; Tovar-Sánchez et al., 2008), and the subsection Racemiflorae (*Q. conzattii*, *Q. urbanii*, *Q. radiata* and *Q. tarahumara*) (McCauley et al., 2007).

The section *Lobatae* (red oaks) is endemic to the New World; members of this section are most abundant in the mountains of Mexico and Central America. The section *Quercus* (white oaks) is represented both in humid and dry-arid areas, with a wider distribution (González-Rivera, 1993; Nixon, 1993b; Zavala, 1998; Valencia, 2004). Red oaks are mainly distributed in the western, southern and southeastern areas of Mexico, which are considered to be the humid parts of the country (Nixon, 1993b; Zavala, 1998).

We consider red oaks as a suitable model for the study of the biogeography of 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). The MTZ is a complex zone where Nearctic and Neotropical faunas superimpose; it includes the montane areas of the southwestern United States, Mexico and almost all Central America.

In this study, the section *Lobatae* of the genus *Quercus* is used to define areas of biological importance for conservation. 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. In order to determine the most important areas for red oak conservation, a complementarity analysis was performed based on species richness and species rarity. We also compared the priority areas for conservation of red oaks of Mexico and Central America derived from this study with the current protected natural areas in these countries following the outlines of the systematic conservation planning (Margules and Pressey, 2000) to propose new areas for the protection of red oaks in Mexico and Central America. In this way, we attempt to answer the following questions: Do current Natural Protected Areas (NPAs) really serve to protect target species and are they sufficient? Which NPAs can be extended in coverage to efficiently protect species and forest stands? Which criteria can be used to propose new NPAs for species protection?

2. Materials and methods

2.1. Distributional data and recognition of species

Distributional data for 75 red oak species from Mexico and Central America were obtained from a review of herbarium specimens deposited 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, as 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 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. Thus, we had a database composed of 70 species of red oaks for Mexico. Seventeen species are registered for Central America, and five of them are exclusive to this region: *Q. costaricensis*, *Q. gulielmi-trealeasi*, *Q. hondurensis*, *Q. rapurahuensis*, and *Q. seemanni*. In addition, reviews, monographs, and floristic studies were reviewed (Muller, 1942, 1951; Martínez, 1951, 1953, 1954, 1959, 1965, 1966, 1974; Standley and Steyermark, 1952; McVaugh, 1974; Burger, 1977; Espinosa, 1979; Valdéz 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, and distributional maps for each of the 75 species were obtained using GIS ArcView ver. 3.2 (ESRI, 1999).

2.2. Biogeographic analysis

The biogeographic analysis was performed using three different units:

1) We used political divisions of Mexico and the countries of Central America as follows: states for Mexico, districts for Belize, provinces for Costa Rica and

Panama, and departments for Guatemala, El Salvador, Honduras, and Nicaragua (Fig. 1a).

2) 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 the following floristic provinces: (i) California, (ii) Sierra La Laguna, (iii) northern Altiplano Mexicano, (iv) southern Altiplano Mexicano, (v) Tamaulipas, (vi) Sierra Madre Oriental, (vii) Sierra Madre Occidental, (viii) Serranías Meridionales, (ix) Valle de Tehuacán-Cuicatlán, (x) Depresión del Balsas, (xi) Sierra de los Tuxtlas, (xii) Planicie Costera del Golfo, (xiii) Planicie Costera del Pacífico, (xiv) Serranías Transístmicas, and (xv) Sierra de Talamanca. A same biogeographic framework was earlier tested by Contreras-Medina et al. (2007) for gymnosperms, but in this work we also undertook an additional analysis, dividing three of the provinces of Rzedowski (1978) previously considered as non-monophyletic (sensu Luna et al., 1999; Morrone, 2005). These areas were: the Sierra Madre Oriental divided into three different parts: (vi-a) northern (specifically Sierra Plegada), (vi-b) central and (vi-c) southern; the Sierra Madre Occidental in two parts: (vii-a) north-central and (vii-b) southern; and the Serranías Meridionales in six parts: (viii-a) Faja Volcánica Transmexicana, (viii-b) Sierra Madre del Sur, (viii-c) Jalisco, (viii-d) Guerrero, (viii-e) Oaxaca, and (viii-f) Isthmus (Fig. 1b).

3) We decided to use grid-cells to analyze same-size units as Mexican and Central American political divisions and provinces have different sizes. The distribution of the 75 red oak species was analyzed using 183 grid-cells of 1° x 1° latitude/longitude (Fig. 1c).

2.3. 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 dividing the number of species present in one area by the total number of species considered (in our case 75 species). 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 '0' for all other units; if one species was found in two units, its score was '0.5', in three units was '0.33', and so on. We then 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 distribution, but this index is correlated more with richness than endemism, as 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 distribution [corrected weighted endemism of Crisp et al. (2001)]. To obtain the corrected weighted endemism index, the weighted endemism index was divided 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 the first index are considered as centers of richness and in the second index as centers of endemism. Units values for both indices ranged from 1 to 10 (Table 2).

2.4. Complementarity analysis and conservation

A complementarity analysis to determine the richest areas in species and endemism was also conducted with the objective of preserving the majority of species in minimal spaces (Vane-Wright et al., 1991; Margules and Pressey, 2000; Margules et al., 2002; Sarkar et al., 2006). This analysis allowed us to determine the importance of each political division, floristic province or grid-cell in the conservation of red oaks, identifying the minimum number of areas where maximum biological diversity was found.

Complementarity consists of the selection of two or more areas with the highest number of critical species (Vane-Wright et al., 1991). The first area contains the highest number of endemic species, and the second the highest number of endemic species (as well as non endemic species) non present in the first area, using an iterative algorithm (Kirkpatrick, 1983). The complementarity value of a pair of areas is given by the number of species not shared between areas.

The complementarity of areas has been measured with two different types of algorithms: 1) richness-based in which the selection of areas is undertaken using criteria of species richness alone, selecting the first area as that with the highest number of species, and choosing the second area based on the high number of complementary species when compared with the first area; and 2) rarity-based in which selection of areas is undertaken using only the criteria of rarity of species, 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 (Margules et al., 1988; Vane-Wright et al., 1991; Csuti et al., 1997; Margules et al., 2002; Rodrigues and Gaston, 2002).

Five methods to calculate complementarity were used as criteria to prioritize the important areas for conservation of red oaks in Mexico and Central America; the first two were richness-based and the last three rarity-based. 1) In the first method, the areas with the highest species richness were selected using only a richness index. The area with the highest richness index was selected, and subsequently deleted from the matrix. This is an iterative method, so the richness indices were recalculated and the highest quotient for the remaining areas was obtained, selecting the area with the highest richness and the highest number of complementary species, until the 75 species included in the study for Mexico and Central America, were all found in the selected areas. 2) The second method was similar in process to the first, but was based on the weighted endemism index; the first priority area was selected as the one with the highest weighted endemism value. The species represented in that area were then deleted, and the index iteratively recalculated with the rest of the areas and species. 3) The third method considered as a priority those areas including species 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. 4) The fourth method prioritized areas that contained species with restricted distributions, using the higher weighted endemism index. Finally, 5) the fifth method prioritized areas based on the highest corrected weighted endemism index, with the goal of detecting areas that adhere to species irreplaceability criteria, as the corrected index leaves out richness bias.

Based on the above analyses, we selected important areas for conservation using endemism and richness criteria for Mexican and Central American red oaks, focusing on three different goals: 1) determining the states/districts/departments/provinces richest in species and endemism; 2) determining the floristic provinces richest in both parameters combined; and 3) finding grid-cells with species restricted to a single one; in this case, endemics are considered as narrow endemics. Based on the above criteria, we can solidly propose conservation areas based on the present-day distribution of red oaks.

3. Results

3.1. Political division analysis

In this study, we considered 75 species of red oaks for Mexico and Central America based on available herbarium specimens and published scientific reports. From this information, 58 (77.3%) red oak species were endemic to Mexico and 5 (6.6%) to Central America. Table 2 shows that richness indices near 0 represent localities with a smaller number of species, while values near 1 represent areas with high species richness. Following these indices, the richest Mexican states with respect to red oak species were Jalisco (0.34667 richness index, 26 species), Oaxaca (0.32 index, 24 species), Veracruz and Hidalgo (0.2533 index, 19 species each), Chiapas, Nuevo León and Puebla (0.22667 index, 17 species each), and Chihuahua and Durango (0.2133 index, 16 species each). Mexican states with fewer species were Baja California Sur (one species, 0.0133), Baja California Norte (two species, 0.0267), Aguascalientes, Colima and Morelos (six species each, 0.08), and Distrito Federal and Tlaxcala (seven species each, 0.0933). 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 (0.1733), followed by El Salvador, Honduras and Nicaragua with six species each (0.08). In Costa Rica and Panama five species (0.0667) were registered, and in Belize only two species (0.0267) were registered. The Francisco Morazán department of Honduras was the richest subregion with six (0.0667) 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.

The weighted endemism values showed the highest value for Jalisco state (6.59), followed by Nuevo León (6.04). 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. Veracruz and Puebla had indices with intermediate values. For the Central American countries, San José and Alajuela provinces in Costa Rica, as well as Chimaltenango department in Guatemala and Francisco Morazán department in Honduras, showed the highest values of weighted endemism (Fig. 2b).

