

Copyright Notice

This electronic reprint is provided by the author(s) to be consulted by fellow scientists. It is not to be used for any purpose other than private study, scholarship, or research.

Further reproduction or distribution of this reprint is restricted by copyright laws. If in doubt about fair use of reprints for research purposes, the user should review the copyright notice contained in the original journal from which this electronic reprint was made.

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

Garcillán, Pedro P.^{1*}; Ezcurra, Exequiel¹ & Riemann, Hugo²

¹Instituto Nacional de Ecología, Av. Periférico Sur 5000, Delegación Coyoacán, 04530 México D.F., Mexico;

²Colegio de la Frontera Norte, Abelardo L. Rodríguez 2925, 22320 Tijuana, Mexico;

*Corresponding author; Fax: +52 55 54245485; E-mail pedrop@ine.gob.mx

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.

Nomenclature: Wiggins (1980); Hickman (1993); Skinner & Pavlik (1994); International Legume Database & Information Service, www.ildis.org/legumes.html

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 \times 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_j) 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

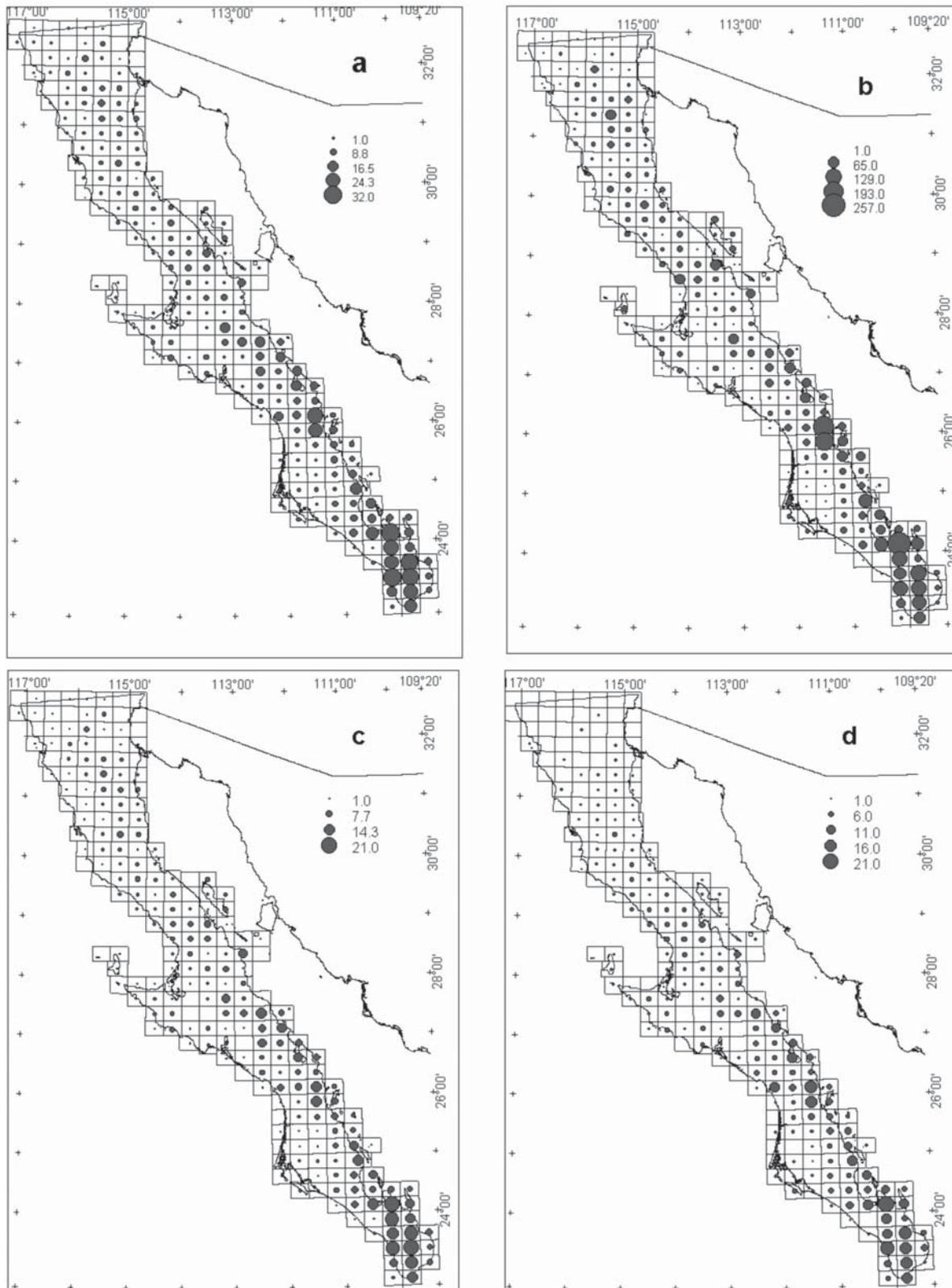


Fig. 1. Geographic distribution of (a) species richness of woody legumes; (b) collection effort measured in number of collected specimens of woody legumes per cell; (c) richness of genera of woody legumes; (d) richness of endemic species of woody legumes in Baja California. The size of each dot is proportional 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 latitude 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):

$$s = \frac{abh}{a + bh} \quad (1)$$

