UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO

INSTITUTO DE ECOLOGÍA
DOCTORADO EN CIENCIAS BIOMÉDICAS

VARIACIÓN ESPACIAL DE LA DIVERSIDAD EN VEGETACIÓN DESÉRTICA Y SU APLICACIÓN EN LA MODELACIÓN DE LAS RELACIONES BIODIVERSIDAD – MEDIO AMBIENTE

T E S I S

QUE PRESENTA

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PARA OBTENER EL GRADO DE

DOCTOR EN CIENCIAS

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MÉXICO, D.F.   SEPTIEMBRE 2003

A mis abuelos Cipriano y Luisa,

por enseñarme cada día el mundo, la dignidad, la ternura.

A mis padres y a mi hermana,

por tanto amor, tanto sacrificio, tanto abrazo.

A Charlotte,

por el mar.

AGRADECIMIENTOS

A México, a su gente, que me ha acogido y ofrecido tanto.

A Exequiel Ezcurra, maestro y ejemplo, por el lujo de aprender a su lado y disfrutarlo. Por su compromiso y respeto permanente. Por su inmensa ayuda siempre. Por traerme a México y por mandarme a Morelia. Gracias.

A mis padres, a mi hermana, porque estoy aquí gracias a su trabajo, su sacrificio, su apoyo. Por su inmensa capacidad para abrazar, para dar. Esta tesis está a mi nombre, pero es suya.

A Charlotte, por la enorme ayuda con el trabajo, por los caminos y por los puertos, siempre por ser junto a mí.

A la familia González-Abraham que me dio una familia a este lado y me lo hizo sentir.

A Carlos Montaña y Miguel Franco, que me ayudaron siempre con la mejor disposición.

A Gerardo Bocco, por el curso de Morelia, por su cordialidad siempre.

A mis compañeros del "Lacra", Carlos Martorell, Eduardo Peters, Ernesto Vega y Miguel Gutiérrez, por permitirme la entrada a tan selecto club y por lo mucho que aprendí y me divertí con ellos.

A Juan Fornoni, que desde el primer día me ayudó a ver y entender.

A Lucia por Lucia.

A Lina Ojeda, sin ella Tijuana no hubiera sido igual.

A C.R. Hibbs por su ayuda y su entrañable amistad.

A Elisabet Wehncke, por las wehnckehistorias, por las penas de Unamuno, por las pláticas, por tantas cosas, pero sobre todo por ella.

A Irene Pisanty, porque después de concocerla quiero un poco más al mundo.

A Bárbara Córcega, por su hospitalidad y generosidad sin límite.

A la Negrita, que aun no estando está.

CONTENIDO

RESUMEN

En el presente estudio se analizan los patrones de riqueza y de diversidad α y β de las leguminosas leñosas de la península de Baja California, México. A partir de la revisión de ocho herbarios se digitalizaron 4,205 registros de 78 species y se representaron sobre una cuadrícula de 205 celdas cartográficas (20' longitud $\times$ 15' latitud). Los tamaños del área de distribución geográfica siguieron una distribución log-normal, pero la riqueza florística mostró agregación en algunas celdas donde la riqueza de especies fue mayor de lo esperado por azar. Se puso a prueba la hipótesis de que el patrón encontrado se debe a la intensidad de colecta o al tamaño de área terrestre. Aun así, 16 celdas, situadas en la región de El Cabo y a lo largo de la Sierra de la Giganta, en el sur de la costa del Golfo de California, presentaron una riqueza significativamente alta. El endemismo es elevado, alcanzando 60–70% en el centro de la península, donde se encuentran los desiertos más secos. Se encontró una elevada diversidad β y el recambio de especies en sentido E-W desde la costa del Pacífico hacia la costa del Mar de Cortés se relaciona significativamente con la variación topográfica a lo largo de la península. Un análisis de la similitud entre sitios mostró que las regiones florísticas de la península tienen fronteras bien definidas, y que la similitud florística tiende a mantenerse sobre largas distancias a lo largo del corredor costero del Golfo de California. Finalmente, una clasificación numérica de las celdas basada en sus atributos florísticos diferenció cinco regiones bien definidas que coinciden con regionalizaciones de la península de Baja California propuestas previamente por varios autores basadas en métodos descriptivos, así como con las áreas de endemismos descritas en el primer capítulo. Se concluye que en la península de Baja California los patrones de distribución de especies y las regiones de leguminosas leñosas reflejan las dos principales fuerzas ecológicas que actúan sobre ella: el gradiente climático templado–tropical y el gradiente geográfico E–W existente desde el Océano Pacífico a través de la sierra hasta el Golfo de California y así mismo, el papel crucial que los factores históricos y climáticos han tenido en el teatro ecológico de Baja California.

ABSTRACT

In this study I analyzed the patterns of species richness, and of α and β-diversity, of woody legumes in the Baja California peninsula, Mexico. From the specimen labels of eight herbaria, I digitized 4,205 records corresponding to 78 species, which were projected onto a grid of 205 cartographic cells (20' longitude $\times$ 15' latitude). Geographic ranges were log-normally distributed, but floristic richness was found to be clumped around some cells where the observed richness was significantly higher than expected at random. I tested the hypothesis that this pattern could be attributable to the intensity of collection efforts or to large land surfaces. However, I still found 16 cells, in the Cape Region and along the Sierra de la Giganta in the southern Gulf coast, where richness was significantly high once these two factors were accounted for. Endemism was high, reaching 60–70% in the center of the peninsula, where the driest deserts are found. High β-diversity was found and the E–W turnover from the Pacific coast to the Gulf of California was significantly associated to topographic variation across the peninsula. An analysis of between-site similarities showed that floristic regions in the peninsula have well-defined boundaries, and that floristic similarities tend to extend for long distances along the coastal corridor of the Gulf of California. A numerical classification of the cells based on its floristic attributes separated the peninsula into five well-defined regions that closely match those regionalisations for Baja California previously proposed by various authors using descriptive methods, as well as with the areas of endemism described in the first chapter. I conclude that the species patterns and the ecological regions of woody legumes in the peninsula clearly reflect the two main environmental forces that act on it, namely, the long temperate–tropical climatic gradient, and the dramatic geographic E–W gradient that runs from the Pacific Ocean across the mountain divide into the Gulf of California, and that historical and climatic factors have played an important role in the ecological theater of Baja California.

INTRODUCCIÓN GENERAL

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La península de Baja California ha sido durante su historia un *plus ultra*, un territorio que por encima de su carácter de frontera o límite geográfico ha representado un espacio imaginario al que han sido atraídos a lo largo de los años, pareciera que imantados, individuos peculiares y no tanto, proyectos místicos, utópicos, terrenales fantasías. El naturalista experimenta igualmente una fascinación que no desmerece a otras vivencias más celestiales.

Baja California, la segunda península más larga del mundo despúes de la península malaya, es una estrecha franja de tierra en el NO de México que tiene 1,300 km de largo y 110 km en promedio de ancho, cubriendo un área de 145,000 km^2. Situada entre 23° y 33° N, en la latitud de encuentro de los Reinos Neártico y Neotropical y orientada aproximadamente en dirección N-S, contiene en tan reducido espacio una de las transiciones biológicas más apasionantes del mundo.

Ubicada en el extremo sur peninsular, la región de Los Cabos está conectada geológica y biogeográficamente con el bosque seco tropical de la costa pacífica de México (Axelrod 1979; Pennington et al. 2000) . El noroeste peninsular forma parte de los ecosistemas mediterráneos de la Provincia Florística de California (Peinado et al. 1994; Minnich y Franco-Vizcaíno 1998). Ambos ecosistemas han sido identificados como áreas de gran riqueza en especies y endemismos (Raven 1988; Myers et al. 2000; Ezcurra et al. 2002). Entre ambos extremos, y ocupando la mayor parte de la península (aprox. 80%), se extiende una región árida subtropical de transición, comunicada por su extremo nordeste con el Desierto Sonorense a través de un estrecho corredor de 50 km de ancho y 300 km de longitud (Fig. 1).

Esta porción árida de la península es, a su vez, un aislado "apéndice peninsular" del gran corredor de ecosistemas áridos que abarca Norteamérica desde el sureste del Estado de Washington, en los Estados Unidos, hasta los Estados de Hidalgo y Puebla en el altiplano central de México, y desde el centro de Texas hasta la costa del Pacífico en la península de Baja California. Este gran corredor árido, que cubre casi un millón de km^2 y contiene el 10% de la superficie árida en el mundo (Bailey 1981), ha sido habitualmente dividido en cuatro desiertos (MacMahon 1979; Brown 1982): el desierto frío de la Gran Cuenca y los desiertos cálidos de Mojave, Sonora y Chihuahua.
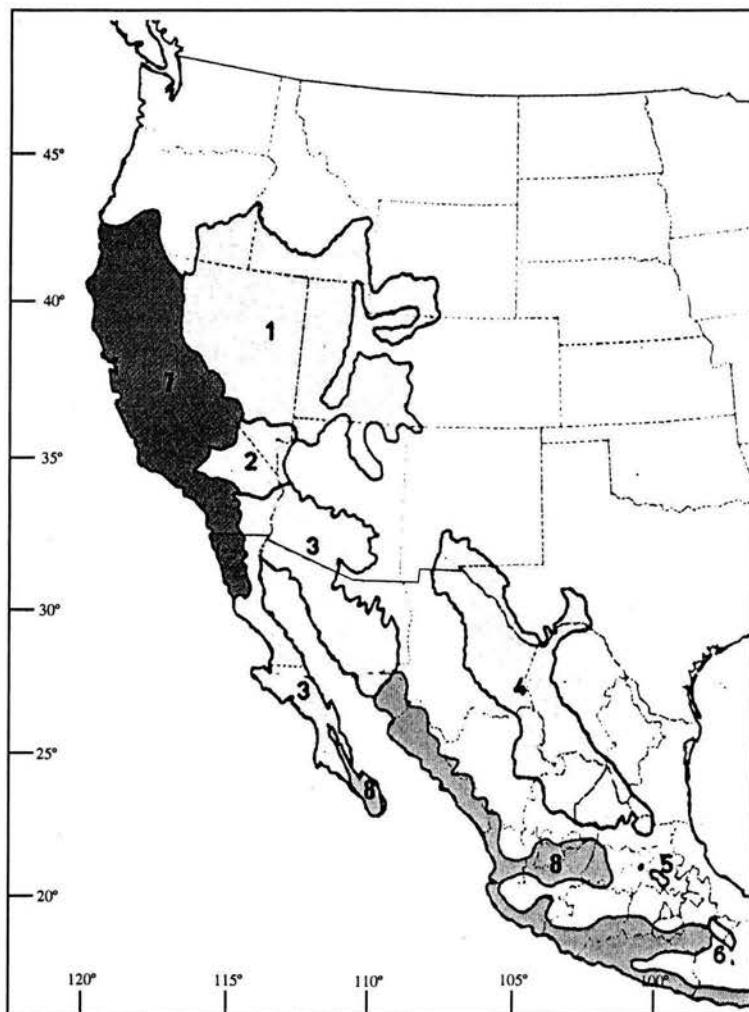
Fig. 1. Regiones áridas de Norteamérica: (1) Gran Cuenca, (2) Mohave, (3) Desierto Sonorense, (4) Desierto Chihuahuense, (5) Valle del Mezquital, y (6) Valle de Tehuacán y Cuicatlán. Regiones no áridas presentes en Baja California: Provincia Florística de California (7) y bosque tropical seco (8). (Modificado a partir de Rzedowski 1973 y Arriaga et al. 1997).

Situados en lo que Fischer y Turner (1978) denominaron zona de transición (20° − 40° latitud), la precipitación en estos desiertos cálidos puede ocurrir en invierno, en verano o ser bimodal. El patrón de precipitación, relacionado con la dinámica estacional de las masas de aire a través de Norteamérica (Neilson 1987), separa los tres desiertos cálidos de Norteamérica (Smith et al. 1997). Conforme uno se mueve de oeste a este, del Mojave hacia el Chihuahuense, disminuye la proporción entre lluvias de invierno y lluvias de verano. El desierto de Mojave y la porción occidental del Desierto Sonorense reciben primordialmente precipitación de invierno, con su estación de crecimiento en primavera, la mayor parte del Desierto Sonorense tiene un régimen de precipitación bimodal, con periodo de crecimiento en primavera y verano, y el Desierto Chihuahuense recibe precipitación dominantemente en los meses de verano. Si bien otros muchos factores participan en la demarcación de estas regiones, los contrastes en la estacionalidad de las precipitación es crucial para marcar diferencias en la composición y la estructura de la vegetación (Brown 1982; Smith et al. 1997).

Geográficamente el Desierto Sonorense puede describirse de manera sencilla como la región que rodea el Golfo de California (también llamado Mar de Cortés) (Shreve 1951). Dicho de otra manera, el Mar de Cortés divide al Desierto Sonorense en dos partes unidas por una estrecha conexión: una parte "continental" o Desierto Sonorense *sensu stricto* y una segunda parte "peninsular" o Desierto de Baja California. Diversos autores consideran el Desierto de Baja California como una región separada del Desierto Sonorense, con su propia singularidad histórica, evolutiva y ecológica (Morafka et al. 1992; Peinado et al. 1994; Riddle et al. 2000; Ezcurra et al. 2002).

Desde el inicio de su formación a finales del Mioceno (aprox. 6 Ma AP), diversas partes de la península o la península en su totalidad han estado sometidas a períodos de aislamiento de variada duración (Axelrod 1979; Murphy 1983; Morafka et al. 1992). La formación de la cadena de montañas, que atraviesa la península de norte a sur, crea una marcada heterogeneidad topográfica. El resultado de estos procesos geológicos ha sido un escenario físico heterogéneo temporal y espacialmente. Sobre este escenario actuaron procesos climáticos, tales como la circulación general de vientos y de corrientes marinas, variables temporal y espacialmente, en especial durante los ciclos glacial-interglacial pleistocénicos (1.8 Ma − 11,000 años AP; Van Devender y Burgess 1985; Van Devender 1990). El resultado evolutivo de la conjunción, histórica y presente, de estos escenarios físico, climático y biológico ha sido la gran diversidad

de especies, formas de vida y comunidades vegetales que contiene la península de Baja California.

En el presente trabajo se hace una aproximación a este complejo y apasionante escenario biológico que constituye Baja California, a través de un grupo de plantas de especial relevancia en los Desiertos Sonorense y de Baja California: las especies leñosas de la familia Leguminosae.