The Mexican states that included endemic species were Baja California Sur with *Quercus devia* and Baja California Norte with *Q. agrifolia* and *Q. peninsularis*. A second important group was integrated by Nuevo León with two exclusive species (*Q. tenuiloba* and *Q. graciliramis*) and six semi-restricted species (species shared with a neighbor state) (*Q. canbyi*, *Q. flocculenta*, *Q. galeanensis*, *Q. hintonorum*, *Q. miquihuanensis*, and *Q. saltillensis*), and Coahuila with one exclusive species (*Q. coahuilensis*) and four semi-restricted species (*Q. flocculenta, Q. gravesii*, *Q. hintonorum*, and *Q. saltillensis*). A third group was formed by the state of Jalisco with two endemic species (*Q. cualensis* and *Q. tuitensis*) and three semi-restricted species (*Q. iltisii*, *Q. radiata* and *Q. urbanii*) (Fig. 2c). In Central America, the department of Huehuetenango in Guatemala and the province of Cartago in Costa Rica had the highest values of corrected weighted endemism. Costa Rica had two endemic species, *Q. costaricensis* and *Q. gulielmi-trealeasi*, and a semi-restricted one, *Q. seemannii*.

3.2. Floristic province analysis

The species richness analysis of the Mexican floristic provinces showed that the highest red oak diversity was concentrated in the Serranías Meridionales (37 species) and the Sierra Madre Oriental (35 species). The Sierra Madre Occidental, the southeastern part of the Altiplano Sur, the Planicie Costera del Pacífico and the Valle de Tehuacán-Cuicatlán were secondary richness zones in Mexico.

In Mexico, seven species were endemic to the Sierra Plegada: *Q. flocculenta, Q. galeanensis, Q. graciliramis, Q. hintonorum, Q. miquihuanensis, Q. saltillensis,* and *Q. tenuiloba,* and two semi-restricted: *Q. canbyi* and *Q. coahuilensis.* Also, *Q. gravesii* an endemic to the Altiplano Norte, can be added to this list as it was found in the irregular montane areas of Coahuila that are remnants of the Sierra Plegada. In the southern Sierra Madre Oriental, only one species was endemic and one semi-restricted: *Q. hirtifolia* and *Q. acherdophylla*, respectively. Five species were endemic to the Serranías Transístmicas: *Q. acatenangensis, Q. crispipilis, Q. duratifolia, Q. hondurensis* and *Q. paxtalensis* and one semi-restricted species, *Q. benthamii*. Five species were endemic to northern Sierra Madre Occidental: *Q. albocincta, Q. durifolia, Q. macvaughii, Q. radiata* and *Q. tarahumara*. Three species were endemic to the Serranías Meridionales of Jalisco: *Q. cualensis, Q. iltisii* and *Q. tuitensis* and two species to the California province: *Q. agrifolia* and *Q. peninsularis*. Sierra Madre del Sur also had two endemic species: *Q. grahami* and *Q. rubramenta*. One endemic species was found for Sierra La Laguna: *Q. devia,* and one species for Depresión del Balsas: *Q. hintonii.* Weighted endemism index values showed the highest value for the Sierra Madre Oriental province followed by the Serranías Meridionales and the Sierra Madre Occidental. For Central America, three species were found to be endemic to the Sierra de Talamanca: *Q. costaricensis, Q. gulielmi-trealeasi* and *Q. seemannii*.

The corrected weighted endemism index showed the highest value for Sierra La Laguna in Baja California Sur due to the restricted distribution of *Q. devia*. The Sierra de Talamanca also had a high value due to the occurrence of three endemic species: *Q. costaricensis, Q. gulielmi-trealeasi,* and *Q. seemannii*. The California region also had high values by the presence of two exclusive species: *Q. peninsularis* and *Q. agrifolia*. A third group with five endemic species each is formed by the Sierra Madre Occidental (*Q. albocincta*, *Q. durifolia*, *Q. macvaughii, Q. radiata* and *Q. tarahumara*) and the Serranías Transístmicas (*Q. acatenangensis, Q. crispipilis*, *Q. duratifolia*, *Q. hondurensis* and *Q. paxtalensis*).

When we analyzed species richness with the Sierra Madre Oriental, the Sierra Madre Occidental and the Serranías Meridionales divided into different sections (see methods), the areas richest in species were: Serranías Meridionales of Jalisco (24 species), southern Sierra Madre Oriental (21 species), Sierra Madre del Sur (20 species), southern Altiplano and Valle de Tehuacán-Cuicatlán (19 species each), and the Planicie Costera del Pacífico (18 species). A group with intermediate species richness was found in the northern Sierra Madre Oriental and in the Serranías Transístmicas with 16 species each (Fig. 3a).

The highest value of weighted endemism index (Fig. 3b) was found in the northern Sierra Madre Oriental, followed by the Serranías Transístmicas, and nor-central Sierra Madre Occidental. The Serranías Meridionales of Jalisco and the Sierra Madre Occidental had secondary importance, as did the Sierra Madre del Sur and the southern Sierra Madre Oriental. The Pacific coast had an intermediate weighted endemism index value.

Corrected weighted indices (Fig. 3c) were the highest in the California region and Sierra de la Laguna as well as in the Sierra de Talamanca in Central America.

Other important areas are located in the northern Sierra Madre Oriental, Sierra Madre Occidental and Serranías Transístmicas.

3.3. Grid-cell analysis

Grid-cell analysis showed two centers of species richness, with one located in the west in the Serranías Meridionales of Jalisco (0.30667 richness index, 23 species), and the other in the east where the Sierra Madre Oriental converges with the Sierra Madre del Sur (0.20667 index, 20 species) (Fig. 4a). Areas with secondary importance in terms of species richness include the Faja Volcánica Transmexicana, northern Sierra Madre Oriental, southern Sierra Madre Occidental, Sierra Madre del Sur and part of the Serranías Transístmicas, strictly in the Sierra Madre de Chiapas and the volcanic chains of Guatemala, all located in the Mexican Transition Zone.

The northern part of the Sierra Madre Oriental and the Serranías Meridionales of Jalisco had the highest weighted endemism indices. The southern Sierra Madre Oriental at its border with the northern Sierras of Oaxaca was of secondary importance zone; as were the Sierra Madre del Sur and the Sierra Madre de Chiapas and the volcanic chains of Guatemala (included in the Serranías Transístmicas), as well as a smaller part of the southern extreme of the Sierra Madre Occidental (Table 2, Fig. 4b).

Corrected weighted endemism index values showed that the Sierra La Laguna was the site with most restricted species distribution. A secondarily important area was located in the northern part of the Sierra Madre Oriental, specifically in the Sierra Plegada that continues through the northern Altiplano. A third important area corresponded to the Serranías Meridionales of Jalisco (Fig. 4c). In Central America, the most important area was found in the Sierra de Talamanca, with the highest values of corrected weighted endemism occurring due to the presence of three endemic species: *Quercus costaricensis, Q. gulielmi-treleasi* and *Q. seemanii*. Another important area was found in northwestern Honduras, in the central Chortis plateau, and in the western part of the Sierra de Comayagua; the Sierra Madre de Chiapas-Guatemala also had a relatively an high index value.

3.4. Complementarity

Complementarity analysis was undertaken considering political divisions, floristic provinces, and grid-cells with determinations based on species richness and weighted endemism (Table 3). For complementarity species richness-based and complementarity species rarity-based, weighted endemism and corrected weighted endemism were considered (Table 4). In all cases, complementarity analysis showed 12 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 five algorithms used, 12 Mexican states were defined as high priority for red oak conservation: Jalisco, Nuevo León, Chiapas, Hidalgo, Coahuila, Chihuahua (Sonora), Baja California Norte, Baja California Sur, Guerrero (Oaxaca) and Estado de México.

The complementarity analysis based on richness and weighted endemism index prioritized the states of Jalisco, Nuevo León and Chiapas, followed by the states of Baja California Sur, Estado de México and Coahuila (Table 3). According to the species rarity complementarity algorithm and corrected weighted endemism index, the most important states for conservation were Baja California Norte, Baja California Sur, Coahuila, Nuevo León, Jalisco and Estado de México, followed by Chiapas, Hidalgo, Chihuahua, and Guerrero. In Central America, the provinces of San José and Alajuela in Costa Rica, the region that includes the departments of Comayagua, Francisco Morazán, La Paz and Yoro in Honduras, Nueva Segovia and Matagalpa in Nicaragua, Chiquimula and Zacatepequez in Guatemala, and the district of Cayo in Belize were considered to be of high priority (Table 4).

The complementarity analysis divided by floristic provinces showed nine important areas for red oak conservation: Sierra Madre Oriental, Serranías Meridionales, Serranías Transístmicas, Sierra Madre Occidental, Sierra de Talamanca, California, Depresión del Balsas, Sierra La Laguna, and Altiplano Norte, in order of importance (Tables 3 and 4). All analyses gave similar results, with the exception of the analysis based on rarity using the corrected weighted index that gave a different order of importance: Sierra La Laguna, Sierra de Talamanca and California, followed by the Depresión del Balsas, the Sierra Madre Occidental and the Serranías Meridionales (Table 4).

When we considered separate sections within the Sierra Madre Oriental, Sierra Madre Occidental and Serranías Meridionales, the analysis showed eleven key units for red oak conservation: in order of importance, northern Sierra Madre Oriental (Sierra Plegada), Serranías Transístmicas, north-central Sierra Madre Occidental, Serranías Meridionales of Jalisco, southern Sierra Madre Oriental (Hidalgo-Oaxaca), Sierra de Talamanca, California, Sierra Madre del Sur, Depresión del Balsas, Sierra La Laguna and Altiplano Norte (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 Sierra Plegada, Serranías Transístmicas, and Sierra Madre Occidental; for the fifth algorithm the three priority areas were Sierra La Laguna, California and Sierra de Talamanca.

Finally, the complementarity analysis generated 34 priority grid-cells, which composed 11 areas of importance for red oak conservation. These eleven priority areas were: California, Sierra La Laguna, northern Sierra Madre Occidental (bordering the states of Chihuahua and Sonora), southern Sierra Madre Occidental (in the southern part of the state of Durango), Serranías Meridionales of Jalisco (in the central part of the state), northern Sierra Madre Oriental (Sierra Plegada and its continuation as isolated patches through the Altiplano Norte), southern Sierra Madre Oriental (in the adjacent parts of Hidalgo, Puebla and Veracruz), Depresión del Balsas (in the southwestern extreme of the state of Mexico), Sierra Madre del Sur of Guerrero, Serranías Transístmicas, and Sierra de Talamanca (Fig. 5c). Priority varied depending on the algorithm used, but the three areas that appeared as priorities in the majority of the cases were the Sierra Plegada, Serranías Meridionales of Jalisco and southern Sierra Madre Occidental, with the exception of the fifth algorithm that gave Sierra La Laguna, Serranías Meridionales of Jalisco, and Sierra Plegada of Nuevo León as priority areas.