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 $h \rightarrow \infty$), and b is the rate at which new species are found at the beginning of the collection process (i.e. when $h \rightarrow 0$). 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):

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

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 $\rho \rightarrow 1$, 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:

$$s_i = k + d\rho_i \quad (3)$$

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

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

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

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

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:

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

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 km².

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

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

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).

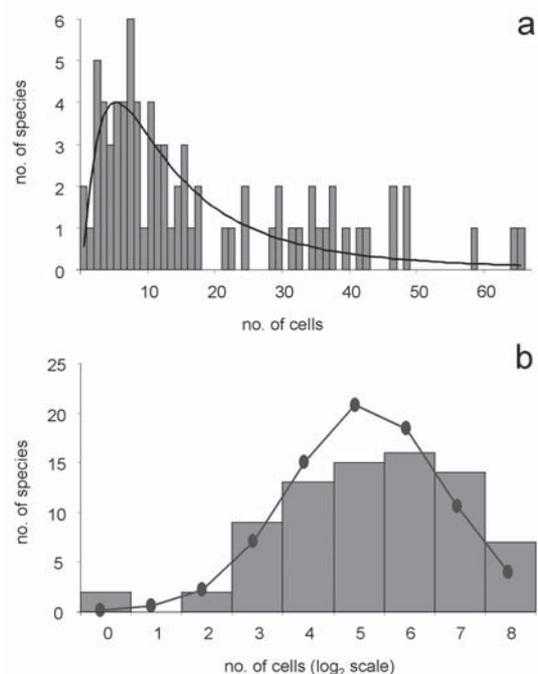


Fig. 2. Frequency distributions of the geographic ranges of woody legumes in Baja California. **a.** No. of cells on a linear scale; **b.** No. of cells on a logarithmic axis. In both plots, the continuous line marks the predicted values of the log-normal distribution, and at both scales, the observed 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 sarcocaulous Central Desert clearly fall into this last category.

Geographic ranges

Each species occupied, on average, 17.8 map cells (some 11521 km²). The distribution was markedly skewed, with the majority of species occupying less than 10 cells (ca. 7000 km²), and three widespread species occupying more than 57 cells (ca. 40000 km²). 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