Debido a su complicada historia biogeográfica y a sus conexiones con el bosque seco de la costa del Pacífico, estos desiertos son regiones ricas en especies arbóreas, particularmente leguminosas, y en plantas columnares de gran tamaño (Robichaux 1999; Dimmit 2000), lo que les otorga un llamativo aspecto arborescente con gran volumen de biomasa aérea. Además de su importancia numérica y fisionómica, las leguminosas leñosas son cruciales en el funcionamiento de las comunidades de estas zonas áridas, por su capacidad para modificar las críticas condiciones ambientales, mejorando las relaciones hídricas, térmicas y nutricionales en sus proximidades, estableciendo de esta manera auténticas "islas de fertilidad" bajo sus copas (ver referencias en Garcillán et al. 2003).

La familia Leguminosae es cuantitativamente uno de los grupos dominantes de la flora leñosa peninsular. Esta flora leñosa comprende aproximadamente 670 especies y representa 22 % del total de 3,000 especies (Shreve y Wiggins 1964; Wiggins 1980; León de la Luz y Domínguez-Cadena 1989; Lenz 1992; León de la Luz y Coria-Benet 1993; León de la Luz et al. 1995). Las leguminosas, con 80 especies, representan 12 % de la flora leñosa, siendo la primera familia en número de especies arbóreas y la segunda en número de arbustivas después de las Asteraceae.

El concepto de diversidad biológica ha sido dividido en dos componentes fundamentales (Whittaker 1960, 1972): (1) riqueza local o diversidad α, referida al número de especies presentes en un hábitat o área relativamente homogénea, y (2) diversidad β o diversidad entre hábitats, referida al recambio de especies entre áreas o hábitats distintos. En la península de Baja California se han realizado numerosos estudios sobre los patrones de riqueza de especies en diversos grupos de animales (Stager 1960; Truxal 1960; Seib 1980; Due y Polis 1986; Taylor y Regal 1978; Williams 1980; Murphy 1983; Brown 1987; Wiggins 1999; Johnson y Ward 2002; Rojas-Soto et al. 2003), pero apenas existen esfuerzos semejantes para grupos de plantas (Riemann 2001). Estos trabajos se han dirigido a examinar las tendencias generales de

la riqueza de especies, diversidad α, a lo largo de la península, y en gran número dirigidas al examen del denominado por Simpson (1964) "efecto peninsular" (disminución del número de especies conforme nos alejamos del istmo peninsular). En su mayoría la referenciación geográfica es relativamente imprecisa o está referida a unidades espaciales muy extensas (ver sin embargo, Riemann 2001; Rojas-Soto et al. 2003), y en ningún caso se realiza un análisis desde la perspectiva de la diversidad β.

El propósito general de esta tesis fue analizar el patrón completo de diversidad, incluyendo los componentes α y β, de las especies de leguminosas leñosas como una contribución al conocimiento biogeográfico y ecológico de la península de Baja California.

En el Capítulo I (Garcillán et al. 2003) se presenta el análisis de la diversidad α de especies de leguminosas leñosas y se propone para ello un modelo predictor de la riqueza de especies que incorpora dos factores que la condicionan de manera significativa: el tamaño del área y la intensidad de colecta realizada en la misma. Son numerosos los estudios que establecen la existencia de una relación entre estos dos factores y la riqueza de especies en un área determinada. Por esta razón, el objetivo fundamental de este análisis fue la determinación del patrón de riqueza de especies de leguminosas leñosas existente más allá de estos dos "artefactos experimentales", es decir, de las áreas de riqueza de especies significativamente alta o baja debido a causas naturales.

En el Capítulo II se analiza el patrón de diversidad β, es decir, su intensidad y distribución geográfica. Para ello se proponen distintas expresiones del recambio de especies, o diversidad β, y se analiza su relación con los dos ejes ecológicos fundamentales que actúan sobre la península: el gradiente climático templado-tropical en sentido norte-sur y el gradiente entre la costa del Pacífico y la costa del Golfo de California producido por la cadena montañosa transpeninsular. Finalmente, se propone una regionalización florística de Baja California a partir de una clasificación numérica con base en la presencia y la distribución de las leguminosas leñosas. Las fronteras de esta regionalización son interpretadas a la luz del patrón de diversidad β y comparada con otras regionalizaciones propuestas por diversos autores (Shreve 1951; Truxal 1960; Shreve y Wiggins 1964; Murphy 1983; Williams 1980; Peinado et al. 1994, entre otros).

En el Apéndice I se presenta la relación de las especies utilizadas en el estudio, junto con información biogeográfica sobre la naturaleza de su área de distribución y su presencia en cada una de las regiones florísticas establecidas.

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CAPÍTULO I

DISTRIBUCIÓN Y RIQUEZA DE LEGUMINOSAS LEÑOSAS EN BAJA CALIFORNIA, MÉXICO

Distribution and species richness of woody dryland legumes in Baja California, Mexico

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Abstract. We analysed the biogeographic patterns of woody legumes in the Baja California peninsula, NW Mexico. From the specimen labels of eight herbaria, we digitized 4205 records from 78 species, and projected them onto a grid of 205 cartographic cells (20' longitude × 15' latitude). Most species followed distribution patterns that coincide with floristic subdivisions of the peninsula. Endemism is high, reaching 60 - 70% in the centre of the peninsula, where the driest deserts are found and where significant floristic changes took place during Pleistocene glacial events. The number of cartographic cells (i.e. their geographic ranges) were log-normally distributed, as has been reported for many other taxa. Floristic richness was found to be clumped around some cells where the observed richness is significantly higher than could be expected from chance variation. We tested the hypothesis that these 'hotspots' could be attributable to great collection efforts or to large land surfaces, but we still found 16 cells where richness is significantly high once these two factors are accounted for. Species richness and micro-endemism increase towards the south, conforming to Rapoport's rule that predicts that species ranges become smaller towards the equator while richness increases. The floristic hotspots for woody legumes in Baja California occur in the Cape Region and along the Sierra de la Giganta in the southern Gulf Coast, where 77% of the total peninsular legume flora can be found. These hotspots are mostly unprotected, and should be considered priority areas for future conservation efforts.

Keywords: Biogeographic range; Desert; Endemism; Facilitation; Latitudinal pattern; Leguminosae.

Introduction

Woody legumes are, together with giant columnar cacti, one of the most distinctive elements of the Sonoran and Baja Californian Deserts (Dimmitt 2000; Ezcurra et al. 2002). The subtropical character of these deserts, their biogeographic connection with the dry tropical forests of the Pacific coast of Mexico, and especially the bi-seasonal nature of their rainfall (Hastings & Turner 1965; Ezcurra & Rodrigues 1986), have allowed the development of a conspicuous arboreal flora (Felger et al. 2001) that makes this region physiognomically quite distinct and very different from other deserts in North America (Shreve 1951). In these arborescent deserts, woody legumes play a crucial role: Their capacity to ameliorate the harsh environmental conditions under their canopies makes individual trees true fertility islands and safe sites for a myriad of organisms (McAuliffe 1990; Smith et al. 1997). Among the many positive interactions that woody legumes have with other species, they can act as 'nurse plants' by facilitating the establishment of other species under their protective shade (e.g. Turner et al. 1966; McAuliffe 1984; Fowler 1986; Yeaton & Romero-Manzanares 1986; Franco & Nobel 1989; Valiente-Banuet et al. 1991; Suzán et al. 1996), a mechanism of vital importance in the renewal of desert vegetation. The facilitation process relies on three basic mechanisms: (1) the improvement of hydrological conditions for seedlings (Shreve 1931; Turner et al. 1966; Nobel 1989; Nobel & Geller 1987; Franco & Nobel 1989; Valiente-Banuet et al. 1991; Valiente-Banuet & Ezcurra 1991); (2) the improvement of soil fertility (García-Moya & McKell 1970; Romney et al. 1980; Montaña et al. 1988), and (3) the improvement of microclimatic conditions, especially reduced temperature and radiation, which leads to the formation of safe microhabitats (Steenbergh & Lowe 1977; Valiente-Banuet & Ezcurra 1991).

Because of their capacity to regulate the environment and to supply resources or refuge for other species,

desert woody legumes are true 'environmental engineers' (*sensu* Jones et al. 1994). Although they are not in danger of extinction, cutting of these trees for wood, charcoal, and land clearing is putting the safe sites they harbour under dangerous risk (Franks 1999). Recent reports have underscored the need to understand and protect the biodiversity of woody legumes and other desert keystone species, in order to ensure the long-term survival of the desert communities as a whole (Búrquez & Quintana 1994; Nabhan 2000; Suzán et al. 1999). This paper describes the biogeographic patterns of the woody legumes of the Peninsula of Baja California, in Mexico, to identify patterns of rarity and endemism, and to pinpoint areas of significantly high species richness as potential targets for future conservation efforts.

Study area

Baja California is a long, narrow peninsula in NW Mexico, with an area of almost 145 000 km² (including the islands of the Sea of Cortés). It is ca. 1300 km long and, on average, ca. 100 km wide, and runs in a NW-SE direction (Fig. 1). Its northwestern slopes are covered by mediterranean scrub fed by winter Pacific rains, while its southern tip —the Cape Region— is covered by dry tropical scrubs and forests fed by late summer cyclones called *chubascos*. The rest of the peninsula is covered by dry deserts, which may receive both winter and summer rains, usually in very low and variable amounts.

The peninsular flora comprises some 3000 species (Shreve & Wiggins 1964; Wiggins 1980; León de la Luz & Domínguez-Cadena 1989; Lenz 1992; León de la Luz et al. 1995), 670 of which are woody plants. With 80 species, the *Leguminosae* comprise 12% of the total woody flora. The legumes are the family with the highest number of trees, and the second family in number of woody shrubs, after the *Asteraceae*. Various studies have analyzed the biogeographic patterns of different faunal groups in the peninsula (Taylor & Regal 1978; Williams 1980; Murphy 1983; Due & Polis 1986; Brown 1987; Upton & Murphy 1997; Grismer 2002), but similar studies on plants are lacking.

Methods

We worked in total with 78 species of woody legumes (App. 1) belonging to 32 genera within the three legume subfamilies (*Mimosoideae*, $n = 34$; *Faboideae*, $n = 25$; *Caesalpinoideae*, $n = 19$). We discarded all introduced species, and two rare native species (*Caesalpinia pulcherrima* and *Leucaena brandegeei*) for which we found no records in the herbarium collections we visited.

We checked four herbaria in Mexico (MEXU, ENCB, HCIB and BCMEX), and four in the United States (SD, UC, CAS, DS). For each specimen we captured the species identity and the geographic information on the collection site. When geographic coordinates were missing, we approximated them by locating the site from the description in the label. When the label description was insufficient to locate the collection site, we discarded the information from that specimen. We discarded approx. 20% of all the specimens checked, and we finally formed a database with 4205 geo-referenced records for a total of 78 species. Although we only registered in detail the records within the Peninsula of Baja California, we also registered qualitatively if the species had records outside the peninsula.

We divided the Peninsula of Baja California into 228 cartographic cells, each ca. 20' in longitude and 15' in latitude (see Fig. 1; each cell corresponds to a chart at a scale of 1 : 50 000 published by Mexico's National Institute of Statistics, Geography, and Informatics [INEGI], and covers ca. 698 km², although they may vary slightly in size). Cells ($n = 23$) without collection records were not included in the analysis.

Based on the herbarium and geographic information, we constructed two numeric matrices of 78 species × 205 geographic cells. One of them (a frequency matrix) contained in each element (i, j) the number of specimens collected for a given species (i) in a given cell (j), while the other (a presence-absence or incidence matrix) contained in each element a 1 if the species had been collected in that cell, or a 0 if the species had not been collected. The elements of the frequency matrix added to a total of 4205 records, while the incidence matrix totaled 1284 presences. Adding all the elements for each column (i.e. geographic cell) of the frequency and incidence matrices, we could estimate, respectively, the collection effort (h) or the species richness (α_i) in each cell.

Geographic ranges

For each species, we estimated from the incidence matrix its distributional range within Baja California as the number of cells where each species was found, i.e. as the sum of incidences for each species over all cells. We then analyzed the statistical distribution of ranges for the whole floristic set, comparing it with the lognormal distribution, under the null hypothesis that geographic ranges, as an estimate of abundance, are lognormally distributed (Preston 1960; May 1975; Rapoport 1975). Based on the ancillary information collected from the herbarium specimens, we also classified each species (App. 1) according to its distribution in the continent as: (1) endemics (*E*), for species whose distribution is restricted to the Peninsula of Baja California; (2) regional
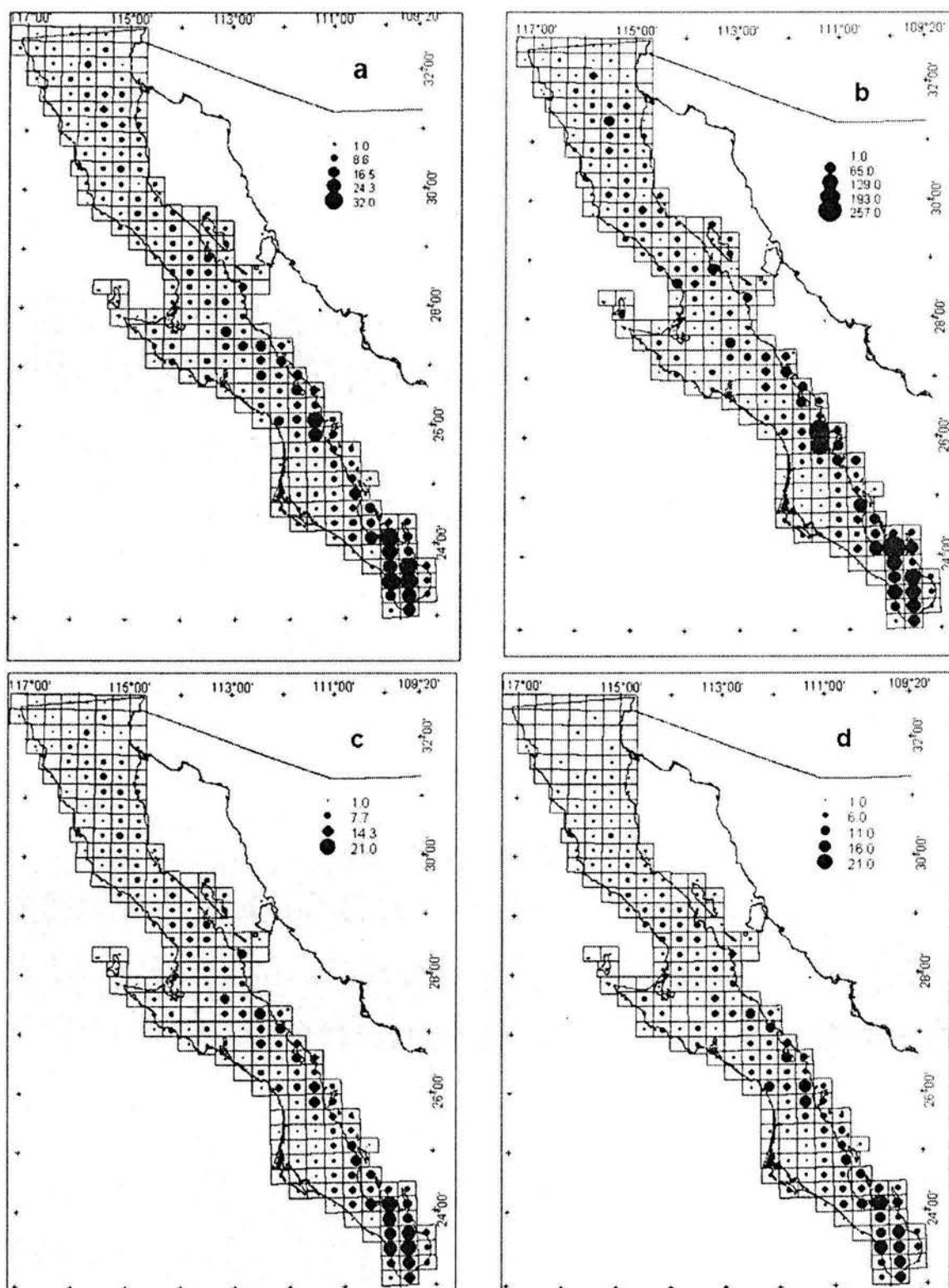
Fig. 1. Geographic distribution of (**a**) species richness of woody legumes; (**b**) collection effort measured in number of collected specimens of woody legumes per cell; (**c**) richness of genera of woody legumes; (**d**) richness of endemic species of woody legumes in Baja California. The size of each dot is proportional to the frequency value observed for that cartographic cell.

species (R), for species that are also found in the larger Sonoran Desert or in the California Biotic Province, and (3) continental species (C), for woody legumes that are widely distributed in North America, extending beyond the borders of Baja California, the Sonoran Desert, and the California Biotic Province (we classified as endemics some species that are also marginally present in the midriff islands of the Sea of Cortés and in the coastal fringe of the midriff in the Mexican State of Sonora).