4. Discussion and conclusions

4.1. Patterns of richness and endemicity

Quercus is the most diverse genus of trees and shrubs in Mexico (Villaseñor, 2004). Most of the species diversification of red oaks occurred in Mexico, with a lesser amount occurring in Central America and only one species, *Quercus 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 altitudinally and latitudinally (Axelrod, 1975; Hooghiemstra, 2006).

It is important to emphasize the importance of conducting conservation biogeography using different units of analysis. In the case of megadiverse countries like Mexico and some countries of Central America, conservation decisions are undertaken considering political boundaries, rather than natural criteria. Political divisions are used because conservation policies are implemented independently by each country or even in some by each state (Dávila-Aranda et al., 2004). Floristic provinces represent natural regions with a common geological origin; those used in this study were very useful and can be proposed as a biogeographic framework for future studies on the conservation biogeography on Mexican and Central American species. The grid-cell units provide 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).

Previous studies on Mexican oaks never have intended to show the different patterns of richness and endemism of this group of vascular plants (e.g. González-Rivera, 1993; Zavala, 1998; Nixon, 2003b; Valencia, 2004), and only included the part corresponding to the richness and endemism of political divisions. Our study is the most comprehensive in terms of herbarium specimens and bibliographic information compiled, and it represents the most complete biogeographic analysis conducted until today.

The Faja Volcánica Transmexicana has been suggested as a bridge between the species of the north and west to the south (e.g., Delgadillo et al., 2003; Salinas-Moreno et al., 2004) and as region with a great diversity of species (Rzedowski, 1978; Fa and Morales, 1993). Our data did not support the hypothesis of a species rich area of red oaks (Zavala, 1998) for the Faja Volcánica Transmexicana. However, Tovar-Sánchez and Oyama (2004) suggested that the Faja Volcánica Transmexicana constitutes a hybrid zone where interspecific gene flow occur between oak species from the West and the East.

Endemism of red oaks is concentrated in the Mexican Transition Zone and in the Sierra de Talamanca. The Faja Volcánica Transmexicana lacks endemic species as well as the Serranías Meridionales of Isthmus and Guerrero. When we contrasted our analysis of provinces with the proposal of Rzedowski (1978), we also identified some patterns that were not revealed when the regions were considered as single units. As treated by Rzedowski (1978), the entire Serranías Meridionales includes six endemic red oak species; when we used floristic units and divided the Serranías Meridionales into six units, smaller-scale patterns were revealed, with the Serranías Meridionales of Jalisco including three endemic species (*Q. cualensis*, *Q. tuitensis* and *Q. iltisii*), the Sierra Madre del Sur including two endemic species (*Q. grahami* and *Q. rubramenta*) and one species represented in both Serranías (*Q. nixoniana*).

An inconvenience of endemic analysis is that the corrected weighted endemism index is only efficient when areas include only restricted-distribution species; thus, when areas include several species with wide distribution, i.e., the Serranías Meridionales of Jalisco, this index does not reflect the importance of species with restricted distribution. These factors gave odd results, i.e., the Serranías Meridionales of Jalisco with three restricted species, appeared to be of secondary importance to the Depresión del Balsas and California provinces, which have one and two species each.

Few studies have conducted on the species richness and endemism of red oaks in Central America, so there is a lack of data with which compare our results. Despite the decrease in species richness and endemism in this region as compared to Mexico, the ecological role and dominance of the genus in the montane forests of Central America is crucial, as documented by Kappelle et al. (1992) for the Sierra de Talamanca, Islebe (1996) for Guatemala, and Mejía and Hawkins (1995) for Honduras.

Following Contreras-Medina et al. (2007), we identified seven hotspots for red oaks based on areas with the highest average of endemism richness, weighted endemism and corrected weighted endemism species indices. These hotspots are, in order of importance, the following: 1) Serranías Meridionales of Jalisco, 2) Sierra

Plegada, (3) southern Sierra Madre Oriental-Sierra Madre del Sur in Oaxaca, 4) southern Sierra Madre Occidental, (5) Depresión del Balsas, (6) Sierra Madre del Sur of Guerrero, and (7) Sierra Madre de Chiapas.

4.2. Selection of areas for conservation based on richness and endemism of red oak species

In general, different units of analysis (i.e., political divisions, floristic provinces, and grid-cells) gave similar results. The four areas with the highest species richness were: 1) Serranías Meridionales of Jalisco, 2) southern Sierra Madre Oriental, 3) Sierra Norte de Oaxaca, and 4) Sierra Plegada. The Faja Volcánica Transmexicana is not a rich area for red oaks as many earlier works had suggested for other groups of organisms (e.g., Rzedowski, 1978; Fa and Morales, 1993). The weighted endemism index, which is an approximation of endemism found in an area that is influenced by the species richness, identified the following important areas: 1) Sierra Plegada, 2) southern Sierra Madre Oriental, 3) Serranías Meridionales of Jalisco, 4) Sierra Madre Occidental, and 5) Serranías Transístmicas. Finally, the corrected weighted endemism index (which eliminates the bias of richness and optimally reflects the importance of species with restricted distributions), showed that the most important areas were: 1) California, 2) Sierra La Laguna, 3) Sierra Plegada, 4) Serranías Transístmicas, and 5) Sierra de Talamanca.

To delimit important areas for red oak conservation, an intersection of the resultant polygons for the complementarity analysis was undertaken using political divisions, floristic provinces and grid-cells of 1° x 1°. Using this method, 10 priority conservation areas were recognized for Mexico and three for Central America, based both on total species richness and restricted distribution of species; this allowed us to redraw the polygons based in physiographic information (Fig. 6).

In terms of the implementation of systematic conservation planning (Margules and Pressey, 2000; Sarkar et al., 2006), we must conserve zones that have not been decreed as NPAs. Nine of the 13 important areas suggested in this study for red oak conservation are within zones with some type of protection; however, careful analysis of the localities of these red oaks reveals they are not necessarily found within the protected areas but rather in the vicinity. In Mexico, there are 14 areas with official protection that include red oaks (second column, Table 5).

The conservation biogeography approach focuses attention on range-restricted species (one form of rarity) as a conservation priority (Rodrígues and Gaston, 2002). The current Mexican and Central American NAPs protect 31 species of red oaks (41%), as well as 2,259,011 ha of the land inhabited by these species. Of this land, 63.19% belongs to Mexico, 1.91% to Guatemala, 6.33% to Honduras, and 28.57% to Costa Rica.

We propose to increase the coverage of the protected areas following the guidelines of the Priority Conservation Regions for Mexico (PCRM) (Arriaga et al. 2000), which include areas with high biodiversity and endemism rates. Uniting the PCRM guidelines with our results for red oak conservation areas, we propose that the coverage of 11 NPAs can be extended by 748,845 ha as suggested in Table 5 (fifth column).

We also propose 16 new areas covering 1,007,523 ha for the conservation of red oaks (Table 5, seventh and eighth columns) in sites that are not officially protected at this time. All these areas have been diagnosed as biologically and ecologically important for other groups of organisms and have been named as Priority Terrestrial

Regions (PTRs) by Arriaga et al. (2000). Many of these areas include cloud forests, which harbor a high biodiversity and are considered to be one of the most fragile ecosystems in Mexico and the Neotropics (Luna et al., 2006; Churchill et al., 1995; Hamilton et al., 1994). Zones with congruent distributions of red oaks and PTRs are mainly located in the southern Sierra Madre Oriental, Sierra Madre del Sur, Altos de Chiapas, Sierra Madre de Chiapas and Sierra de Comayagua; also, at the Sierra Plegada, the Serranías Meridionales of Jalisco and peripheral areas of the Depresión del Balsas where small fragments of cloud forests are located. It is of vital importance to study the extension and limits of the decreed NPAs and to propose new areas of conservation, not only for red oaks, but for the conservation of the ecosystems associated with this genus, including mixed forests, oak forests, pine-oak forests, coniferous forests, and cloud forests (Challenger, 1998).

With this proposal, the 75 species of red oaks of Mexico and Central America could be conserved, including those with restricted distribution. This will protect 748,845 ha of additional land if only current coverage increased, and nearly 1,007,523 if 16 new NPAs are created. In total, this covers 1,756,368 ha of temperate forests. In addition, for the case of red oaks in Mesoamerica, it is necessary to implement a general program of protection and conservation for the whole geographic range in order to preserve not only species richness and endemism but all biological processes that can occur at a large geographic scale. The response of forest species to global threats such as climatic changes, considered as the most serious threat to plant biodiversity (Malcolm et al., 2006), can only be studied at the global scales by focusing, for example, on the genetic basis of physiological responses of tree species distributed in different local climates (e.g., Hamrick, 2004; Scotti-Saintaigne et al., 2004; González-Martínez et al., 2006). Examples of evolutionary process frequently occur among oak species are hybridization, introgression, genetic assimilation, interspecific gene flow, and pollen swamping. 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 above do not necessarily occur in the main centres of species richness or endemism but in other geographic regions where species meet, increasing not species richness but genetic diversity by intensive gene flow (Tovar and Oyama, 2004; Tovar et al., 2008) or by promoting other biological process such as plant insect interactions (Tovar and Oyama, 2006a, b). In Mexico, an example of this is found in the Faja Volcánica Transmexicana, area with a low richness and endemism value, but that acts as a center of gene flow among species. Finally, deforestation rates for oak forests in Mexico ranged from 5,000 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 endemisms.