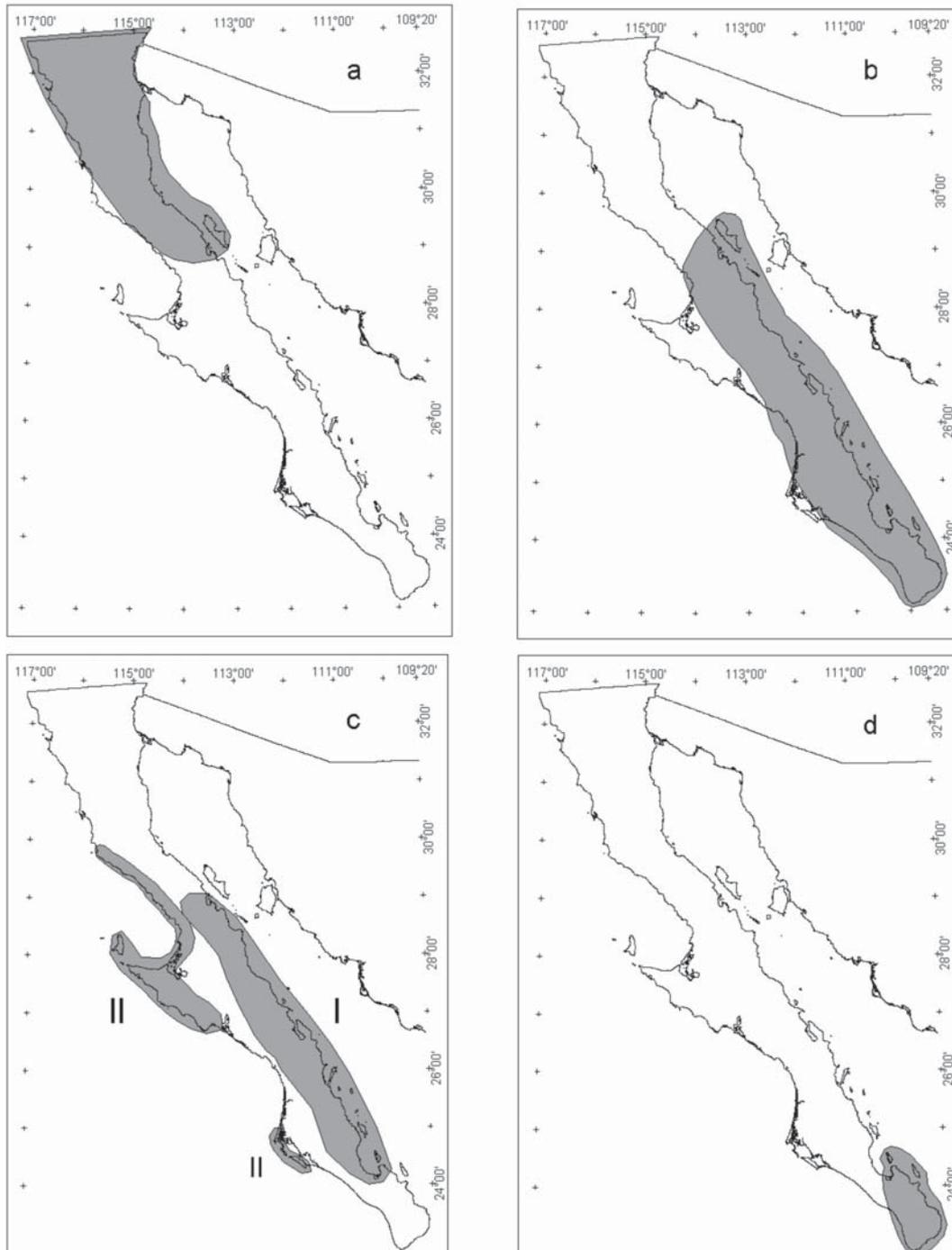


Fig. 3. Patterns of geographic ranges of woody legumes in Baja California: **a.** North; **b.** South-Centre; **c.** Central Gulf Coast (I) and Pacific Coast (II); **d.** Cape Region. The ratios endemic:regional:continental species is 1:6:5 for the North; 13:1:1 for the South-Centre; 6:2:1 for the Central 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.