By visually comparing the observed distribution maps of the 78 species, we identified six well-defined patterns of geographic distribution within the peninsula, and classified each of the species into one of the different patterns. These areas where many species tend to coincide were later used for the interpretation of other observed biogeographic trends.

Latitudinal effects

Species richness and endemism. We plotted species richness (α) of each cell against the latitiude of the cell. Additionally, we then calculated, for each geographic cell and for latitudinal bands of 15', the relative endemism, i.e. the proportion of endemic species with respect to the species richness of the cell or the band (E/α_i).

Latitude and species range. We calculated mean latitude for each species as the mean of the central latitude of all the cells in which the species was present, and plotted these values against its geographic range. Because some northern species have continuous, distributions north of the peninsula (into the California Biotic Province, or the Northern Sonoran and Mojave Deserts), we separated these from the analysis.

Biodiversity 'hotspots'

We tested whether the observed patterns of species richness (α) could be attributed to random variation, or whether they should be ascribed to some systematic cause. Firstly, we calculated the frequency distribution of species richness in the geographic cells, and tested it against a Poisson distribution as the null model for a random distribution of counts. Thus, we were able to identify cells that departed significantly from the Poisson model, either because they had a very high, or a very low number of species. We then proceeded to test whether these departures from the random null model could be attributable to collection biases introduced by (a) the effect of collection effort, or (b) the land area of the cell.

The effect of collection intensity. It is well-known that as collection effort increases in any given area, the number

of species found increases in a non-linear fashion, less than proportionally to the number of specimens, eventually approaching an asymptote that corresponds to the true richness of the area. The models that describe this relationship have been called 'accumulation functions' (e.g. Soberón & Llorente 1993; Flather 1996; Moreno & Halffter 2000). Of these, one of the most commonly used is Clench's model (Soberón & Llorente 1993):

$$s = \frac{abh}{a + bh} \tag{1}$$

where s is the species richness estimated for a given collection effort h, a is the asymptotic richness for well-collected areas (i.e. when $h \to \infty$), and b is the rate at which new species are found at the beginning of the collection process (i.e. when $h \to 0$). Although this model fits reasonably well most collection processes, it was not meant to compare different areas but to describe the accumulation process in any given area. When more than one area is involved, collectors often make a choice on where to collect based on how many uncollected species they are able to find for a given number of new specimens. Thus, we want a predictor of species richness that is based not on the absolute collection effort (measured as the number of specimens), but on the relative effort (measured as the number of species identified relative to the number of specimens collected). For this purpose, we re-wrote Clench's equation by solving for α as a function of (s/h):

$$s = a - \left(\frac{a}{b} \cdot \frac{s}{h} \right) \tag{2}$$

Let us now define the redundancy of a collection in a given area as $\rho = 1 - s/h$. If $\rho = 0$, each species is only supported by one voucher specimen, while if $\to 1$, then each species is supported by a large number of collected specimens. Thus, we can now re-write Eq.(2) in order to express the expected number of species in geographic cell i as a function of the redundancy of the collection effort in that same cell:

$$s_i = k + d\rho_i \tag{3}$$

where k and d are linear constants that can be estimated from simple regression by fitting for all the 205 cells of the peninsula the observed species richness (α_i) against the redundancy of the collection effort (ρ_i). With the parameters of the fitted equation, we can calculate for each cell the expected species richness (s_i), as predicted by the redundancy of the collection effort.

Effect of land area. One of the most common models used to describe the species-area relationship is the 'power function' model, $s = cA^z$, where s is the number of species present in an area of size A, z an exponent (showing values < 1 for the curve to be convex), and c is

a coefficient of proportionality (Arrhenius 1921; Preston 1962; MacArthur & Wilson 1967). For the 205 cells of our data set, this model can be re-written as $\alpha_i = cA_i^z$, where α_i is the species richness predicted by the model for a cell i whose land area is A_i. It also follows that for a cell of standard area A_0 the expected floristic richness will be $\alpha_0 = cA_0^z$. From these equations, it can be deduced that, if the expected richness (α_0) of a cell of standard land area (A_0) is known, the expected richness (α_i) of a cell with a different land area (A_i) can be calculated as

$$\alpha_i = \alpha_0 \left(\frac{A_i}{A_0}\right)^z \qquad (4)$$

If we make now (A_0) the land area of the cells for an average number of species, and if we replace the symbol for the expected richness α_0 by its equivalent s_i (the species richness expected after correcting for collection effort), then it follows that

$$\alpha_i = s_i \left(\frac{A_i}{A_0}\right)^z \qquad (5)$$

That is, the expected number of species in cell i, corrected for land area, can be simply derived from the collection-corrected richness (s_i), the ratio between the actual land area of the cell and the standard land area (A_i/A_0), and the exponent of the power function (z). It can also be shown that, in order to fulfill the condition that the sum of expected richness values for all cells equals the sum of the observed frequencies (a necessary condition for the analysis of frequency residuals), then the value of the standard cell area is equal to the exponentially-weighted average of all cell land areas:

$$A_0 = \left(\frac{\sum s_i A_i^z}{\sum s_i}\right)^{(1/z)} \qquad (6)$$

In order to estimate the value of the parameters, we randomly selected 20 cartographic cells, and added to each cell a random fraction of the contiguous eight cells, creating thus 20 area samples of geographic size ranging between one and nine cells (Dunn & Loehle 1988). The species richness in these cells of variable size was regressed against area using the log-log transformed model ($\log S = \log c + z \log A$), and the exponent z was estimated ($z = 0.498$). With this value, we estimated the average land area (A_0), which was 594 km^2.

A test for significant richness. Finally, the expected species richness for each cartographic cell was calculated by putting Eqs. (6) and (3) together:

$$\alpha_i = \left(k + d\rho_i\right) \cdot \left(\frac{A_i}{A_0}\right)^z \qquad (7)$$

where the parameters k and d are derived from the regression of species richness against collection redundancy, the exponent z is estimated from the species-area regression, and the standard cell area A_0 is calculated from the exponentially-weighted average of all cell land areas.

We then calculated the Pearson residuals (ε) between the observed and the predicted species richness values ($\varepsilon_i = (\alpha_i - \alpha_i)/\sqrt{\alpha_i}$), where α_i is the value predicted by Eq. (6). Because species richness values are discrete counts with expected Poisson distributions, the Pearson residuals should behave asymptotically as normal deviates (Everitt 1992), and their significance can be calculated from the Normal distribution. Thus, all cells having species richness values significantly higher than those predicted by the combined effect of the redundancy of the collection and the land area of the cell, can be plotted in the map as areas where biodiversity is higher than expected by either chance factors, by the effect of reiterated collection, or by the effect of large land areas (Mourelle & Ezcurra 1996). Finally, because by testing for significance of the residuals in 205 cells we run the risk of increasing the probability of type-I errors, we applied a Bonferroni correction on the acceptance threshold for significant residuals (Sokal & Rohlf 1995).
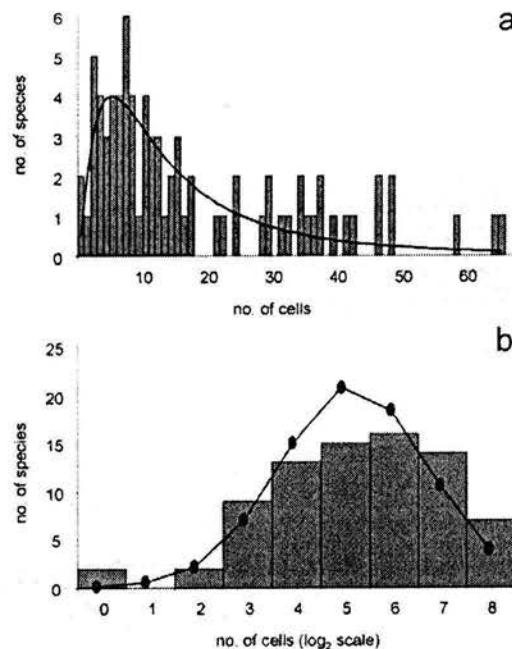

Fig. 2. Frequency distributions of the geographic ranges of woody legumes in Baja California. a. No. of cells on a linear scale; b. No. of cells on a logarithmic axis. In both plots, the continuous line marks the predicted values of the log-normal distribution, and at both scales, the observed histogram did not differ significantly from the predicted lognormal series ($P \gg 0.05$).

Results

The number of legume species in the cells varied between 1 and 32 (Fig. 1a), with the highest species richness towards the Gulf Coast and the Cape Region, east and south of the peninsula. Turner et al. (1995) reported similar patterns of richness for woody legumes in the Sonoran Desert region. Similar trends were found for the richness of genera (Fig. 1c), and for the richness of endemic species (Fig. 1d). The Pacific incline of the peninsula, although poor in legumes, has a relatively high proportion of endemic species. The collection effort varied greatly at the scale of our study: while some cells were represented in the collections by only one specimen, other cells yielded more than 200 specimens (Fig. 1b). As we expected, the effort of collectors seems to be the result of two factors, namely accessibility and floristic richness. Indeed, many cells with high species richness have been collected intensely and repeatedly, but also those cells that are nearer to the trans-peninsular highway are more collected than those removed from easy access. Additionally, many areas that are poor in legumes have been intensely collected, possibly because they present other interests for biologists. Areas such as the temperate forests of the Sierra de San Pedro Mártir, or the spectacular sarcocaulescent Central Desert clearly fall into this last category.

Geographic ranges

Each species occupied, on average, 17.8 map cells (some 11521 km^2). The distribution was markedly skewed, with the majority of species occupying less than 10 cells (ca. 7000 km^2), and three widespread species occupying more than 57 cells (ca. 40000 km^2). The observed distribution of ranges did not differ significantly from the lognormal distribution model (Fig. 2a, b), as has been reported repeatedly for other taxa (e.g., Willis 1922; Preston 1960; Rapoport 1975; Anderson 1977; Gaston 1990; Brown et al. 1996). All three subfamilies showed similar range distribution patterns.

With the exception of nine species distributed throughout the peninsula, all other 69 species could be classified into one of five distribution patterns (Fig. 3a-d): North (Lower Colorado Valley and mediterranean scrubs of the California Biotic Province, $n = 12$ species); Central Gulf Coast ($n = 9$); Pacific Coast ($n = 4$); South-Center ($n = 15$); and Cape Region (granitic tip of the peninsula, $n = 29$). Although poor in total richness, the fog deserts of the Pacific coast have a large proportion of endemics (Figs. 3c and 4c). The non-endemic flora of the Cape Region is composed mostly of species of wide continental distribution, while the non-endemic species in the rest of the peninsula are dominated by legumes of regional distribution.

Latitudinal effects

Species richness tends to increase towards lower latitudes, with two outstanding peaks of high diversity: the Cape Region and the Sierra de la Giganta (Fig. 4a). The same trend was observed for all subfamilies, although it was more marked for the Mimosoideae, a group of high tropical affinities. Within the group of endemic species, woody legumes in the south showed smaller ranges than species of central and northern affinities, i.e, micro-endemism is concentrated towards the Cape Region (Fig. 4b). Finally, the proportion of endemic species in latitudinal bands was quite constant south of the midriff region (ca. 60 - 70%, decreasing to around 50% in the Cape Region), but decreased rapidly north of 29° Latitude, as the California Biotic Province and the Lower Colorado Valley replace the Baja Californian deserts (Fig. 4c).

Biodiversity 'hotspots'

The distribution of species richness in cells was highly clumped: The mean richness per cell was 6.27, and the variance : mean ratio was 6.4, departing significantly ($P < 0.0001$) from the expected value of unity for random frequency values (Greig-Smith 1984; Hayek & Buzas 1997). Furthermore, the observed distribution also departed significantly from the random expectation of a Poisson distribution (Fig. 5).

The effect of collection intensity. The relationship between the number of species and the number of specimens collected fitted significantly to Clench's model (Fig. 6a). Furthermore, when the data were regressed against collection redundancy, it was found to conform significantly to the expected linear model (Fig. 6b). Indeed, the cells where the collection effort has been more redundant are, on average, better represented in the collections than those cells where redundancy is low.