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Figure legends

Figure 1. Units used in biogeographic analysis: (a) Political division for Mexico, Guatemala, Belice, El Salvador, Honduras, Nicaragua, Costa Rica and Panama; (b) Floristic provinces used for red oaks based and modified from Rzedowski (1976), Takhtajan (1986) and Morrone (2001): (i) California; (ii) Sierra La Laguna; (iii) northern Altiplano Mexicano and (iv) southern Altiplano Mexicano; (v) Tamaulipas; (vi) Sierra Madre Oriental; (vii) Sierra Madre Occidental; (viii) Serranías Meridionales; (ix) Valle de Tehuacán-Cuicatlán; (x) Depresión del Balsas; (xi) Sierra de los Tuxtlas; (xii) Planicie Costera del Golfo; (xiii) Planicie Costera del Pacífico; (xiv) Serranías Transístmicas; and (xv) Sierra de Talamanca; and, (c) Grid-cells of 1° x 1° latitude/longitude.

Figure 2. Biogeographic analysis using political division: (a) Ranges of species richness in each states/districts/departments/provinces of Mexico and Central America; (b) Ranges of weighted endemism index; (c) Ranges of corrected weighted endemism index in each political division. Ranges can be consulted in Table 2.

Figure 3. Biogeographic analysis using floristic provinces: (a) Ranges for species richness in each floristic province; (b) Ranges for weighted endemism index value of each floristic province; (c) Ranges for corrected endemism index value of each floristic province. Ranges can be consulted in Table 2.

Figure 4. Biogeographic analysis using grid-cells of 1° x 1° latitude/longitude: (a) Ranges for species richness in each grid-cell; (b) Ranges for weighted endemism index

value in each grid-cell; (c) Ranges for corrected weighted endemism index value of each grid-cell. Ranges can be consulted in Table 2.

Figure 5. Prioritary areas based in complementarity: (a) Political division; (b) Floristic provinces; (c) grid-cells 1° x 1° latitude/longitude.

Figure 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) Serranía Meridional de Jalisco, (6) Sierra Plegada, (7) southern Sierra Madre Oriental, (8) Depresión del Balsas, (9) Sierra Madre del Sur, (10) Altos de Chiapas, (11) Sierra Madre de Chiapas, (12), Sierra de Comayagua, (13) Sierra de Talamanca.

Table 1. Number of oak species in Mexico and countries of Central America.

Country	**Number of species**	**Section *Lobatae***	**Section *Protobalanus***	**Section *Quercus***	**References**
Mexico	>200				Martínez (1951-1974)
	150-200				Rzedowski (1978)
	173-213				González-Rivera (1993)
	135 (150)	55	4	76	Nixon (1993)
	140	71	4	65	Zavala (1998)
	161	76	4	81	Valencia (2004)
	160-165				Nixon (2006)
Guatemala	24	12		12	Muller (1942)
	27	14		13	Standley & Steyermark (1952)
	25-26				Nixon (2006)
Belize	8	3		5	Muller (1942)
	9				Nixon (2006)
Honduras	13	6		7	Muller (1942)
	14-15				Nixon (2006)
El Salvador	8	4		4	Muller (1942)
	8-10				Nixon (2006)
Nicaragua	3	1		2	Muller (1942)
	12	6		6	Breedlove (2001)
	14				Nixon (2006)
Costa Rica	16	9		7	Muller (1942)
	12	6		6	Burger (1977)
	14				Nixon (2006)
Panama	9	4		5	Muller (1942)
	10	5		5	Muller (1960)
	12				Nixon (2006)

Table 2. Range values by political division, floristic provinces, and grid-cells obtained for richness index, weighted endemism and corrected weighted endemism of red oaks, ranged from 1 to 10.

RANGES FOR RICHNESS INDEX

	Political Divisions		Floristic Provinces		Grid-cells	
1	0.013333	0.046667	0.013333	0.044000	0.013333	0.042667
2	0.046667	0.080000	0.044000	0.074667	0.042667	0.072000
3	0.080000	0.113333	0.074667	0.105333	0.072000	0.101333
4	0.113333	0.146667	0.105333	0.136000	0.101333	0.130667
5	0.146667	0.180000	0.136000	0.166667	0.130667	0.160000
6	0.180000	0.213333	0.166667	0.197333	0.160000	0.189333
7	0.213333	0.246667	0.197333	0.228000	0.189333	0.218667
8	0.246667	0.280000	0.228000	0.258667	0.218667	0.248000
9	0.280000	0.313333	0.258667	0.289333	0.248000	0.277333
10	0.313333	0.346667	0.289333	0.320000	0.277333	0.306667

RANGES FOR WEIGHTED ENDEMISM

	Political Divisions		Floristic Provinces		Grid-cells	
1	0.032258	0.688118	0.285256	1.222802	0.022727	0.259009
2	0.688118	1.343977	1.222802	2.160348	0.259009	0.495292
3	1.343977	1.999837	2.160348	3.097894	0.495292	0.731574
4	1.999837	2.655696	3.097894	4.035440	0.731574	0.967856
5	2.655696	3.311556	4.035440	4.972985	0.967856	1.204138
6	3.311556	3.967415	4.972985	5.910531	1.204138	1.440420
7	3.967415	4.623275	5.910531	6.848077	1.440420	1.676702
8	4.623275	5.279134	6.848077	7.785623	1.676702	1.912984
9	5.279134	5.934994	7.785623	8.723168	1.912984	2.149266
10	5.934994	6.590853	8.723168	9.660714	2.149266	2.385549

RANGES FOR CORRECTED WEIGHTED ENDEMISM

	Political Divisions		Floristic Provinces		Grid-cells	
1	0.024642	0.068886	0.095085	9.095085	0.022727	0.047980
2	0.068886	0.113131	0.185577	9.185577	0.047980	0.073232
3	0.113131	0.157375	0.276068	9.276068	0.073232	0.098485
4	0.157375	0.201620	0.366560	9.366560	0.098485	0.123737
5	0.201620	0.245864	0.457051	9.457051	0.123737	0.148990
6	0.245864	0.290109	0.547543	9.547543	0.148990	0.174242
7	0.290109	0.334354	0.638034	9.638034	0.174242	0.199495
8	0.334354	0.378598	0.728526	9.728526	0.199495	0.224747
9	0.378598	0.422843	0.819017	9.819017	0.224747	0.250000
10	0.422843	1.000000	0.909509	9.909509	0.250000	1.000000

Table 3. Complementarity analysis richness-based. In the first column, the highest richness index was used as priority, deleting the species of the selected area and recalculating iteratively the index. In the second column, the weighted endemism area is the priority, and then are deleted the species present in the selected area and recalculating iteratively the index.