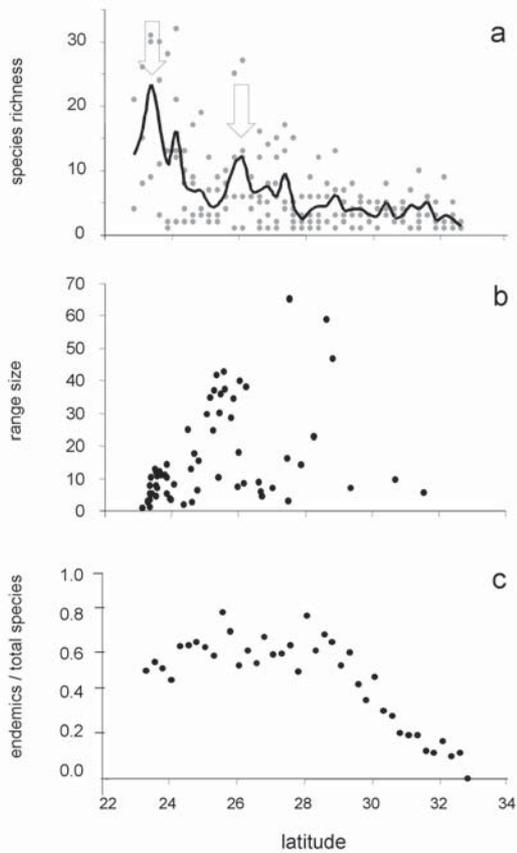


Fig. 4. a. Relationship between latitude and richness of woody legumes in 205 cartographic cells of Baja California. The continuous line marks the mean richness for each latitudinal band, and the arrows mark the latitudinal location of the Cape Region and the Sierra de la Giganta. **b.** Relationship 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'.

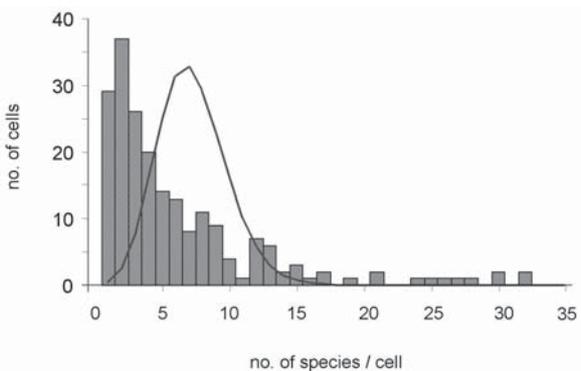


Fig. 5. Statistical distribution of species richness of woody legumes in the 205 cells. The bars mark the observed frequencies, the continuous line shows the expected Poisson values. The observed values differed very significantly from the expected random distribution ($G = 467$; $df = 12$; $P << 0.0001$).

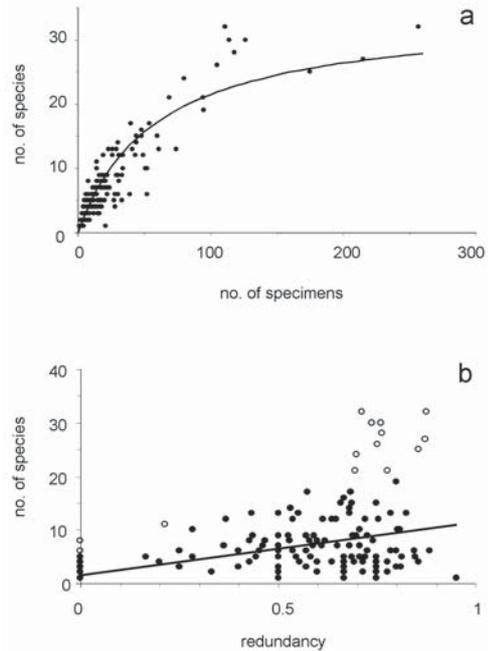


Fig. 6. a. Relationship between the number of species and collection effort (estimated as the number of collected specimens) for the 205 cartographic cells. The line shows Clench's model, fitted by non-linear regression ($r^2 = 0.89$; $P << 0.0001$). **b.** Relationship between the number of species and collection redundancy (ρ_i , an estimate of relative collection effort). The line shows the linear model linking redundancy and the estimate of richness ($r = 0.44$; $P << 0.0001$). The open dots indicate cells where the observed species richness was significantly higher than the predicted value (see Text).