Hotspots of significant richness. Sixteen cells were found where, after correcting for the effects of collection intensity and land area, the floristic richness still departed significantly from a random distribution (Fig. 7). These cells are located very clearly along the Southern Gulf Coast of the peninsula, and throughout the Cape Region, two biotic subdivisions of the Baja Californian drylands where the richness of woody
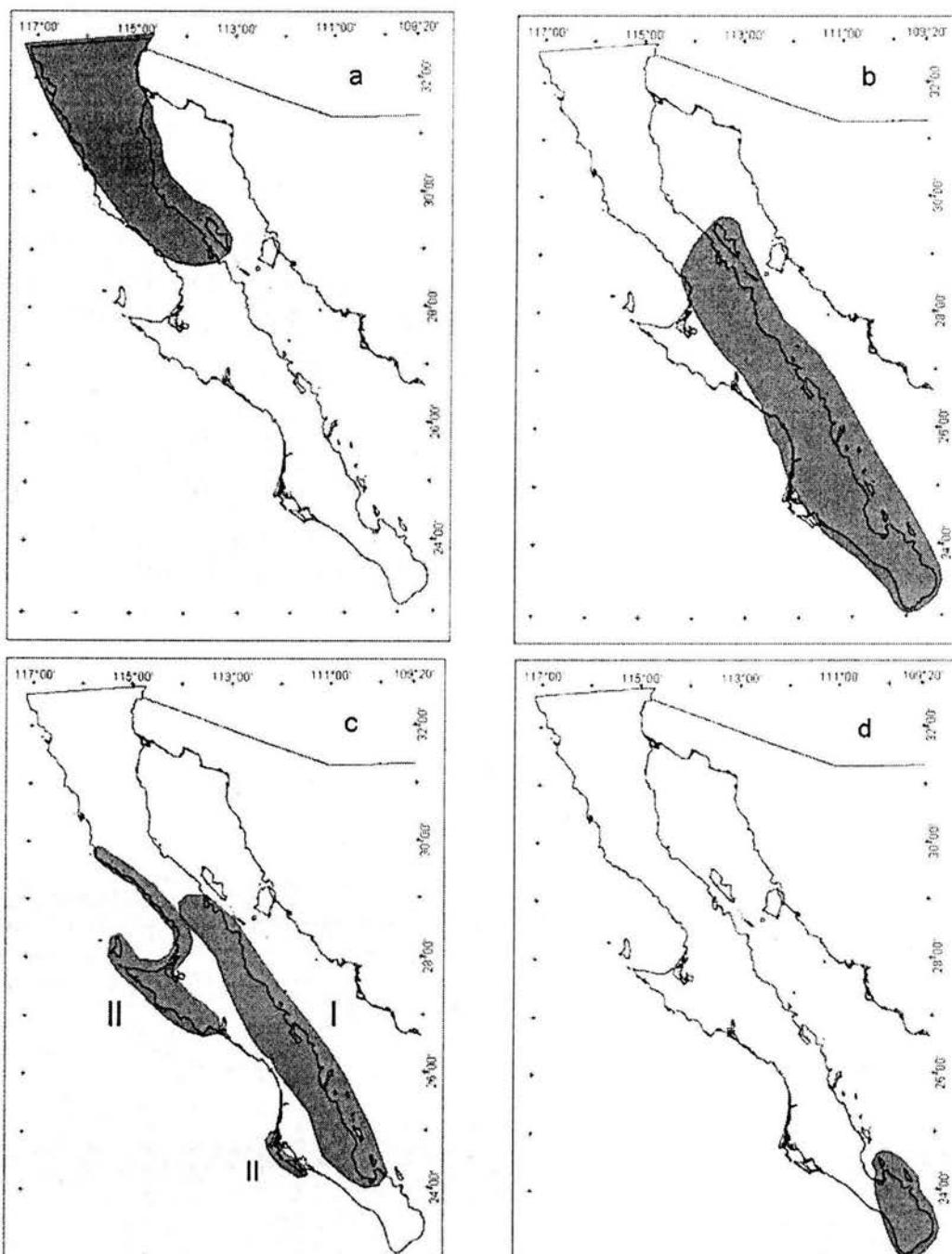
Fig. 3. Patterns of geographic ranges of woody legumes in Baja California: **a.** North; **b.** South-Centre; **c.** Central Gulf Coast (I) and Pacific Coast (II); **d.** Cape Region. The ratios endemic:regional:continental species is 1:6:5 for the North; 13:1:1 for the South-Centre; 6:2:1 for the Central Gulf Coast; 4:0:0 for the Pacific Coast; and 12:2:13 for the Cape Region.

legumes is much higher than could be expected by chance variation. Sixty species –77% of the total flora – are present in these cells, which jointly conform less than 8% of the region's terrestrial surface. The only species not found in these high-diversity cells are the 12 species of northern distribution, the four species associated to the Pacific Coast, and two rare legumes: *Eysenhardtia peninsularis*, restricted to the center of the peninsula, and *Senna pallida*, found only in a small part of the Pacific coast in the Cape Region.
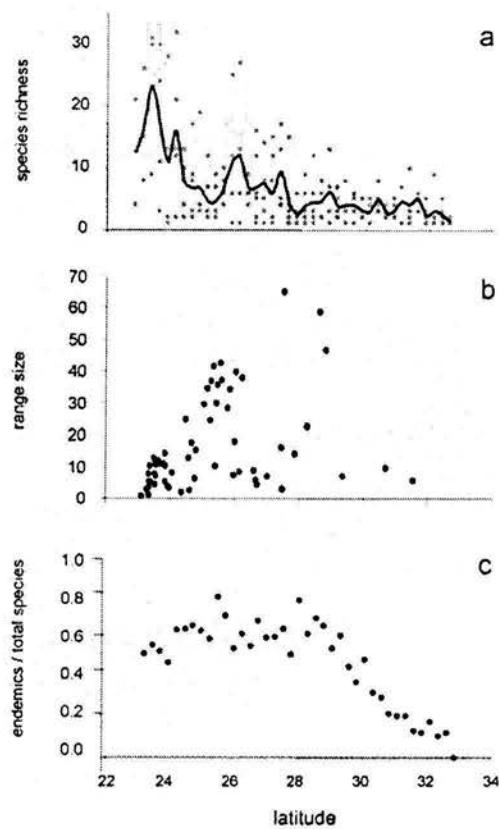
Fig. 4. a. Relationship between latitude and richness of woody legumes in 205 cartographic cells of Baja California. The continuous line marks the mean richness for each latitudinal band, and the arrows mark the latitudinal location of the Cape Region and the Sierra de la Giganta. **b.** Relationship between the range size of endemic species (measured as the no. of cells where the species has been collected) and its mean latitude (measured as the average latitude of all cells where the species is present). **c.** Proportion of endemic species in latitudinal bands of 15'.
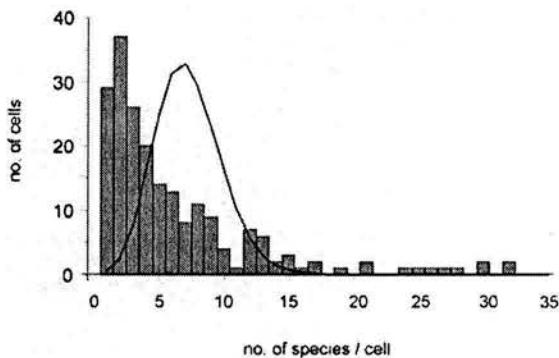

Fig. 5. Statistical distribution of species richness of woody legumes in the 205 cells. The bars mark the observed frequencies, the continuous line shows the expected Poisson values. The observed values differed very significantly from the expected random distribution ($G = 467$; $df = 12$; $P \ll 0.0001$).
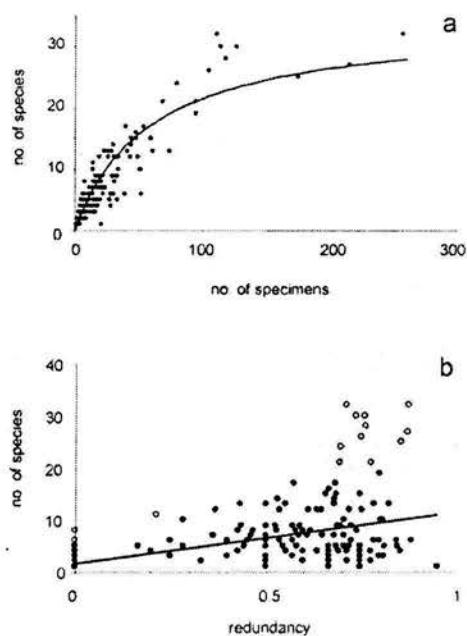
Fig. 6. a. Relationship between the number of species and collection effort (estimated as the number of collected specimens) for the 205 cartographic cells. The line shows Clench's model, fitted by non-linear regression ($r^2 = 0.89$; $P \ll 0.0001$). **b.** Relationship between the number of species and collection redundancy (ρ_i, an estimate of relative collection effort). The line shows the linear model linking redundancy and the estimate of richness ($r = 0.44$; $P \ll 0.0001$). The open dots indicate cells where the observed species richness was significantly higher than the predicted value (see Text).
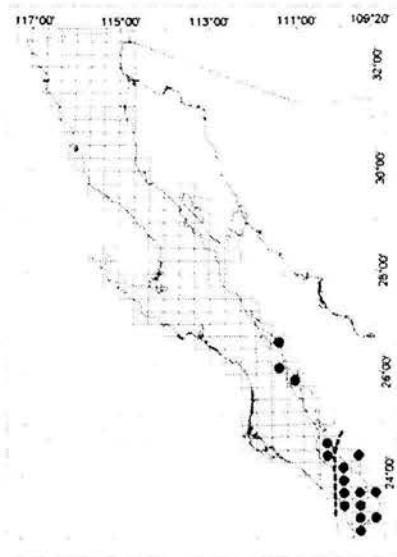
Fig. 7. Biodiversity 'hotspots' of extraordinarily high species richness for woody legumes in the peninsula of Baja California. The dotted line shows La Paz geologic fault, which separates the Cape Region from the rest of the peninsula.

Discussion

With very few exceptions, most species seemed to follow well-defined distribution patterns that coincide well with Shreve's (1951) subdivisions of the Baja California Peninsula: (1) the northern mediterranean sclerophyllous scrubs; (2) the Lower Colorado microphyllous desert; (3) the Central Gulf Coast's hot sarcocaulescent desert; (4) the Pacific Coast fog-fed, sarcophyllous scrubs; (5) the crassicaulescent deserts of the South, and (6) the tropical scrubs and dry forests of the Cape Region. Endemism is high throughout most of the peninsula, and especially in its central part, possibly as a result of its 6 million years of isolation from the mainland, as reported by Murphy (1983), and by Due & Polis (1986), among others, for other taxa. The proportion of endemic species, however, is not correlated with species richness, and tends to be relatively high in the isolated, legume-poor coastal scrubs of the Pacific.

Many biogeographic patterns and trends, described for other taxa, are also found in the woody legume flora of Baja California: The species abundances, as estimated by their geographic ranges, conformed very closely to the lognormal distribution of abundances, as described and predicted by many authors (e.g., May 1975; Pielou 1975; Preston 1980; Magurran 1988) who have postulated the lognormal as the null random model of species abundance. It is interesting to note that, although the distribution of species ranges fits to the lognormal distribution, the scatter of these ranges in space is not random but tends to concentrate in some geographic areas. Indeed, some cartographic cells showed significantly more species than could be expected by chance, and clearly formed well-defined 'hotspots' of floristic richness.

Legume species richness is correlated with latitude, as has been amply reported for many other groups (e.g., Pianka 1966; Stevens 1989; Rosenzweig 1992; Rohde 1998). A full 73% of the legume flora of Baja California is restricted to the southern half of the peninsula. Additionally, the species' ranges tend to decrease towards the tropics, confirming again a well-reported phenomenon known as 'Rapoport's rule,' which predicts that micro-endemism increases towards the equator (Stevens 1989; Mourelle & Ezcurra 1997). However, the proportion of endemic species is higher in the central part of the peninsula, as many tropical leguminous trees of widespread distribution in continental Mexico are also present in the dry forests of the Cape Region.

The causes of extremely high endemism in the isolated central part of the peninsula are possibly related to the evolutionary history of the region during the Pleistocene Epoch (1.8 MYBP). During this period,

some 15-20 glacial-interglacial cycles occurred (Imbrie & Imbrie 1979; Van Devender & Burgess 1985), and during the glacial phases, which occupied as much as 95% of the Epoch, temperate woodlands and the sclerophyllous chaparrals occupied large parts of the peninsula and the dry scrub became fragmented and retreated into hot, climatically stable, lowlands (Van Devender 1990; Riddle & Honeycutt 1990; Grismer & McGuire 1993; Peinado et al. 1994). Conversely, during the interglacial phases, which were warmer and drier, the woodlands and chaparrals retreated north or high-up into the mountains, and the lowlands became again covered by arid scrubs. It is likely that the succession of long glacial periods followed by short interglacials may have generated the local extinction of species with strict tropical affinities, which found refuge in the climatically stable tropical lowlands of the Cape Region, and secondarily in the hot lowlands of the Lower Colorado Valley (Peinado et al. 1994). At the beginning of the Holocene (ca. 11000 YBP) the current dry, warm deserts expanded (Axelrod 1979, 1981), and the dryland species spread from these refuges, possibly giving origin to the northern and southern patterns described in Fig. 4. The less drought-tolerant tropical species, however, must have been limited by the dry nature of the early Holocene (the Hypsithermal climatic interval, 8000-4000 YBP; Spaulding 1991) and mostly remained in the hot lowlands of the Cape Region, with a secondary expansion corridor in the southern Gulf Coast, along the wetter, warm canyons of the Sierra de la Giganta.

Other authors have given other reasons for the high floristic richness of the Cape Region. Some argue that when the Cape Region drifted from its original location off the coast of Jalisco (some 6 MYBP), it must have transported a significant section of the seasonal dry tropical forest of the Pacific coast, which, as noted by Gentry (1995) is exceptionally rich in legumes. This original species pool was maintained in relative isolation from the rest of the peninsula during the Miocene and the mid-Pliocene (Murphy 1983; Riddle et al. 2000; Carreño & Helenes 2002), and kept relatively stable climatic conditions (Axelrod 1958, 1979). Under this interpretation, the Cape Region is simply an ancestral relict of the Pacific dry forests of Jalisco. Other researchers, on the other hand, argue that, because of its different origin, the Cape Region has a geologic substrate dominated by granite, which is markedly different from the extrusive substrates, mostly basalt, that are found on the ranges in its vicinity (see León de la Luz 2000, and references therein). The main argument behind this last line of reasoning is that the floristic transition between the Cape Region and the peninsular deserts occurs abruptly around the La Paz Fault, sharp N-S line that separates both geologic origins.

Conclusions

1. The geographic ranges of legume species in Baja California follow very closely the lognormal assumptions of random differences in abundance from one species to the next.

2. The spatial distribution of ranges, however, is clumped around well-defined hotspots of species richness.

3. Species richness and micro-endemism increase towards the tropical tip of the peninsula, conforming well to the predictions of Rapoport's rule.