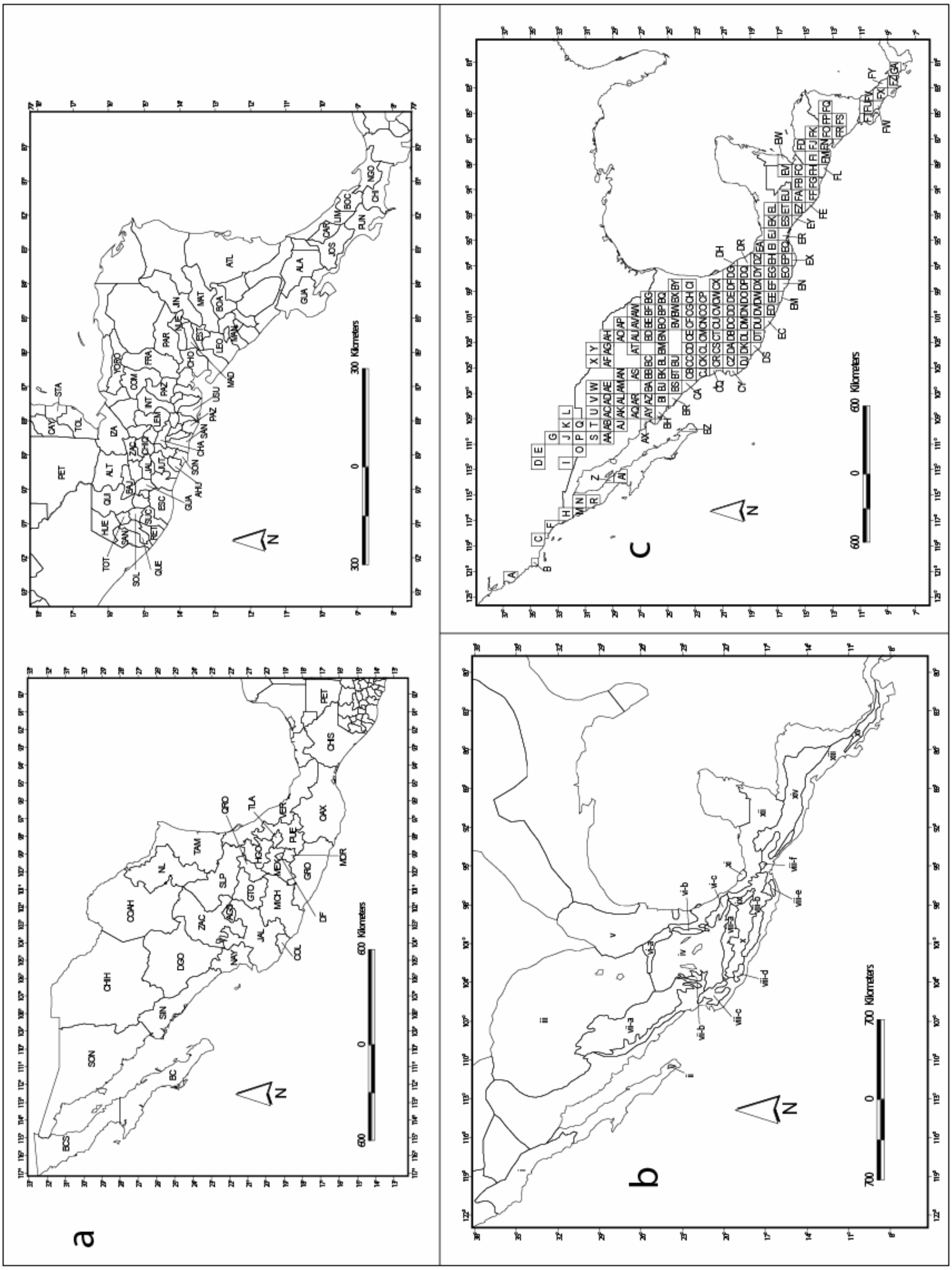
Complementarity for richness index in political divisions					**Complementarity for Weighted Endemism in political divisions**				
Order	AREA	Richness index	Additional species	All species	**Ord**	AREA	Weighted Endemism	Additional species	All species
1	JAL/MEX	0.360000	27	27	1	JAL/MEX	6.590853	27	27
2	NL/MEX	0.186667	14	41	2	NL/MEX	5.953968	14	41
3	CHIS/MEX	0.133333	10	51	3	CHIS/MEX	2.805723	10	51
4	HGO/MEX	0.080000	6	57	4	BC/MEX	2.000000	2	53
5	CHIH/MEX	0.080000	6	63	5	CHIH/MEX	2.000000	6	59
6	ALA,JOS/CR	0.053333	4	67	6	HGO/MEX	1.587302	6	65
7	OAX,GRO/MEX	0.026667	2	69	7	COAH/MEX	1.000000	1	66
8	BC/MEX	0.026667	2	71	8	MEX/MEX	1.000000	1	67
9	COAH/MEX	0.013333	1	72	9	BCS/MEX	1.000000	1	68
10	MEX/MEX	0.013333	1	73	10	ALA,JOS/CR	0.626190	4	72
11	BCS/MEX	0.013333	1	74	11	OAX,GRO/MEX	0.500000	2	74
12	CHIQ,ZAC/GUA; CAY/BEL; CHA,USU,MOR/SAL; FRA,COM,PAZ,YOR/HON; MAT,NUE/NIC	0.013333	1	75	12	CHIQ,ZAC/GUA; CAY/BEL; CHA,USU,MOR/SAL; FRA,COM,PAZ,YOR/HON; MAT,NUE/NIC	0.083333	1	75
Complementarity for richness index in floristic provinces					**Complementarity for Weighted Endemism in floristic provinces**				
1	SMJ	0.320000	24	24	1	SMORN	9.660714	16	16
2	SMORN	0.200000	15	39	2	STI	7.257118	16	32
3	STI	0.146667	11	50	3	SMJ	6.570635	18	50
4	SMORS	0.093333	7	57	4	SMOCC	5.000000	6	56
5	SMOCC	0.066667	5	62	5	SMORS	3.083333	6	62
6	TALA	0.040000	3	65	6	TALA	3.000000	3	65
7	SMS	0.040000	3	68	7	SMS	2.250000	3	68
8	BAL	0.026667	2	70	8	CALI	2.000000	2	70
9	CALI	0.026667	2	72	9	BAL	2.000000	2	72
10	ALTIN	0.026667	2	74	10	ALTIN	1.500000	2	74
11	LAGU	0.013333	1	75	11	LAGU	1.000000	1	75
Complementarity for richness index in grid-cells					**Complementarity for Weighted Endemism in grid-cells**				
1	CZ	0.306667	23	23	1	CY	2.385549	13	13
2	CH	0.160000	12	35	2	BW	2.150641	12	25
3	DQ	0.106667	8	43	3	DQ	1.482285	14	39
4	EZ	0.080000	6	49	4	EZ	1.088095	6	45
5	AK,AJ	0.066667	5	54	5	BZ	1.000000	1	46
6	FU,FX	0.053333	4	58	6	ED	0.790909	4	50
7	ED,EE	0.040000	3	62	7	CK	0.773779	7	57
8	A,H,R	0.026667	2	64	8	BO	0.750000	2	59
9	AU,AV	0.026667	2	66	9	CH	0.642857	2	61
10	DN,DV	0.026667	2	68	10	FU,FX	0.615909	4	65
11	BP	0.026667	2	70	11	DN,DV	0.500000	1	66
12	CY	0.013333	1	71	12	AK,AJ	0.463462	4	70
13	BZ	0.013333	1	72	13	A,H,R	0.309524	2	72
14	CC,CK,CL	0.013333	1	73	14	EK,ET,EU,FA,FF,FG	0.166667	1	73
15	EK,ET,EU,FA,FF,FG	0.013333	1	74	15	EV,FD,FH,FI,FJ,FO,FP	0.125000	1	74
16	EV,FD,FH,FI,FJ,FO,FP	0.013333	1	75	16	Y,AG,AH,AO,AP,AT,AU,AV,AW,B,	0.083333	1	75

Table 4. Complementarity analysis rarity-based. In the first column, the number inside the parenthesis indicates the number of areas in which are found the restricted species and number outside indicate how many endemic species in each area. In the second column, the priority criteria is the restricted species with the weighted endemism index. In the third column, the priority criteria used is the corrected weighted endemism index.

Complementarity for rarities species in political divisions					**Complementarity for Weighted Endemism in political divisions**					**Complementarity for Corrected Weighted Endemism in political divisions**				
Ord	AREA	Rarity*	Additional species	All species	**Ord**	AREA	Weighted Endemism	Additional species	All species	**Order**	AREA	Corrected Weighted	Additional species	All species
1	JAL/MEX	2(1)	27	27	1	JAL/MEX	6.590853	27	27	1	BC	1.000000	2	1
2	NL/MEX	2(1)	14	41	2	NL/MEX	5.953968	14	41	2	BCS	1.000000	1	3
3	CHIS/MEX	2(1)	10	51	3	CHIS/MEX	2.805723	10	51	3	COAH/MEX	0.392424	10	13
4	BC/MEX	2(1)	2	53	4	BC/MEX	2.000000	2	53	4	NL/MEX	0.355581	8	21
5	COAH/MEX	1(1)	3	56	5	COAH/MEX	1.833333	3	56	5	JAL/MEX	0.253494	26	47
6	MEX/MEX	1(1)	2	58	6	MEX/MEX	1.111111	2	58	6	MEX/MEX	0.181799	2	49
7	BCS/MEX	1(1)	1	59	7	BCS/MEX	1.000000	1	59	7	CHIS/MEX	0.179467	10	59
8	OAX(GRO)	2(2)	4	63	8	OAX	1.544444	4	63	8	GRO/MEX	0.178810	2	61
9	HGO(PUE)	1(2)	3	66	9	HGO	1.083333	3	66	9	HGO/MEX	0.149134	5	66
10	CHIH,SON/MEX	2(3)	4	70	10	CHIH,SON/MEX	1.166667	4	70	10	SON/MEX	0.226367	4	70
11	ALA,JOS/CR	1(5)	4	74	11	ALA,JOS/CR	0.626190	4	74	11	ALA/CR	0.114782	4	74
12	CHIQ,ZAC/GUA; CAY/BEL; CHA,USU,MOR/SAL; FRA,COM,PAZ,YOR/HON; MAT,NUE/NIC	**1(12)**	1	75	12	CHIQ,ZAC/GUA; CAY/BEL; CHA,USU,MOR/SAL; FRA,COM,PAZ,YOR/HON; MAT,NUE/NIC	0.083333	1	75	12	CAY/BEL	0.089046	1	75
Complementarity for rarities species in floristic provinces					**Complementarity for Weighted Endemism in floristic provinces**					**Complementarity for Corrected Weighted Endemism in floristic provinces**				
1	SMORN	**7(1)**	16	16	1	SMORN	9.660714	16	16	1	LAGU	1.000000	1	1
2	STI	**5(1)**	16	32	2	STI	7.257118	16	32	2	TALA	0.728571	5	6
3	SMOCC	**5(1)**	10	42	3	SMJ	6.570635	18	50	3	CALI	0.666667	2	8
4	SMJ	**3(1)**	13	55	4	SMOCC	5.000000	5	55	4	SMORN	0.603795	16	24
5	TALA	**3(1)**	3	58	5	SMORS	3.083333	7	62	5	SMOCC	0.508791	11	35
6	SMS	**2(1)**	4	62	6	TALA	3.000000	3	65	6	STI	0.453570	13	48
7	CALI	**2(1)**	2	64	7	SMS	2.250000	3	68	7	ALTIN	0.425170	2	50
8	SMORS	**5(1)**	6	70	8	CALI	2.000000	2	70	8	SMJ	0.296642	13	63
9	ALTIN	**1(1)**	2	72	9	ALTIN	1.500000	2	72	9	SMS	0.265138	5	68
10	BAL	**1(1)**	2	74	10	BAL	1.500000	2	74	10	BAL	0.248975	2	70
11	LAGU	**1(1)**	1	75	11	LAGU	1.000000	1	75	11	SMORS	0.230290	5	75
Complementarity for rarities species in grid-cells					**Complementarity for Weighted Endemism in grid-cells**					**Complementarity for Corrected Weighted Endemism in grid-cells**				
1	BZ	1(1)	1	1	1	CY	2.385549	13	13	1	BZ	1.000000	1	1
2	CY	1(1)	13	14	2	BZ	1.000000	1	14	2	CY	1.000000	13	14
3	BP	2(2)	11	25	3	BW	2.150641	12	26	3	BO	0.180051	6	20
4	BW	1(2)	3	28	4	DN	0.863497	8	34	4	BW	0.179220	8	28
5	DN	1(2)	8	36	5	BO	0.750000	2	36	5	BX	0.150058	1	29
6	BX,CY	1(2)	1	37	6	CH	0.726190	3	39	6	DV	0.090356	7	36
7	EZ	2(3)	8	45	7	DQ	1.202121	7	46	7	ES	0.107407	7	43
8	DF,DQ	1(3)	6	51	8	EZ	1.088095	6	52	8	DG	0.102579	3	46
9	CK	1(3)	6	57	9	CK	0.607112	6	58	9	CL	0.079857	4	50
10	ED(EE)	2(4)	4	61	10	ED	0.790909	4	62	10	ED	0.088335	4	54
11	AU,AV	1(4)	2	63	11	FU,FX	0.615909	4	68	11	FX	0.153977	4	58
12	AJ,AK	1(5)	4	67	12	AJ,AK	0.463462	4	72	12	DQ	0.087791	4	62
13	FU,FX	1(5)	4	71	13	A,H,R	0.309524	1	73	13	AJ	0.076374	5	67
14	A,H	1(6)	2	73	14	EK,ET,EU,FA,FF,FG	0.166667	1	74	14	N,Z,AI	0.166667	1	68
15	EK,ET,EU,FA,FF,FG	1(6)	1	74	15	EV,FD,FH,FI,FJ,FO,FP	0.125000	1	75	15	ET	0.078126	2	70
16	EV,FD,FH,FI,FJ,FO,FP	1(8)	1	75						16	BP	0.175442	1	71
										17	AHR	0.154762	1	72
										18	EV	0.085227	1	73
										19	BF	0.087121	1	74
										20	CZ	0.084753	1	75

Table 5. Systematic conservation planning. The first column lists the prioritary areas based in complementarity for red oaks. The second column the current natural areas with official protection. The cover landscape with current protection in third column, and the number of species protected in fourth column. In fifth column specify the area suggested for increment in areas with protection current, and the number of species protected in sixth column. In seventh column are shown those areas without protection, the landscape covered in eighth column, and number species protected in ninth column.

SUGGESTED IMPORTANT AREAS FOR RED OAKS WITH OFFICIAL PROTECTION	NAMES OF THE PROTECTED AREAS	CURRENT PROTECTED AREA (HA)	NUMBER OF SPECIES CURRENTLY PROTECTED	SUGGESTED INCREMENT IN AREA IN THIS STUDY (HA)	NUMBER OF SPECIES PROTECTED INCLUDING THE INCREMENTED AREA	SUGGESTED IMPORTANT AREASFOR RED OAKS (WITHOUT OFFICIAL PROTECTION)	AREA TO PROTECT (HA)	NUMBER OF SPECIES PROTECTED
1. SIERRA SAN PEDRO MÁRTIR	PN SAN PEDRO MÁRTIR	72,909	1	121794	2			
		72909		**121794**				
2. SIERRA LA LAGUNA	RB SIERRA LA LAGUNA	112437	1					
		112437						
3. SIERRA TARAHUMARA	APFF CAMPO VERDE	108067	1	75219	6	YECORA	159096	
	APFF TUTUACA	363440	4	115552	10			
	APFF PAPIGOCHIC	243639	0	246459	5			
	PN CASCADA DE BASSESEACHIC	5911	0					
		721057		**437230**			**159096**	
4. SIERRA MADRE OCCIDENTAL	RB LA MICHILIA	9421	2	12684		GUACAMAYITA	45917	4
						RIO JESUS MARIA	174049	6
						SIERRA LOS HUICHOLES	88274	8
		9421		**12684**			**308240**	7
5. SERRANIAS MERIDIONALES DE JALISCO						SIERRA VALLEJO	33391	6
						CABO CORRIENTES	35373	10
							68764	
6. SIERRA PLEGADA	PN CUMBRES DE MONTERREY	177395	6	108155	8	CAÑON DE ITURBIDE	35659	
						PUERTO PURIFICACION	48100	4
						PEÑA NEVADA	60149	6
		177395		**108155**			**143908**	6
7. SIERRA MADRE ORIENTAL SOUTHERN	RB BARRANCA DE METZTITLAN	96043	10			MESÓFILOS HIDALGO	69231	15
	APRN CUENCA RIO NECAXA	41692	10					
	PN EL CHICO	2729	5					
		140464					**69231**	
8. DEPRESION DEL BALSAS						SIERRA NANCHITITLA	32014	6
						NEVADO DE TOLUCA	45568	10
							77582	
9. SIERRA MADRE DEL SUR						SIERRA GUERRERENSE	82828	11
						CAÑON ZOPILOTE	42420	9
							125248	
10. ALTOS DE CHIAPAS	LAGUNAS DE MONTEBELLO	6396	3			MESOFILOS LOS ALTOS	23748	2
						HUITEPEC	31706	4
		6396					**55454**	
11.SIERRA MADRE DE CHIAPAS	RB EL TRIUNFO	119183	6					
	RB/ZV VOLCAN TACANA	8963	1	9993	2			
	ZV VOLCAN TAJOMULCO	12494	1	19414	4			
	ZV VOLCÁN LACANDON	4313	0	12812	4			
		144953		**42219**				
12. SIERRA DE COMAYAGUA	PN LA TIGRA	23821	2					
	PN CELAQUE	26640	3					
	PN MONTAÑA COMAYAGUA	18480	2					
	RVS CORRALITOS	5730	0					
	RVS MIXCURE	8060	0					
	RB MONSERRAT	2240	0	10024	4			
	RB MONTECILLOS	13120	3					
	RB HIERBABUENA	3510	1					
	RB OPALACA	14660	1					
	RB GUAJIQUIRO	6700	1					
	RB CERRO EL UYUCA	1138	3	16739	6			
	AUM CARIAS BERMUDEZ	4535	1					
		128634		**26763**				
13. SIERRA DE TALAMANCA	PN LA AMISTAD	193477	3					
	RF CORDILLERA VOLCANICA	61049	3					
	RF LOS SANTOS	60212	2					
	PN TAPANTI	58482	2					
	PN CHIRRIPO	50557	1					
	PN BRAULIO CARILLO	47781	1					
	ZP MONTEVERDE	26790	2					
	RF RIO MACHO	22110	1					
	ZP LAS TABLAS	19998	2					
	PN JUAN CASTRO BLANCO	14512	0					
	RB ALBERTO MANUEL BRENES	7832	1					
	ZP CERROS DE ESCAZU	7205	1					
	PN VOLCAN POAS	6533	1					
	ZP RIO NAVARRO	6489	2					
	ZP RIO TORO	4322	2					
	ZP CUENCA RIO TUIS	4130	1					
	ZP CARAIGRES	3217	1					
	ZP CERRO LA CARPINTERA	2395	1					
	RF GRECIA	2312	2					
	PN VOLCAN IRAZU	2008	1					
	RVS LA MARTA	1295	0					
	PN VOLCAN TURRIALBA	1261	0					
	OTRAS AREAS (11)	3436	0					
		607403						
TOTALS		**2121069**	**32**	**748845**	**37**		**1007523**	**55**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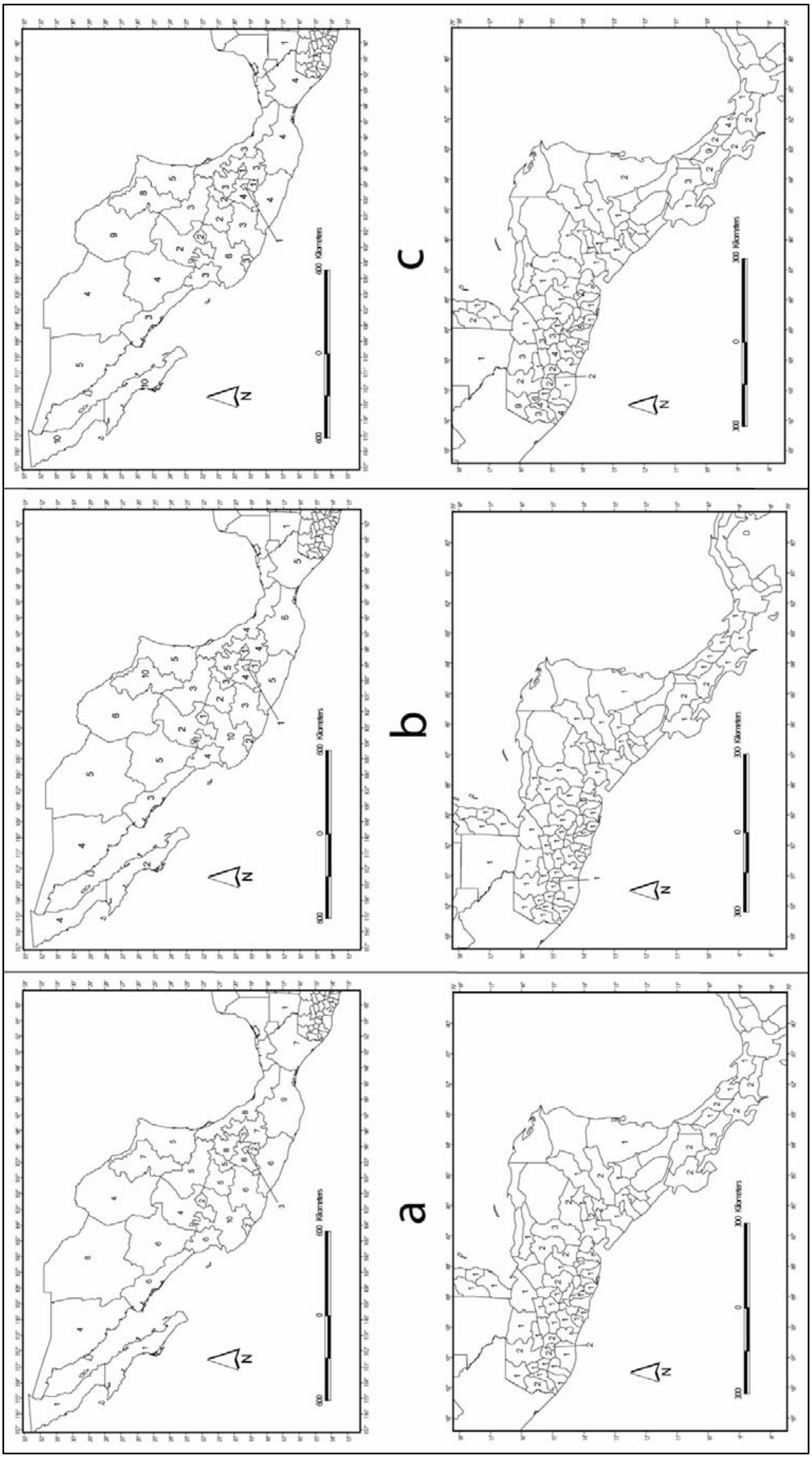