4. The proportion of endemic species, however, tends to peak towards the center of the peninsula, where the driest deserts are found, and where significant floristic changes took place during Pleistocene glacial events.

5. The floristic hotspots for woody legumes in Baja California occur in the Cape Region and along the Sierra de la Giganta in the southern Gulf Coast, where 77% of the total peninsular legume flora can be found.

6. These hotspots are mostly unprotected, and should be considered priority areas for future conservation efforts.

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CAPÍTULO II

REGIONES BIOGEOGRÁFICAS Y DIVERSIDAD BETA DE LEGUMINOSAS LEÑOSAS EN LA PENÍNSULA DE BAJA CALIFORNIA, MÉXICO

Biogeographic regions and β-diversity of woody dryland legumes in the Baja California peninsula, Mexico *

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Abstract

We analyzed the floristic turnover, or β-diversity patterns, of woody legumes in Baja California, a 1,300 km long peninsula in NW Mexico that runs in a predominantly N–S direction. From the specimen labels of eight herbaria, we digitized 4,205 records from 78 species, and projected them onto a grid of 205 cartographic cells (20' longitude × 15' latitude). We found that E–W turnover from the Pacific coast to the Sea of Cortés was high (ca. 60% change from one cell to the next), and significantly associated with topographic variation across the peninsula. An analysis of between-site similarities showed that floristic regions in the peninsula have well-defined boundaries, and that floristic similarities tend to extend for long distances along the coastal corridor of the Sea of Cortés. Finally, a numerical classification of Baja California based on the floristic attributes of the cells separated the peninsula into five well-defined regions that coincide very closely with regionalisations previously proposed by various authors using descriptive methods, and with the areas of endemism described for the peninsula in a previous paper. We conclude that the ecological regions of woody legumes in the peninsula clearly reflect the two main environmental forces that act on it, namely, the long temperate–tropical climatic gradient, 1,300 km long, and the dramatic E–W gradient that runs from the Pacific Ocean across the mountain divide into the Sea of Cortés in approximately 100 km.

(5,569 words)

Introduction

The peninsula of Baja California, a narrow sliver of land 1,300 km long, around 110 km wide on average (ranging from 40–200 km), and covering 145,000 km^2 in area, contains in its limited area one of the most spectacular biological transitions in the world. Its northwestern part receives winter rains from Pacific storm fronts, and belongs to California Floristic Province (Minnich & Franco-Vizcaíno 1998). Its southern tip receives the late-summer cyclones called *chubascos*, and is covered by a unique variant of the dry tropical forests of the Mexican Pacific coast (Martin et al. 1999; Robichaux & Yetman 2000). Both these ecosystems have been identified as biological hotspots of richness and endemism (Myers et al. 2000; Ezcurra et al. 2002). Additionally, the northeastern part of the peninsula contains a corridor, 300 km long, that continues the Lower Colorado Region of the Sonoran Desert along the coast of the Sea of Cortés (or Gulf of California). Lying within these extremes, the rest of the peninsula is a long arid corridor with scanty, random, bi-seasonal precipitation that connects the temperate ecosystems of the north with the dry tropical ecosystems of the south (Fig. 1).

A second axis of variation is given by Baja California's mountainous backbone, which runs along the centre of the peninsula from north to south, with few interruptions. This generates two contrasting watershed slopes: the Pacific slope, whose climate is controlled by the cold upwellings of the N–S California current, with winter rains and coastal fogs, and the Gulf slope, hotter and with a higher proportion of monsoon-type summer rains. These two axis of climatic variation, N–S and E–W, form the core of all the different biogeographic subdivisions that have been proposed for the peninsula (e.g., Shreve 1951; Wiggins 1980; Murphy 1983; Peinado et al. 1994; Arriaga et al. 1997).

Additionally, climate variations during the Quaternary in the region have induced the formation of a series of "sky-islands" in the highest ranges, where remnants of the ancestral Madro-Tertiary temperate flora, which covered the region during the Pliocene, still survive in isolation (Axelrod 1958, 1979; Van Devender 1990; Riddle & Honeycutt 1990). Similarly, the deep,

moist canyons that dissect the mountain slopes harbour palm oases with relicts of tropical vegetation types (Grismer & McGuire 1993; Arriaga & Rodríguez-Estrella 1997). Thus, as a result of its complex topography, climate, and evolutionary history, Baja California is one of the most spatially-diverse regions of the world, where in expanses of less than 100 km contrasting combinations of different climates and environments can be found, which occur thousands of kilometres apart in larger continental areas (Ezcurra 2001).

Baja California harbours some 3,000 plant species, 670 of which are woody trees and shrubs (Shreve & Wiggins 1964; Wiggins 1980; Lenz 1992; León de la Luz et al. 1995, 1999). The peninsula, however, is largely covered by sparse desert vegetation, which locally is relatively species poor. Its great biological diversity, thus, seems to be more due to spatial heterogeneity and ensuing species turnover (β-diversity) than to a high local species richness (α-diversity). In this paper we attempt to explore and test this statement using the woody legumes of the peninsula as a test group.

In a previous paper we analysed the distributional patterns and hotspots of species richness within the peninsula (Garcillán et al. 2003). For the present study, we investigated the means through which high species turnover can maintain an elevated regional diversity in spite of low local richness. For this purpose, we tested the following simple hypotheses: (a) that the peninsula has a high β-diversity relative to other, more homogeneous, regions; (b) that, because the peninsula lies largely in a N–S direction, the floristic similarity between different areas of the peninsula is related to the differential influence of the east and west divides and the corridors they have formed during evolutionary history; and, (c) that the ecological regions of the peninsula reflect the two main environmental forces that act on it, namely, the long N–S climatic gradient, and the short, sharp E–W gradient that runs from the Pacific Ocean across the mountain divide into the Sea of Cortés.

Methods

Woody legumes are one of the most distinctive elements of the Sonoran and Baja Californian Deserts (Dimmitt 2000; Ezcurra et al. 2002). They play a crucial role as fertility islands and safe sites for many desert species (McAuliffe 1990; Smith et al. 1997), and can act as "nurse plants" by facilitating the establishment of other species under their canopy. A detailed description of the study group, its importance as a cornerstone life-form, and the dataset used, can be found in Garcillán et al. (2003), and references therein.

We worked with 4,205 georeferenced records from the 78 species of woody legumes of Baja California, belonging to 32 genera within the three legume subfamilies, and digitized from herbarium labels from nine herbaria. Following Riemann (2001), we divided the Peninsula of Baja California into 228 cartographic cells, each approx. 20' in longitude and 15' in latitude. Twenty-three cells contained no collection records, and were not included in the analysis, which thus consisted only of 205 cells.

Based on herbarium and geographic information, we constructed a presence-absence or incidence matrix (78-species × 205-cells) containing in each element a 1 if the species had been collected in that cell, or a 0 if the species had not been collected. The elements of the matrix totalled 1,284 presences. Adding all the elements for each column (i.e., geographic cell) of the matrix, we could estimate the species richness (α_i) in each cell.

Species turnover along E–W transects

Because of the large latitudinal span and the predominant N–S direction of the peninsula of Baja California, and because of the longitudinal mountain ranges that divide the Pacific from the Sea of Cortés, we also analyzed species turnover along E–W transects, going from one coast to the other. For this, we used the simple model proposed by Schluter and Ricklefs (1993), which is in turn related to Whittaker's (1960) and Harrison, Ross and Lawton's (1992) models:

$\gamma = n.\beta.\bar{\alpha}$, where γ is the total richness (i.e., the number of species in the whole transect), $\bar{\alpha}$ is the mean species richness of the transect cells, β is the mean species turnover from one cell to the next, and n is the number of cells in the transect. That is, the product $n.\beta$ measures how many times larger total species richness is compared to mean cell richness. From this, it can be

deduced that a simple estimate of β-diversity in a transect is given by the ratio $\beta = \gamma/(n.\bar{\alpha})$. Using this model, we calculated β-diversity within each of the 38 transects that comprise the peninsula and plotted the values against transect latitude.

In order to test whether β-diversity is related to landscape heterogeneity, we calculated for each transect a series of estimates of topographic variation. For this purpose, we measured in each cell its maximum altitude and the altitude of six points distributed regularly within the cell. With this information we estimated the maximum altitude of the transect (a measure of abruptness of the peninsular divide), the mean altitude (by averaging all point measurements), and the standard deviation of both measures (an estimate of the topographic ruggedness within the transect). We then correlated the β-diversity estimated for each transect against the estimates of topographic variation.

Species turnover between transects (N–S turnover)

We also calculated the turnover between adjacent E–W transects, using the same model described above: $\beta = \gamma/(n.\bar{\alpha})$, where γ is the total richness of both transects together, $\bar{\alpha}$ is the average species richness of the pair of transects, β is the mean species turnover from one transect to the next, and n is the number of transects (i.e., $n = 2$). With this model, we calculated the β-diversity between the 38 transects of the peninsula, and plotted its values against the latitude of the boundary between transect pairs. We also tested for a statistical relationship linking between-transect turnover and landscape heterogeneity, as described in the previous section.

Floristic affinity between regions

In order to test for affinities between floristic regions, we used Rapoport's "barriers and corridors" method (Rapoport 1975; Rapoport & Ezcurra 1979; Mourelle & Ezcurra 1996). This approach consists in selecting a reference, or base, cell located in the central part of previously defined biogeographic regions, and calculating the similarity of all the rest of the cells against the base. In this case, similarity is defined as the proportion of species from the base cell that are also present in another cell. When the similarity values are plotted on a map, it is possible to

see how high-similarity corridors are distributed, and hypotheses on the regional distribution of similarity can be made.

Floristic similarity and geographic distance

Turnover, or β-diversity, has been also estimated from the way floristic similarity between sites decreases with distance (Condit et al. 2002). Following this approach, we calculated all the pairwise floristic similarity values between all the 205 cells with plant records in the peninsula, using Jaccard's index of similarity (Hengeveld 1990). Additionally, we calculated all the pairwise geographic distance values between the cells. We then regressed the similarity values against the distances, and fitted to these values the exponential decay model $S_d = S_0 . e^{-kd}$ (Preston 1962; Whittaker 1972; Okubo & Levin 1989; Nekola & White 1999), where S_d is the predicted similarity between sites that are separated by a distance d ; S_0 is the mean floristic similarity between immediately adjacent sites (similar to the "nugget" effect in semivariograms; see Nekola & White 1999), and k is a parameter that depends on the intensity of turnover. Using non-linear regression, we fitted this model to the whole dataset, and also to the subset of all cells in the Pacific slope (i.e., the Pacific floristic corridor) and to a second subset of all cells lying in the Sea of Cortés side of the divide (i.e., the Gulf corridor). Through simple z-tests using the standard error of the estimated parameters, we compared the S_0 and k values of the three datasets.

Floristic classification

Finally, we performed a numerical classification of the 205 cells based on their floristic attributes. For this purpose, we submitted the presence-absence matrix to a divisive multivariate classification procedure. We used Noy-Meir's (1973) method, based on partitioning the group of cells into two subsets along the first axis of a Principal Component Analysis (PCA). The partitioning criterion we used was minimizing the within-group variance along the first axis. Once the original matrix was divided into two subgroups, we tested for the one with the largest floristic variance (estimated from the trace of the variance-covariance matrix) and divided it again to form three groups, which were evaluated for their floristic variance. The group with the largest variation was again selected, and the procedure was iteratively repeated. At each step,

we evaluated the significance of the partition by comparing the variance explained by the first axis against the predicted values of the broken–stick distribution (Jackson 1993). The divisive procedure was stopped when the broken–stick test indicated that the residual floristic variation in the subgroups could be attributed to chance. Finally, because PCA is a two-way scoring procedure similar to Correspondence Analysis (CA; see Ezcurra 1987, and references therein), we used the divisive algorithm to produce a list of indicator species, similarly to the TWINSPAN algorithm based on divisions along CA axes (Hill 1979).

Results

Species turnover along E–W transects

Beta diversity within E–W transects varied between 0.40 and 0.82, with a mean value of 0.62 (Fig. 2a). That is, on average within a transect more than 60% of all species are replaced from one cell to the next. Latitudinally, we found no significant trend in within-transect turnover. However, four regions of high E–W turnover could be identified by simple visual inspection of the plot (Fig. 2a). These were (1) the northern Sierra de la Laguna (23° – 24° Lat. N), (2) the Magdalena–Sierra de la Giganta transects (25° – 26° N), (3) The Vizcaíno–Sierra de San Francisco transects (27° – 28° N), and (4) the Mediterranean–Lower Colorado transects (30° – 32° N), which include the high northern ranges of San Pedro Mártir and Sierra de Juárez. All these transects cross over high mountain ranges of abrupt topography. In agreement with this observation, we found that transect β-diversity was significantly correlated ($r = 0.51, P < 0.001$) with the standard deviation of transect altitude, a measure of topographic heterogeneity (Fig. 2b).

Species turnover between transects (N–S turnover)

N–S turnover between adjacent transects varied less than E–W turnover, and showed values ranging between 0.55 and 0.79, with a mean value of 0.64 (Fig. 2c). That is, on average from one transect to the next more than 60% of all species are replaced. We found no significant latitudinal trend in between-transect turnover; one region of high N–S turnover could be

identified by visual inspection of the plot, found at 28° N, in the mid part of the peninsula, and a second one at 33° N, near the Mexico–U.S. border.

Floristic affinity between regions

We selected seven base cells in the central part of the main biogeographic regions of Baja California shown in Fig. 1. Of these, only six maps are shown in Fig. 3a–f. We did not map the results for the Magdalena region, as this part of the peninsula only has a few generalist species recorded in it, and its cells had high similarity with almost all of the rest of the peninsula. The results for each base cell are as follows:

(a) *Mediterranean Region.* We chose as base cell an area of chaparral ca. 32° N. The high similarity cells followed a N–S corridor along the mountains of the Mediterranean Region, with an abrupt limit towards the Lower Colorado Region. Some 20–40% of the temperate woody legumes found in the chaparral follow the Madro-Tertiary mountainous backbone of Baja California all the way into the tropical tip of the peninsula. (b) *Lower Colorado Region.* The similarity map for this base cell demarcates a well-defined region that runs along the upper gulf coast (but does not cross over into the Mediterranean ecosystems), showing relatively high similarities down to latitude 29° N. Below this boundary, floristic affinity decreases sharply, but some low affinity values are still observed along the Central Gulf Coast. (c) *Central Desert.* The base cell in the Central Desert showed high similarity with parts of the Mediterranean region, and also with the Vizcaíno Desert and the Central Gulf Coast, a fact that underscores the transitional nature of this area. (d) *Vizcaíno Desert.* The Vizcaíno region also showed high similarity with neighbouring regions, especially with the Central Desert and the Central Gulf Coast, showing, as in the previous case, a presence of many species of wide distribution and a transitional floristic nature. (e) *Central Gulf Coast.* As was the case with the Lower Colorado, the similarity map for the Central Gulf Coast demarcates a very well-defined region that runs along the eastern coast of the peninsula, showing relatively high similarities up to 27° N, i.e., the beginning of the more transitional Vizcaíno region. Southwards, however, this area shows high affinities with the Cape Region. (f) *Cape Region.* The Cape Region, an area of extremely high endemism and species richness within the peninsula (Garcillán et al. 2003), shows a well-defined boundary that runs along the La Paz geologic fault, with a low proportion of its species shared with the Central Gulf Coast.

Floristic similarity and geographic distance

The parameters of Whittaker's exponential model differed significantly from one slope to the other (Fig. 4a–c). For the whole peninsula, the intersect value was $S_0 = 0.199$ (± s.e. = 0.006), and the exponent value was $k = 0.0033$ (± s.e. = 0.0001). For the Pacific slope, the intersect was $S_0 = 0.196$ (± s.e. = 0.005), and the exponent was $k = 0.0039$ (± 0.0001). For the Gulf slope, the intersect was $S_0 = 0.303$ (± s.e. = 0.007), and the exponent was $k = 0.0025$ (± s.e. = 0.0001). The intersect did not differ significantly between the whole peninsula and the Pacific slope, but it was significantly higher ($P \ll 0.00001$) for the Gulf slope. The exponent was somewhat higher for the Pacific slope compared to the whole dataset set ($P = 0.0006$), and very low for the Gulf corridor compared to the other two datasets ($P \ll 0.00001$). In short, both parameters differed significantly from one slope to the other. The Gulf slope had higher expected similarity between neigbouring cells (S_0) and a lower turnover rate (k), implying that, for any geographic distance, it is expected to find higher between-cell similarities in the gulf than in the Pacific slope. Converting the k-values to estimates of half-changes per unit distance, the mean turnover rate for the whole peninsula is 0.48 half changes per 100 km; along the Pacific slope it is 0.56, while for the Gulf it is 0.36.

Floristic classification

The divisive classification procedure was continued until five groups were identified (Fig. 5a–c). Below this level, the variance explained by new divisions did not differ from the predictions of the broken–stick test under the assumption of random variation. The first division separated the northern part of the peninsula from its southern section at around 28° N. Subsequent divisions chiefly separated the cells according to the peninsular divide. Group 1, in the north, corresponds very closely with the Mediterranean region together with the coastal fog-influenced communities of the Vizcaíno Region and the Central Desert. Group 2 is found on the eastern slope of the northern part of the peninsula, and corresponds closely to the Lower Colorado Region. Group 3 is formed by cells in the southern Pacific slope of the Peninsula, where coastal fogs are less important. This is an area of very low richness in woody legumes. Group 4 lies almost entirely within the boundaries of the Cape Region, plus some of the rocky outward islands of Magdalena Bay. This group harbours the species-rich, dry-tropical ecosystems of the

southern tip of the Peninsula. Finally, Group 5 is found along the southern Gulf coast of the peninsula and corresponds well to the ecological region of the Central Gulf Coast. The most characteristic indicator species are: (Group 1) *Prosopis glandulosa* and *Senna purpusii*; (Group 2) *Errazurizia megacarpa* and *Caesalpinia virgata*; (Group 3) *Dalea brandegeei*, (Group 4) *Indigofera fruticosa, Mimosa xantii, Senna villosa,* and *Senna atomaria,* and (Group 5) *Cercidium microphyllum,* and *Prosopis articulata.* A full list of indicator species and their indicator value is provided as an electronic appendix to this paper.

Discussion and conclusions

Species turnover of woody legumes in Baja California is high: On average, more than 60% of the species are replaced from any cell to the next in E–W transects, or between transects for N–S comparisons. Harrison et al. (1992) found an E–W turnover rate of 0.32 for native trees in Britain, with cells of similar size. That is, turnover in Britain is around half of the rate found in our study region. Similarly, using Whittaker's exponential decay model we found for our data set a turnover rate of 0.48 half-changes for each 100 km, a value remarkably higher than rates reported by Condit et al. (2002) for tropical forests in South and Central America (0.08 half-changes per 100 km for a transect between Peru and Ecuador, and 0.28 between Ecuador and Panama), and also 16 times higher than the turnover rate of 0.03 reported by Nekola & White (1999) for lowland boreal spruce forests between Newfoundland and Alaska.

Floristic turnover was unrelated to latitude, but showed a significant correlation to topographic heterogeneity. The turnover rate from north to south was remarkably constant, but the turnover rate from east to west was very strongly associated to landscape variation. This is consistent with the topographic nature of the peninsula; an E–W transect ranging from one sea to the other must necessarily cross the peninsular divide, and hence it would be expected that the ruggedness of the transect would have a strong bearing on floristic change. In contrast, the long coastal plains flanking the peninsula on both sides act as continuous corridors for biological dispersal.

This hypothesis was further corroborated by Rapoport's "barriers and corridors" analysis, which showed clearly that (a) floristic regions in the north and in the south of the peninsula have well-defined boundaries, and (b) that floristic similarities tend to extend in a N–S

direction, especially along the coastal corridor of the Sea of Cortés. The analysis of floristic similarity vs. geographic distance ratified these conclusions further. The similarity between neighbouring sites (S_0) was significantly higher, and the turnover rate (k) was significantly lower, in the Gulf corridor than in the rest of the peninsula. That is, within the general framework of extremely high turnover in Baja California, the coastal corridor of the Sea of Cortés is the area where β-diversity is lower.

Finally, the numerical classification of Baja California based on floristic attributes separated the peninsula into five well-defined regions (Fig. 5c). This regionalisation is coherent with the analyses of β-diversity described previously. Along a N–S gradient, the peninsula is divided into three distinct regions: the northern region, with winter rains that result from coastal upwellings; the central region, dominated by hot subtropical deserts, and the dry tropical ecosystems of the Cape Region. The northern and central regions, in turn, are divided across the short E–W gradient by the mountain divide into the Pacific coastal ecosystems to the west, and the hotter Gulf deserts to the east. Thus, to the north the woody legumes define two floristic regions: (a) the mild Pacific coastal ecosystems, fed primarily by winter rains, and (b) the deserts of the Lower Colorado Valley, with extremely hot summers and a bimodal rainfall pattern (Ezcurra & Rodrigues 1986). In the center, the peninsula separates into two floristic regions: (a) the coastal deserts of Magdalena and El Vizcaíno, and (b) the Central Gulf Coast, which includes most of the mountains of San Francisco, Guadalupe and La Giganta. Finally, in its hot, species-rich southern tip, Baja California forms the Cape Region, covered by dry tropical forests. This numerical classification coincides very closely with the regionalisations of the peninsula proposed by various authors (e.g., Shreve 1951; Wiggins 1980; Murphy 1983; Peinado et al. 1994). Additionally, the long N–S bipolar gradient detected by the classification also coincides closely with the areas of endemism previously described for the peninsula (Garcillán et al. in press), with a reduced group of legume species of northern distribution; another, larger, group of southern affinity, and a low overlap between the two. In the middle, the Central Gulf Coast, the desert region with the highest regional precipitation (Hastings & Turner 1965; Crosswhite & Crosswhite 1982) acts as an efficient northwards corridor for woody legumes of tropical affinity.

We end this paper with the following conclusions: (a) Baja California has an extremely high β-diversity of woody legumes, mostly as a result of its abrupt topography and contrasting influence of the two surrounding seas. (b) Because the peninsula lies chiefly in a N–S direction along a central mountain range, the floristic similarity between different areas is related to the contrasts imposed by the two divides and the long corridors formed along the two coasts. (c) The ecological regions of woody legumes in the peninsula clearly reflect the two main environmental forces that act on it, namely, the temperate–tropical climatic gradient, 1,300 km long, and the dramatic E–W gradient that runs from the Pacific Ocean across the mountain divide into the Sea of Cortés in 100 km or less.