Figure 2

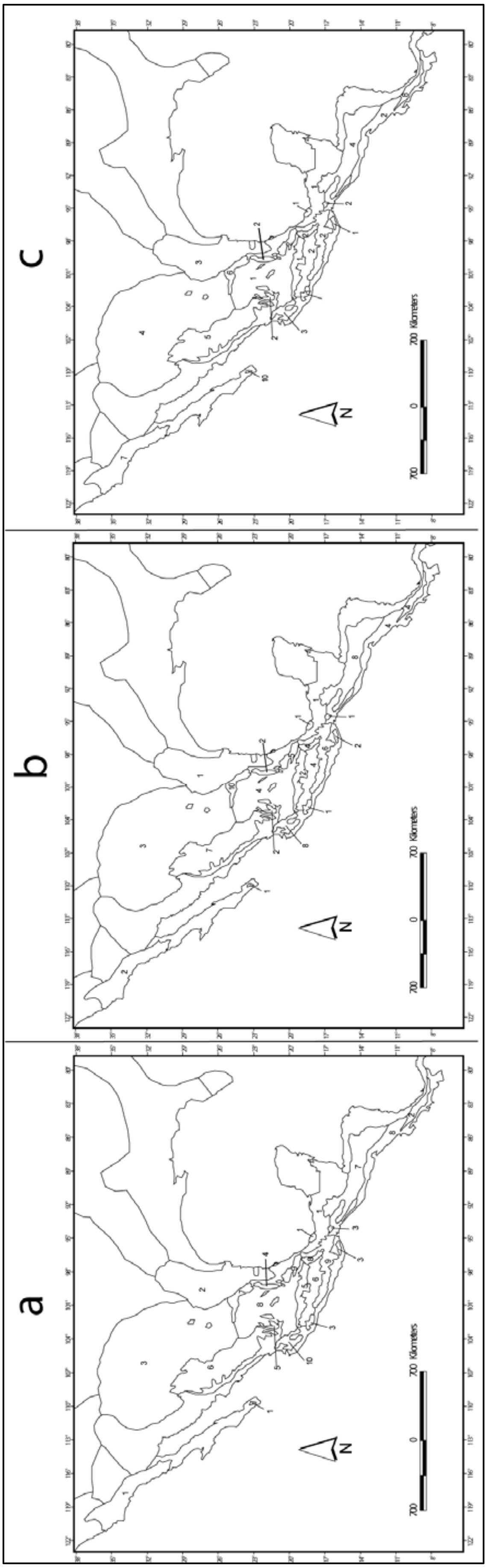

Figure 3

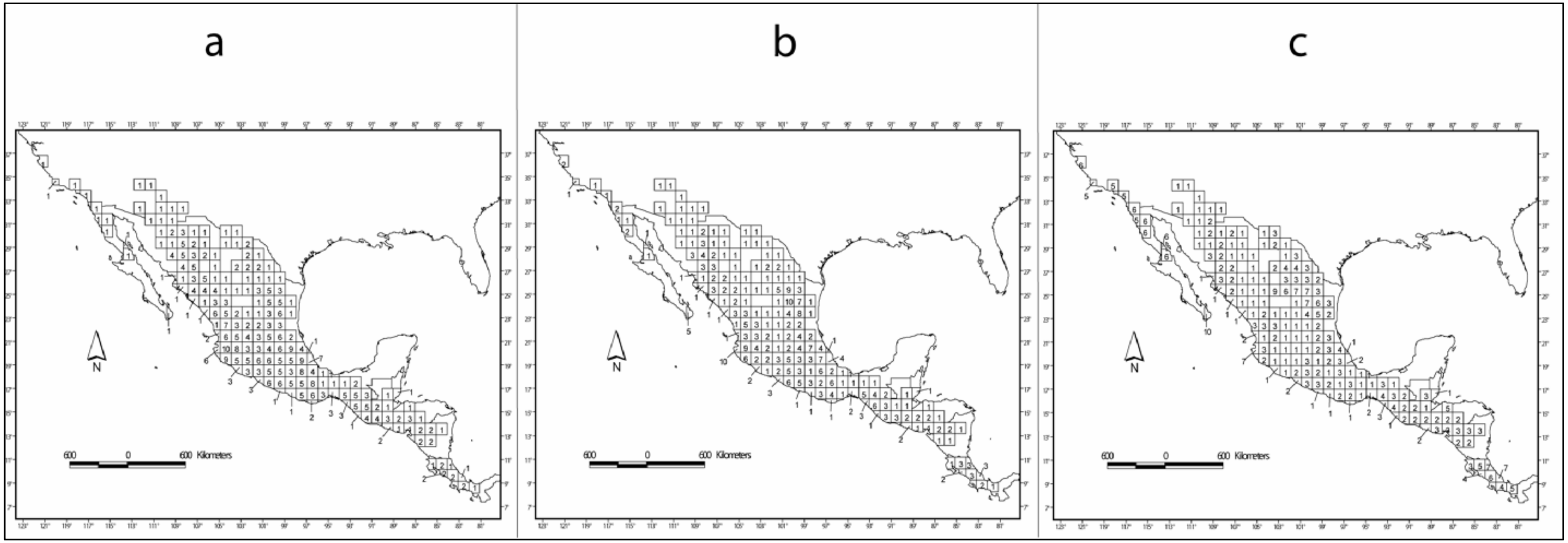

Figure 4

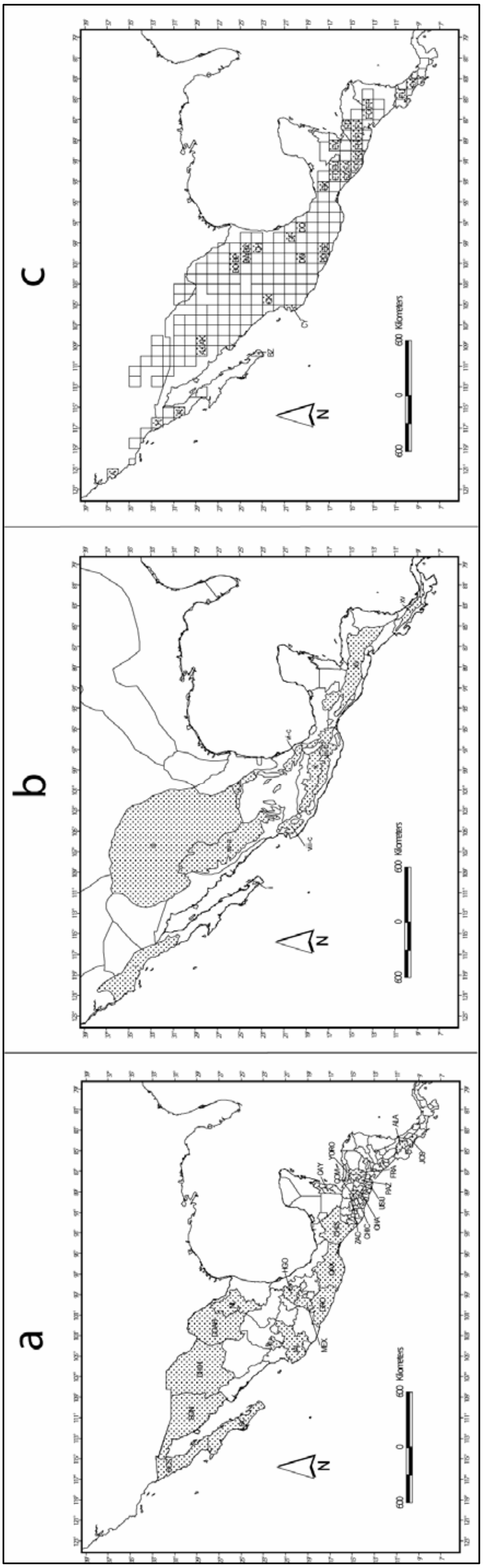

Figure 5

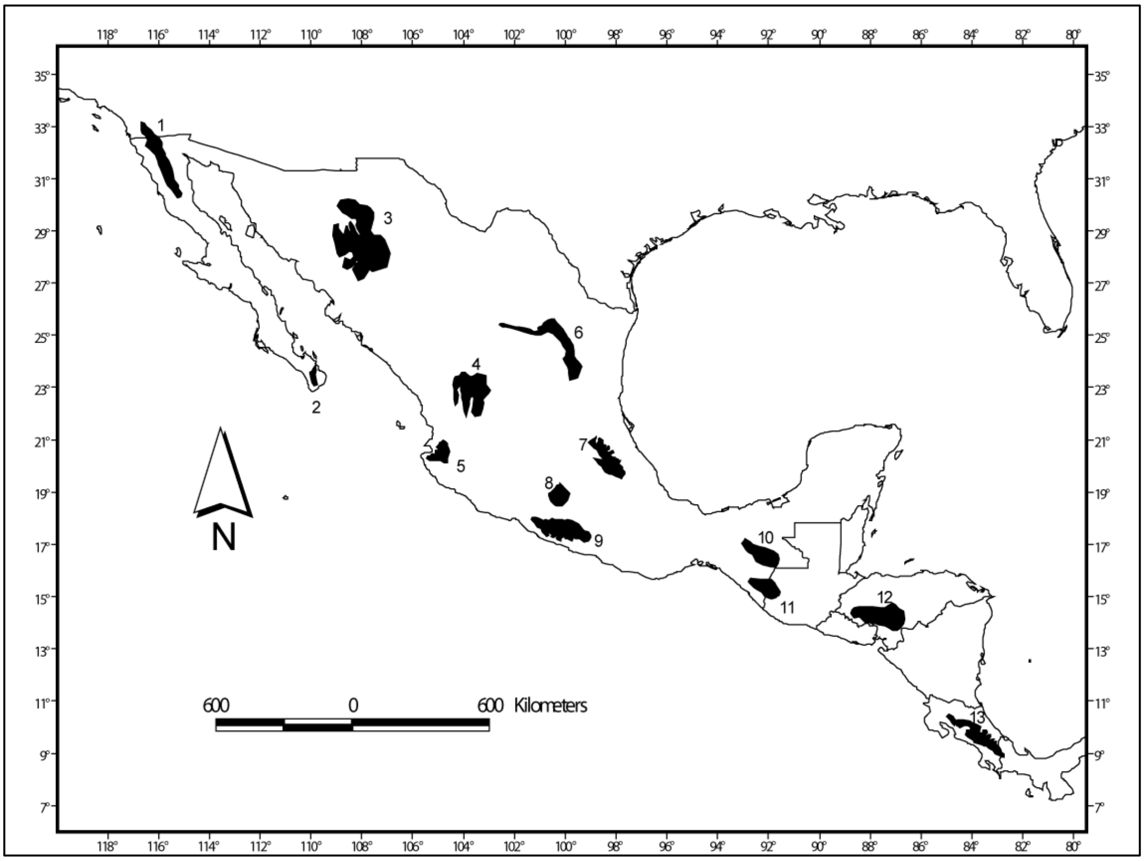
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Figure 6

DISCUSIÓN GENERAL Y CONCLUSIONES

El objetivo general de este trabajo fue la identificación de los patrones de distribución de los encinos rojos de México (aunque el área de estudio se amplió hasta América Central), con el fin de analizar las relaciones históricas de las áreas de distribución. Además, como un objetivo secundario se realizó un estudio areográfico para detectar áreas de mayor riqueza y endemismo para los encinos rojos, y mediante un análisis de complementariedad se determinaron cuáles son las áreas de mayor importancia para la conservación de este grupo, en una propuesta metodológica de la biogeografía para la conservación.

Para determinar los patrones biogeográficos en la distribución de los encinos rojos, se llevó a cabo un análisis de parsimonia de endemismos (PAE por sus siglas en inglés) en el sentido de Morrone (1994). Se utilizaron dos unidades de estudio: por una parte un sistema modificado de las provincias florísticas de Rzedowski (1978) para México y Takhtajan (1986) para América Central, y por otra parte, un conjunto de 158 gradillas de un grado de latitud y longitud. En el caso de las unidades florísticas se obtuvieron dos cladogramas igualmente parsimoniosos que variaron únicamente en la posición de la Sierra de Talamanca. Se reconocen dos clados, uno Neártico con dos subclados definidos, uno en la parte oriental y otro en la parte occidental, lo cual coincide con los trazos generalizados denominados Norteamericano oriental y Norteamericano occidental según Contreras-Medina y Eliosa-León (2001). El segundo clado pertenece a la denominada Zona de Transición Mexicana en sentido estricto, con dos componentes principales: el Mexicano de Montaña y el Mesoamericano identificados por Morrone y Márquez (2003).

El análisis de las gradillas arrojó 50000 árboles igualmente parsimoniosos. En el cladograma de consenso estricto se colapsaron 48 clados, pero se lograron definir 11 clados, de los cuales seis son informativos y el resto constituyen diferentes agrupaciones de áreas pertenecientes al Altiplano Norte (Chihuahuense y Coahuilense). No hay resolución en las relaciones de las áreas del noroeste de México, pero se identifican clados importantes que unen a las Serranías Transístmicas con la Sierra de Talamanca, además de la homogeneidad en los Sistemas Centrales (Faja Volcánica Transmexicana central y oriental, tierras altas del Balsas, Sierra Norte de Oaxaca, Sierra Madre Oriental Hidalguense y Sierra Madre del Sur), separados del clado Neártico oriental, la Meseta Central y Serranías Meridionales de Jalisco + Sierra Madre Occidental sur. Con este análisis la identidad natural de las provincias Sierra Madre Oriental, Sierra Madre Occidental y Faja Volcánica Transmexicana se pone en cuestionamiento, pues es evidente que en dichas provincias existen historias evolutivas diferentes.

A pesar de que el cladograma del PAE define seis clados importantes, la gran cantidad de homoplasias no permiten dilucidar las relaciones entre las áreas, ya que se presenta una politomía general. Por lo tanto, se hicieron análisis adicionales de similitud por agrupamiento de medias no ponderadas (UPGMA por sus siglas en inglés). Las relaciones de similitud ofrecieron un esquema general parecido al PAE, pero difirieron en considerar a los sistemas montanos de América Central como áreas separadas del sureste de México y con mayor parecido a la Sierra de Talamanca. Las relaciones en el norte de México continuaron siendo conflictivas. Los UPGMA trabajan bajo un algoritmo de agrupamiento basado en similitu total. Una alternativa diferente es un análisis con distancias ultramétricas para generar un árbol de unión con el vecino más cercano (NJ por sus siglas en inglés).