Acknowledgements

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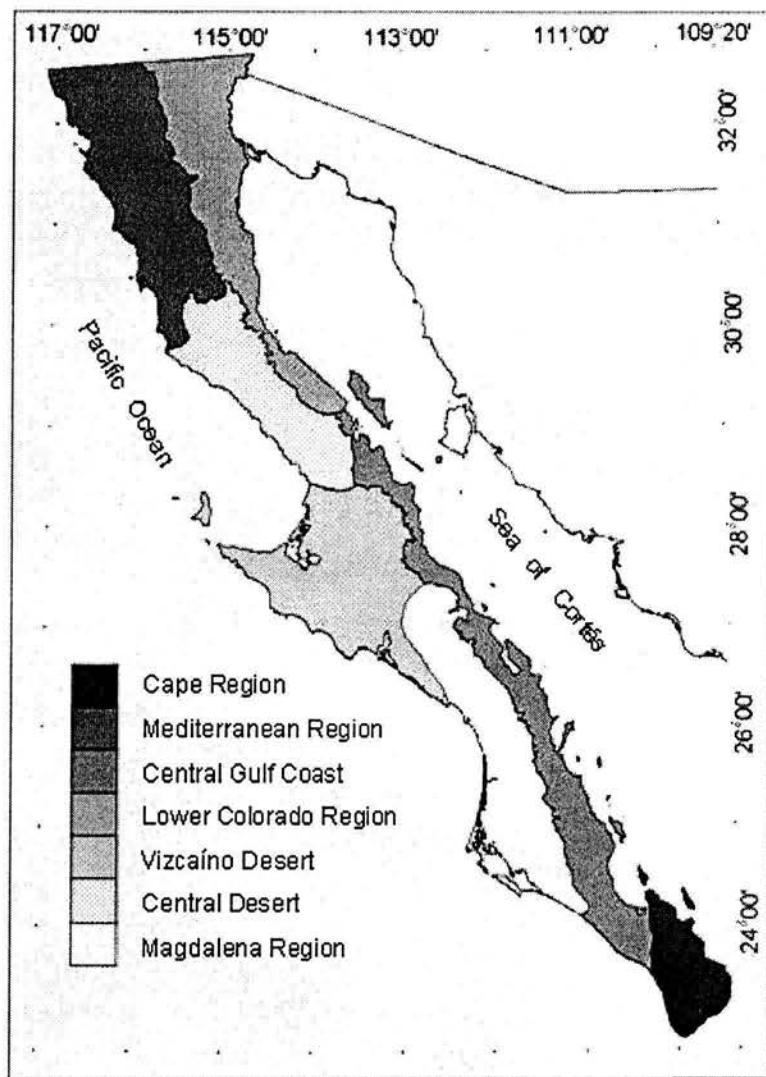
Fig. 1. Floristic regions of Baja California, modified from Shreve (1951), Wiggins (1980), León de la Luz et al. (2000), and Riemann (2001). Subdivisions: (1) Cape Region (dry tropical scrubs and forests); (2) Mediterranean Region (sclerophyllous scrubs); (3) Central Gulf Coast (sarcocaulescent desert); (4) Lower Colorado Region (microphyllous desert); (5) Vizcaíno Desert (sarcophyllous and sarcocaulescent desert); (6) Central Desert (Pacific coast, fog-fed sarcophyllous scrubs), and (7) Magdalena Region (arbocrassicaulescent desert). See Shreve (1951) and Ezcurra et al. (2002) for nomenclatural details.
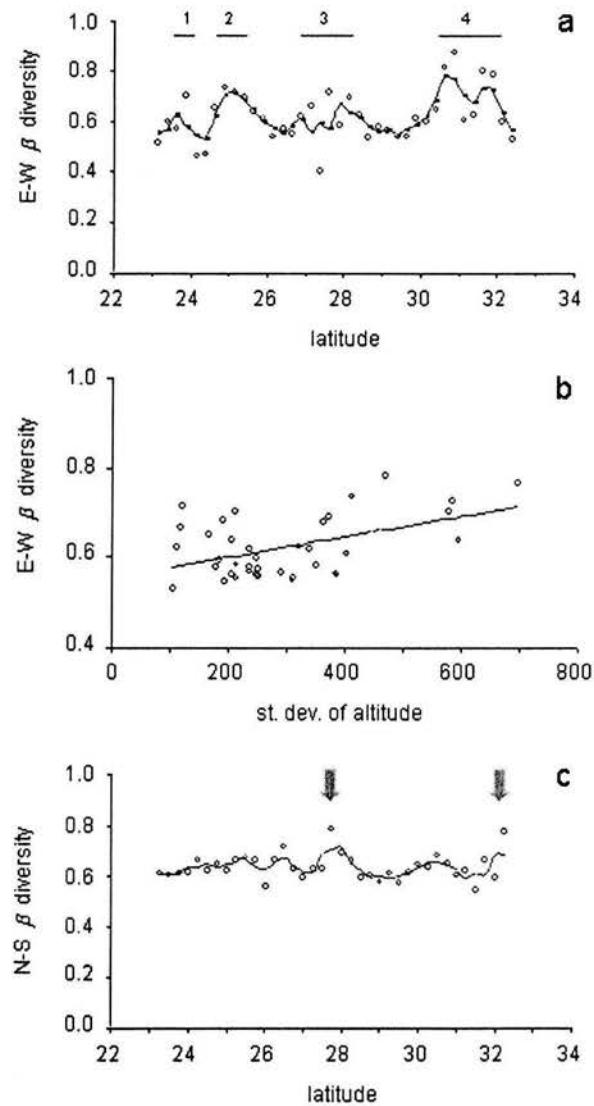
Fig. 2. Relationship between β-diversity along E–W transects and (a) latitude, and (b) standard deviation of altitude. (c) Relationship between β-diversity between N–S transects and latitude. The continuous lines in (a) and (c) show the moving-average trend. The line in (b) shows the regression line ($r^2 = 0.28$; $F_{(1,37)} = 14.7$; $P = 0.0005$). The horizontal lines in (a) show the location of the highest peninsular ranges: (1) La Laguna; (2) La Giganta; (3) San Francisco, and (4) Juárez and San Pedro Mártir. The arrows in (c) indicate the two regions of high N–S β-diversity: the Vizcaíno Desert and the Sierra de Juárez.
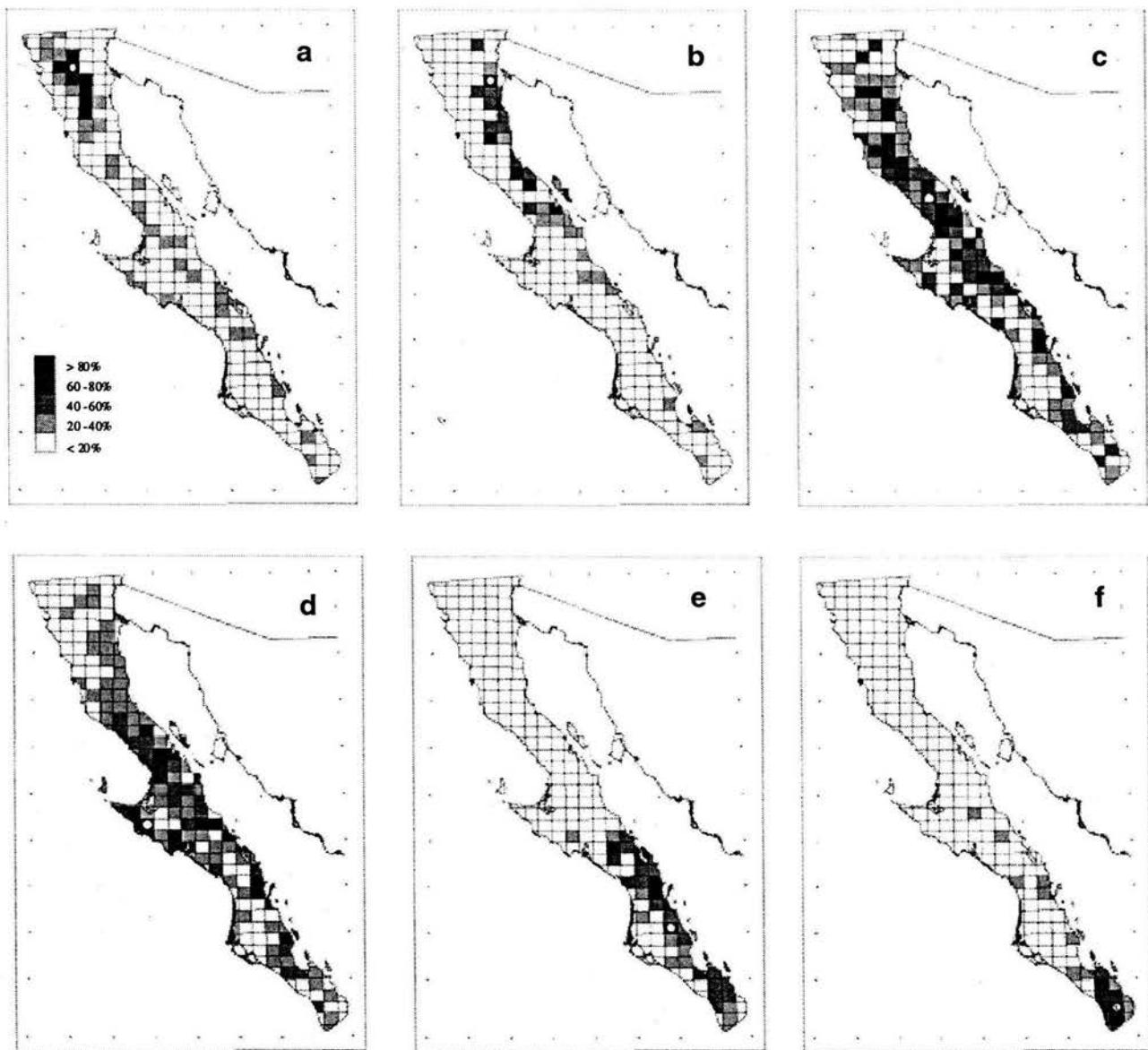
Fig. 3. Floristic affinities of woody legumes among differents regions in the peninsula of Baja California taking as starting points base cells (indicated as black cells with a white circle) in the following regions: (a) Mediterranean Region, (b) Lower Colorado Region, (c) Central Desert, (d) Vizcaíno Desert, (e) Central Gulf Coast, and (f) Cape Region.
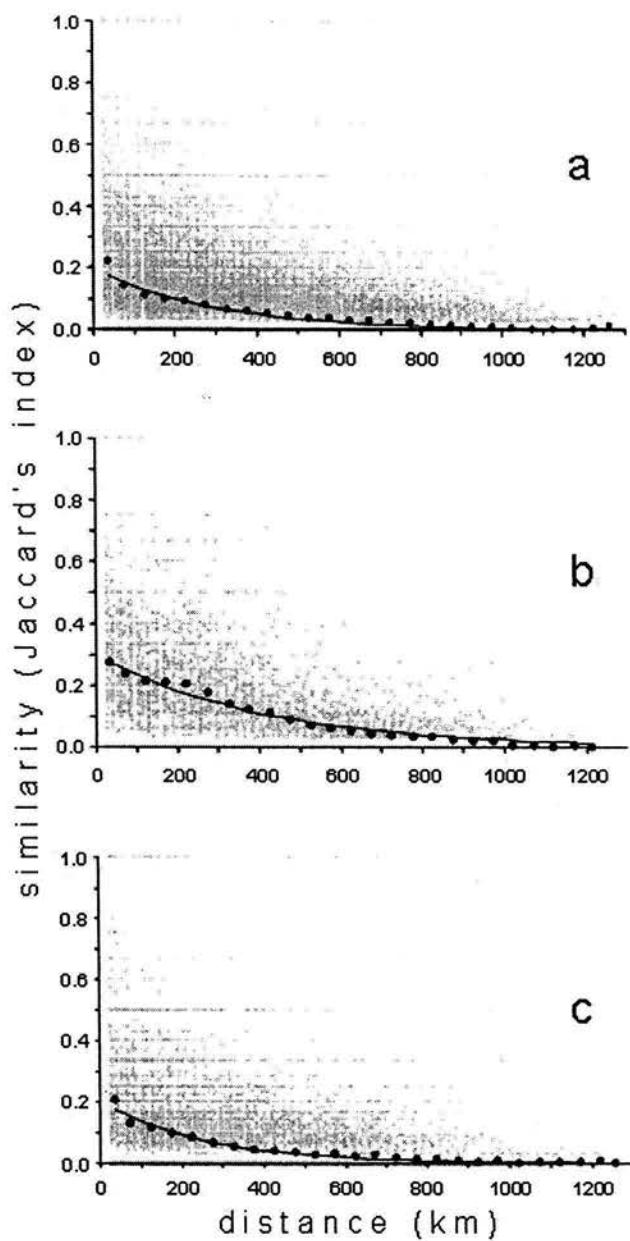
Fig. 4. Similarity between pairs of cells as a function of distance between the cells: (a) whole peninsula (205 cells; $n = 20{,}910$ cross-comparisons), (b) Gulf slope (78 cells; $n = 3{,}003$), and (c) Pacific slope (127 cells; $n = 8{,}001$). The black dots mark the average similarity for each 50 km distance intervals. The lines show Whittaker's exponential model fitted by non-linear regression.
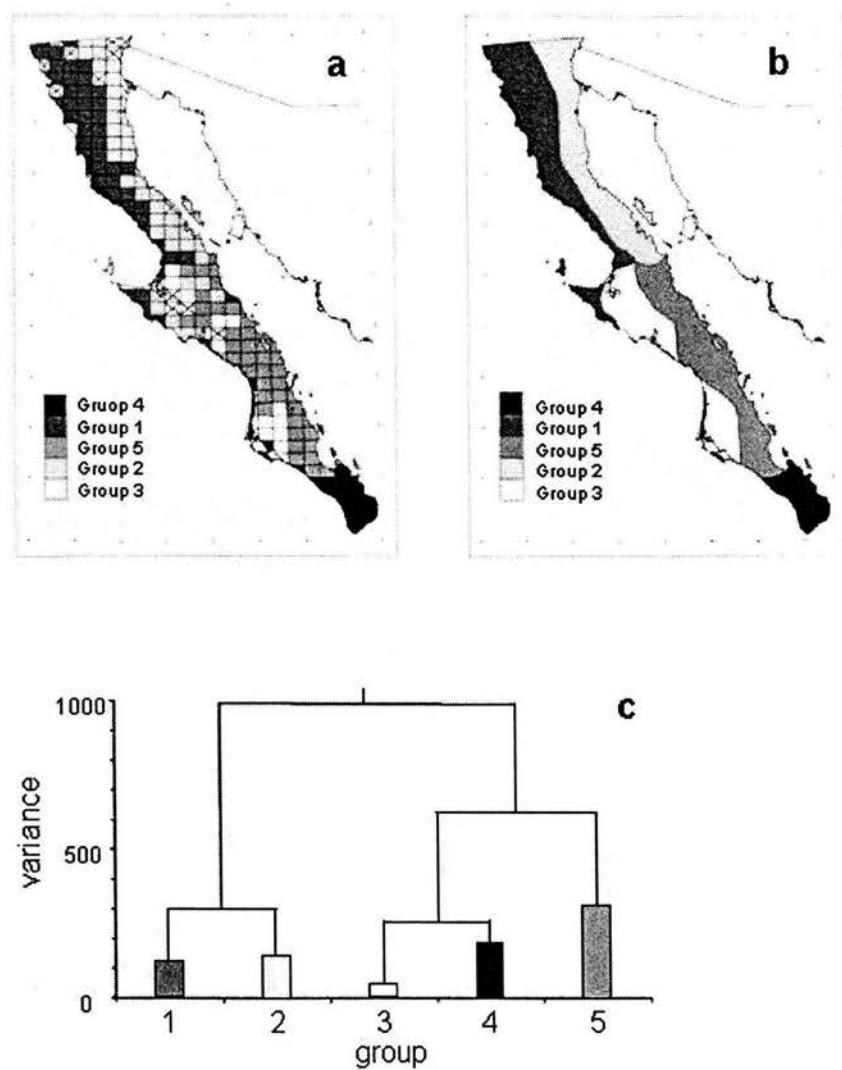
Fig. 5. Floristic regions of Baja California based on the distribution of woody legumes. (a) Groups obtained from divisive multivariate analysis, (b) areographic interpretation of these groups, and (c) dendrogram representing the relationship among groups (branches) and variance within each group (bars). Group 1 corresponds to the Mediterranean Region and Pacific coastal fog deserts; Group 2, Lower Colorado Region; Group 3, Magdalena and Vizcaíno plains; Group 4, Cape Region, and Group 5, Central Gulf Coast and associated mountains.

DISCUSIÓN GENERAL

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Las leguminosas leñosas son un grupo de plantas que integran de manera significativa algunas de las principales coordenadas que han regido, y rigen, el complejo espacio ecológico que es la península de Baja California. Los patrones geográficos de distribución y riqueza de estas especies contienen algunas de las claves que nos permiten interpretar el "teatro ecológico y el drama evolutivo" (*sensu* Hutchinson 1965) que se desarrolla en él.

La distribución de frecuencias de los tamaños de áreas de distribución de las leguminosas leñosas en la península se ajusta a una distribución lognormal, considerada habitualmente como el modelo nulo (May 1975; Pielou 1975; Preston 1980; Magurran 1988), sin embargo la distribución del conjunto de las áreas de distribución en el espacio no es aleatoria, sino que resulta en la presencia de patrones de riqueza bien definidos. El sur peninsular, en concreto la costa del Golfo y la región de Los Cabos, concentra la mayor riqueza de especies, así como la de endemismos y géneros. Además, contiene las áreas de distribución aproximadamente completas de 73% del total de especies, que apenas se solapan a las áreas de distribución del 15% de especies del norte peninsular. En la mitad sur peninsular la región de Los Cabos, a su vez, se diferencia nítidamente del resto. Ésta, contiene gran número de especies, de carácter endémico o distribución disyunta, cuya distribución peninsular está restringida a sus límites, pero al mismo tiempo comparte numerosas especies con la mitad sur de la costa del Golfo.

Esta regionalización de la península, con un norte y sur de fronteras bien definidas, y la disposición en sentido N-S de las similitudes es reflejada por el análisis de "barreras y corredores" de Rapoport. La zona central de la península (27° - 29° N) constituye un área de transición entre ambos extremos, como muestran el máximo de la tasa de recambio de especies en sentido N-S y la afinidad florística entre regiones.

El incremento de la riqueza de especies hacia el sur peninsular se relaciona sin duda con la existencia de un gradiente climático templado–tropical en sentido norte–sur, de lluvias de verano en el sur y de invierno en el norte, y con la afinidad tropical de la familia Leguminosae. No obstante, la peculiaridad del ensamblaje geográfico de las áreas de distribución y la alta proporción de endemismos en el centro peninsular (Bahía de La Paz–Ángel de la Guarda), sugieren la participación de otros factores además del gradiente climático. Éstos están

relacionados con la compleja historia geológica de la península, durante la cual diversas partes de la misma se vieron sometidas a periodos de aislamiento, y sobre todo, con la historia evolutiva de la región a lo largo del Pleistoceno (1.8 Ma – 11,000 años AP).

Durante este periodo tuvieron lugar alrededor de 20 ciclos glacial-interglacial (Imbrie e Imbrie 1979; Van Devender y Burgess 1985) que produjeron como respuesta ciclos asociados de contracción – expansión en la vegetación. Durante las fases glaciales, que abarcaron el 95% de la época, la vegetación templada y esclerófila mediterránea se expandió, ocupando la mayor parte de la península, con la retracción consecuente de la vegetación árido, que se refugió en las partes más calientes y estables. De manera recíproca, en las fases interglaciales, más cálidas y secas, se produjo una retracción de la vegetación templada y del matorral esclerófilo hacia el norte y hacia las zonas más elevadas de las montañas, acompañada de una expansión del matorral árido (Van Devender 1990; Riddle y Honeycutt 1990; Grismer y McGuire 1993; Peinado et al. 1994).

Es probable que durante las fases glaciales la vegetación desértica se refugiara en las zonas de mayor aridez, como el valle del Bajo Colorado o en el caso de las especies de mayor afinidad tropical, en la región de Los Cabos (Cole 1986; Peinado et al. 1994). De igual manera, las condiciones relativamente constantes que mantuvo la costa del Pacífico por la estabilizante influencia marítima (Peinado et al. 1994; Turner et al. 1995) la convirtió en refugio de numerosas especies de carácter xerofítico. Esta puede ser la razón de que actualmente esta zona, a pesar de ser pobre en especies, presente una alta proporción de leguminosas endémicas.

Cuando se produjo la expansión de los desiertos en el inicio del Holoceno (Axelrod 1979, 1981), la vegetación árida se extiendió a partir de las áreas de refugio. En esta dinámica de expansión–retracción, la cadena transpeninsular jugó un papel crucial como barrera y corredor simultáneamente, participando de manera fundamental en el dibujo de la geografía florística peninsular.