A partir de la matriz de presencia y ausencia, se obtuvo un árbol único por NJ que en general resultó congruente con la información generada por el PAE con cuatro ramas principales, pero con poca resolución nuevamente al norte de México. Una ventaja de este método es la obtención de ramas de diferente longitud a lo largo del árbol, pudiendo identificar ramas largas en zonas con presencia de especies de distribución restringida. El NJ minimiza la longitud de las ramas, por lo que utilizar el inverso de la distribución de las especies en lugar de una matriz de presencia / ausencia, por lo que podría generar un árbol de mayor resolución. Al hacer esta modificación en la matriz, se obtuvo un árbol con resolución óptima incluso en el norte de México, además de que la identificación de ramas largas fue más clara. No obstante, las ramas largas no necesariamente son áreas de endemismo, e incluso la Sierra de Talamanca no se identificó como una rama larga.

La identificación de áreas de endemismo se realizó mediante un análisis de redes. A partir de una matriz de simpatría (con una matriz con valores entre 0 y 1, donde 1 representa homopatría total entre dos especies y 0 para alopatría total entre dos especies), se identifican especies intermediarias, v.gr. aquellas especies de amplia distribución que pueden llegar a tener múltiples relaciones de alelopatría con diferentes especies que pueden ocultar patrones de homopatría. Tras la eliminación iterativa de estas especies en las redes, surgen subredes o “cliqués” de especies que viven en simpatría, las cuales se diferencian en nuevos cliqués. Mediante este análisis es posible obtener áreas de endemismo en un sistema de anidamiento. Este sistema de anidamiento de áreas de endemismo, además, fue congruente con los resultados obtenidos con PAE y NJ, con pequeñas diferencias en la interpretación de las relaciones.

El análisis areográfico de los encinos rojos permitió identificar a Oaxaca y Jalisco como las entidades políticas con mayor diversidad de especies de encinos rojos. El utilizar los índices de endemismo ponderado y de endemismo ponderado corregido permitió identificar áreas que son importantes por el número de especies de distribución restringida (endemismos), los cuales se localizan en las Sierras de San Pedro Mártir en Baja California, Sierra La Laguna en Baja California Sur, Serranías Meridionales de Jalisco, Sierra Plegada, Sierra Madre Oriental sur + Sierra Norte de Oaxaca, y por último, en la Sierra de Talamanca.

Tras un análisis de complementariedad basado en criterios de conservación de riqueza y conservación por rareza (especies de distribución restringida), se identifican trece áreas de importancia en la conservación de los encinos rojos en México y América Central, áreas que coinciden en su mayoría con Regiones Terrestres Prioritarias identificadas por Conabio. Se realizó adicionalmente un análisis sobre el número de especies protegidas con las Áreas Naturales Protegidas decretadas en México y en América Central. Se observó que con las áreas actuales se protegen 31 especies (ca. 41% del total de especies), por lo que se propone una modificación de la cobertura de las Áreas Naturales Protegidas, o bien la creación de nuevas áreas de protección, con lo que no solamente se protegen especies de encinos rojos, sino a ecosistemas de vegetación templada de gran importancia, como son los bosques mesófilos de montaña del oriente de México y los bosques de encino y mixtos que son considerados como los tipos de vegetación que albergan la mayor cantidad de vertebrados endémicos.

Es claro que la areografía es un conjunto de técnicas con repercusiones inmediatas en las políticas de conservación, identificando áreas prioritarias en donde se deberían concentrar nuevos estudios que apoyen la conservación de especies, como ejemplo, la conservación de procesos ecológicos y evolutivos, dados a través de estudios de genética de poblaciones de especies particulares.

El presente trabajo es un esfuerzo por proponer nuevas técnicas para el estudio de los patrones biogeográficos de las especies, recalcando la complementariedad de análisis diferentes para llegar a resultados comunes para explicar la historia de las biotas.

Asimismo, es un esfuerzo colectivo por integrar un Atlas Biogeográfico y un Sistema de Información Geográfica de los encinos rojos mexicanos, pero aún la información sobre la distribución de estas especies está lejos de ser completa, ya que aún falta efectuar colectas en áreas poco estudiadas como la Sierra Madre Occidental. Existen zonas mejor estudiadas que otras, como el centro de México, que se concentran cerca de ciudades o caminos principales. No obstante, este trabajo representa la mejor compilación de datos puntuales de distribución de la sección *Lobatae* del género *Quercus*.

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