La vegetación templada se sirvió de la cadena transpeninsular como corredor en sus expansiones y como lugar de refugio en sus periodos de contracción, como el presente. Constancia de ello es la presencia de "sky islands" de vegetación remanente esclerófila repartidas a lo largo de las cumbres montañosas de la península (Axelrod 1958, 1979; Van

Devender 1990; Riddle y Honeycutt 1990; Grismer y McGuire 1993). En el tercio norte peninsular, las elevadas sierras de Juárez y San Pedro Mártir separan bruscamente una vertiente oeste, mediterránea, templada y con precipitaciones regulares de invierno, de una de las regiones más aridas de Norteamérica. Estas cumbres delimitan el área que la vegetación desértica refugiada en el valle del Bajo Colorado utilizó como corredor en su expansión hacia el sur. Al mismo tiempo, en la vertiente oeste encauzan un corredor de afinidad mediterránea que comunica la península de Baja California y la Provincia Florística de California (Mclaughlin 1989; Minnich y Franco-Vizcaíno 1998).

En el sur, la expansión hacia el norte de las especies tropicales menos tolerantes a la sequía, refugiadas en la región de Los Cabos, estuvo probablemente limitada por el periodo de intensa aridez que tuvo lugar en el comienzo del Holoceno (intervalo climático Hipsitermal, 8,000-4,000 años AP; Spaulding 1991), quedando restringidos estos taxa a las zonas bajas de la región de Los Cabos, con un corredor de expansión en el sur de la Costa del Golfo asociado a los cañones y barrancos más húmedos y benignos de la Sierra de la Giganta.

Las tres áreas de procedencia de la flora peninsular (Fig. 1) corresponden con los principales elementos componentes de la misma descritos por diversos autores (p. ej., Wiggins 1960; Peinado et al. 1994): (1) Provincia Florística de California (elementos Madreano y Holártico), (2) valle del Bajo Colorado (elemento Xerofítico-Mediterráneo) y (3) región de Los Cabos (elemento Pantropical). A éstas se podría añadir una cuarta área endógena, en la región del Desierto del Vizcaíno–Desierto Central. Esta zona, separada del Desierto Sonorense por la cadena transpeninsular, habría actuado como centro de origen y diversificación de numerosos taxones exclusivos del Desierto de Baja California.

El efecto de la cadena transpeninsular como barrera diferenciadora entre las dos vertientes se refleja en el distinto comportamiento de la diversidad beta a un lado y otro de la cadena montañosa. La vertiente del Pacífico presenta mayor tasa de recambio de especies con respecto a la distancia que la vertiente del Golfo, la cual mantiene mayor similitud. La diferenciación ecológica entre las dos vertientes no sólo se debe a la sombra orográfica creada por las sierras, en el noreste sobre los frentes invernales procedentes del Pacífico, y en menor medida en el suroeste sobre los "chubascos" procedentes del sureste, sino también a la distinta influencia climática de las dos costas (Humphrey 1974). La costa del Pacífico, aun siendo árida, está en

parte atemperada por la influencia de los vientos frescos del oeste y la corriente marina fría que bordea sus costas. La costa del Golfo es seca y caliente la mayor parte del año. La corriente marina fría de California, que discurre de norte a sur paralela a la costa del Pacífico, provoca sombra de lluvia sobre la tierra colindante en la mitad suroeste peninsular. Simultáneamente, en la costa central del Pacífico, esta corriente produce uno de los tres desiertos de niebla existententes en el mundo (Grismer 2002), con una vegetación rica en líquenes y especies sarcófilas (Nash et al. 1979; Martorell y Ezcurra 2002).

Las cinco regiones resultantes de la clasificación numérica sintetizan significativamente el doble eje de cambio N-S y O-E. En el norte, las leguminosas definen dos regiones florísticas: (a) costa del Pacífico, de precipitaciones de invierno y (b) desierto del Valle del Bajo Colorado, extremadamente caliente y de escasa precipitación, de carácter bimodal (Ezcurra y Rodrigues 1986). En el centro peninsular diferencian dos regiones: (a) desiertos costeros de Magdalena y Vizcaíno y (b) Costa Central del Golfo, que incluye las sierras de San Francisco, Guadalupe y la Giganta. Y finalmente, en su extremo sur, la región de Los Cabos, cubierta por bosque seco tropical. Esta sectorización coincide claramente con las regionalizaciones propuestas por diversos autores (p. ej., Shreve 1951; Wiggins 1980; Murphy 1983; Peinado et al. 1994; Rojas-Soto et al. 2003).

Finalmente, el complejo espacial y temporalmente "teatro ecológico" de la península: con un intrincado proceso de formación, periodos de aislamiento total o parcial y recurrentes cambios climáticos sobre un heterogéneo paisaje topográfico propició el desarrollo de un rico "drama evolutivo". Los capítulos de este "drama evolutivo": extinciones, aislamientos, áreas de refugio, contracción y expansión de poblaciones, especiación, dispersión, inmigración, etc., son responsables de los patrones espaciales de la riqueza y distribución de especies que sustentan los altos valores de diversidad beta existentes a lo largo de toda la península.

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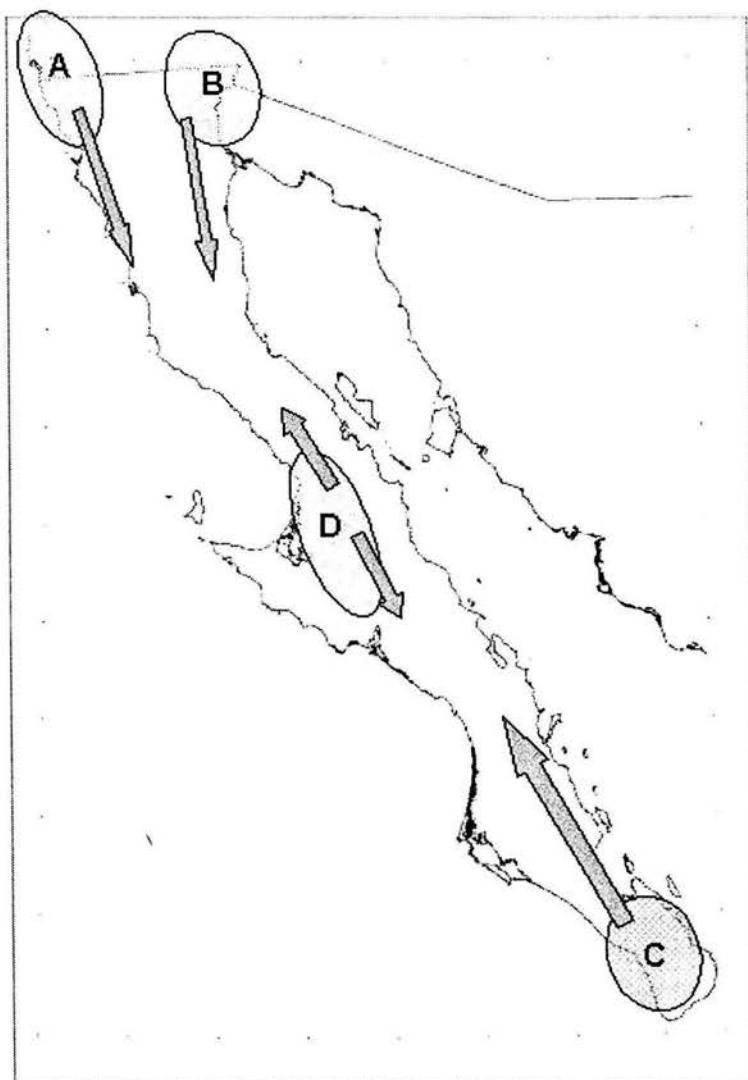
Fig. 1. Centros de origen de la flora peninsular y posibles corredores de dispersión: (A) Provincia Florística de California, elementos mediterráneos, (B) Valle del Bajo Colorado, elementos áridos, (C) El Cabo, elementos tropicales, y (D) Desiertos Vizcaíno–Central, elementos áridos endógenos.

APÉNDICE I

RELACIÓN DE LAS ESPECIES LEGUMINOSAS LEÑOSAS

UTILIZADAS EN EL ESTUDIO

Apéndice I. Lista de leguminosas leñosas de Baja California incluídas en este estudio. Tipos de distribución: *E*: endémica, *R*: regional, y *C*: continental. G-*i*: porcentaje de celdas en el grupo *i* de la clasificación numérica. Celdas: número total de celdas del área de distribución de la especie. El asterisco (*) indica las especies indicadoras en el análisis multivariado divisivo para cada grupo.

Species	D	G-1	G-2	G-3	G-4	G-5	Celdas
Acacia brandegeana I.M. Johnston	E	0	0	4	8	88	24
Acacia cochliacantha Willd.	C	0	0	0	75	25	4
Acacia constricta Bentham	C	25	0	13	0	63	8
Acacia farnesiana (L.) Willd.	C	14	7	7	24	48	29
Acacia goldmanii (Britton & Rose) Wiggins	E	3	3	5	30	59	37
Acacia greggii A. Gray	C	50	37	3	0	11	38
Acacia kelloggiana Carter and Rudd	E	0	0	0	0	100	3
Acacia mcmurphyi Wiggins	E	0	0	0	50	50	6
Acacia pacensis Rudd & Carter	E	0	0	0	25	75	4
Acacia peninsularis (Britton & Rose) Standley	E	0	0	0	46	54	13
Acacia pringlei Brandegee subsp. *californica* Lee, Seigler & Ebinger	R	0	0	0	100	0	3
Aeschynomene nivea Brandegee	E	0	0	0	25	75	28
Aeschynomene vigil Brandegee	E	0	0	0	100	0	10
Amorpha apiculata Wiggins	E	100	0	0	0	0	7
Amorpha californica Torrey & A. Gray	C	82	18	0	0	0	11
Amorpha fruticosa L. var. *occidentalis* Abrams	R	100	0	0	0	0	7
Bauhinia peninsularis Brandegee	C	0	0	0	100	0	4
Brongniartia peninsularis Rose	R	0	0	0	17	83	6
Brongniartia trifoliata Brandegee	E	0	0	0	100	0	3
Caesalpinia arenosa Wiggins	E	0	0	3	30	67	30
Caesalpinia californica (A. Gray) Standley	E	0	0	7	67	27	15
Caesalpinia pannosa Brandegee	E	0	0	17	39	43	23
Caesalpinia placida E.M. Fisher	E	0	0	0	9	91	11
Caesalpinia virgata Bentham	R	14	86*	0	0	0	22
Calliandra californica Bentham	E	28	20	13	9	30	54
Calliandra eriophylla Bentham	C	75	25	0	0	0	4
Calliandra peninsularis (Britton & Rose) Gentry	E	0	0	0	89	11	9
Cercidium floridum Bentham ex. A. Gray subsp. *peninsulare* (Rose) Carter	E	0	0	7	20	73	41
Cercidium microphyllum (Torrey) Rose & Johnston	R	16	20	14	0	50	44
Cercidium praecox (Ruiz, López & Pavon) Harms	C	0	0	22	17	61	23
Chloroleucon mangense (Jacq.) Britton & Rose var. *leucospermum* (Brandegee) Barneby & Grimes	C	0	0	0	100	0	6
Coursetia glandulosa A. Gray	C	0	0	0	90	10	10
Dalea bicolor Willd var. *orcuttiana* Barneby	E	40	26	2	2	30	47
Dalea brandegeei (Rose) Bullock	E	0	0	100*	0	0	4
Dalea purpusii Brandegee	E	0	0	0	0	100	5
Dalea trochilina Brandegee	E	0	0	33	67	0	3
Desmanthus covillei (Britt. & Rose) B. Turner	R	0	0	13	0	88	8
Desmanthus fruticosus Rose	E	0	13	9	26	53	47
Desmanthus oligospermus Brandegee	E	0	0	0	100	0	5
Ebenopsis confine Standley	E	5	8	13	29	45	38
Errazurizia benthamii (Brandegee) Johnston	E	40	7	47	0	7	15
Errazurizia megacarpa (Watson) I.M. Johnston	E	2	65*	9	5	19	43
Erythrina flabelliformis Kearney	C	0	0	0	58	42	12

Eysenhardtia peninsularis Brandegee	E	0	0	50	0	50	2
Haematoxylum brasiletto Karsten	C	0	0	0	90	10	10
Havardia mexicana (Rose) Britton & Rose	R	0	0	0	100	0	5
Hesperalbizia occidentalis (Brandegee) Barneby & Grimes	C	0	0	0	100	0	7
Hoffmannseggia intricata Brandegee	E	0	38	8	0	54	13
Indigofera fruticosa Rose	E	0	0	0	93*	7	14
Indigofera nelsonii Rydberg	E	0	0	0	75	25	4
Indigofera suffruticosa Miller	C	0	0	0	100	0	4
Leucaena lanceolata Watson	C	0	0	0	100	0	3
Lysiloma candidum Brandegee	E	0	0	7	23	70	44
Lysiloma divaricatum (Jacq.) Mcbr.	C	0	0	0	57	43	14
Mimosa aculeaticarpa Ortega var. *biuncifera* Barneby	C	100	0	0	0	0	4
Mimosa distachya Cav.	R	0	0	0	31	69	26
Mimosa epitropica Barneby & León de la Luz	E	0	0	0	100	0	1
Mimosa margaritae Britton & Rose	E	0	0	13	63	25	8
Olneya tesota A. Gray	R	6	20	0	11	63	35
Mimosa xantii A. Gray	C	0	0	0	83*	17	12
Parkinsonia aculeata L.	C	28	4	16	16	36	25
Pickeringia montana Torrey & Gray subsp. *tomentosa* (Abrams) I.M. Johnston	R	100	0	0	0	0	2
Prosopidastrum mexicanum (Dressler) Burkart	E	100	0	0	0	0	8
Prosopis articulata Watson	E	9	6	3	18	65	34*
Prosopis glandulosa Torrey var. *torreyana* (L.Benston) M.C. Johnston	C	51*	7	2	7	33	43
Prosopis palmeri Watson	E	0	0	17	10	72	29
Prosopis pubescens Bentham	C	67	33	0	0	0	6
Psorothamnus emoryi (A. Gray) Rydberg	R	6	33	16	3	41	63
Psorothamnus schottii (Torrey) Barneby	R	18	82	0	0	0	11
Psorothamnus spinosus (A. Gray) Barneby	R	27	73	0	0	0	15
Senna armata (Watson) Irwin & Barneby	R	20	80	0	0	0	5
Senna atomaria (L.) Irwin & Barneby	C	0	0	0	100*	0	12
Senna pallida (Vahl) Irwin & Barneby	C	0	0	0	100	0	1
Senna polyantha (Collad.) Irwin & Barneby	C	0	0	0	0	100	4
Senna purpusii (Brandegee) Irwin & Barneby	E	68*	5	14	0	14	22
Senna villosa (Mill.) Irwin & Barneby	C	0	0	0	92*	8	12
Tephrosia palmeri Watson	E	0	5	0	21	74	19
Zapoteca formosa (Kunth.) H. Hern.	C	0	0	0	100	0	3