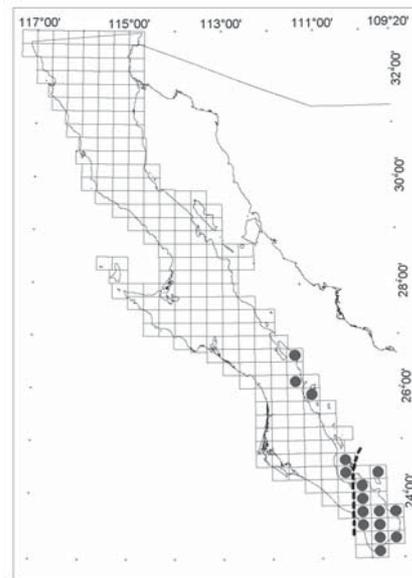


Fig. 7. Biodiversity 'hotspots' of extraordinarily high species richness for woody legumes in the peninsula of Baja California. The dotted line shows La Paz geologic fault, which separates the Cape Region from the rest of the peninsula.

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 sarcocaulous 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.

Acknowledgements. We are grateful Charlotte González and the Huerta-González family for their assistance in checking the herbaria, and Elisabet Wehncke for critically reading the manuscript. This research is part of the first author's doctoral research at the Instituto de Ecología, Universidad Nacional Autónoma de México. The first author gratefully acknowledges the financial support of Mexico's Secretaría de Relaciones Exteriores, and of the Dirección General de Estudios de Posgrado, UNAM, and the facilities generously provided by the Colegio de la Frontera Norte (COLEF) in Tijuana. The authors wish to acknowledge the taxonomic assistance provided by Dr. Jon Rebman of the San Diego Natural History Museum, one of the topmost experts on the floristics of Baja California; Janet Franklin, the Coordinating Editor, and three anonymous reviewers.

References

- Anderson, S. 1977. Geographic ranges of North American terrestrial mammals. *Am. Mus. Novit.* 2629: 1-15.
- Arrhenius, O. 1921. Species and area. *J. Ecol.* 9: 95-99.
- Axelrod, D.I. 1958. Evolution of the Madro-Tertiary geoflora. *Bot. Rev.* 24: 432-509.
- Axelrod, D.I. 1979. *Age and origin of Sonoran Desert vegetation*. Occasional Papers of the California Academy of Sciences, no. 132. San Francisco, CA, US.
- Axelrod, D.I. 1981. Holocene climatic changes in relation to vegetation disjunction and speciation. *Am. Nat.* 117: 847-870.
- Brown, J.H. 1987. The peninsular effect in Baja California: an entomological assessment. *J. Biogeogr.* 14: 359-365.
- Brown, J.H., Stevens, G.C. & Kaufman, D.M. 1996. The geographic range: size, shape, boundaries and internal structure. *Annu. Rev. Ecol. Syst.* 27: 597-623.
- Búrquez, A. & Quintana, M. 1994. Islands of diversity: Ironwood ecology and the richness of perennials in a Sonoran Desert biological reserve. In: Nabhan, G.P. & Carr, J.L. (eds.) *Ironwood: An ecological and cultural keystone of the Sonoran Desert*, pp. 9-27. Occasional Papers in Conservation Biology, Occasional Paper No.1. Conservation International, Washington, DC, US.
- Carreño, A.L. & Helenes, J. 2002. Geology and ages of the islands. In: Case, T.J., Cody, M.L. & Ezcurra, E. (eds.) *A new island biogeography of the Sea of Cortés*, pp. 14-40. Oxford University Press, NY, US.
- Dimmitt, M.A. 2000. Biomes and communities of the Sonoran Desert Region. In: Phillips, S.J. & Wentworth Comus, P. (eds.) *A natural history of the Sonoran Desert*, pp. 3-18. Arizona-Sonora Desert Museum Press, University of California Press, Berkeley, CA, US.
- Due, A.D. & Polis, G.A. 1986. Trends in scorpion diversity along the Baja California peninsula. *Am. Nat.* 128: 460-468.
- Dunn, Ch.R. & Loehle, C. 1988. Species-area parameter estimation: testing the null model of lack of relationship. *J. Biogeogr.* 15: 721-728.
- Everitt, B.S. 1992. *The analysis of contingency tables*. 2nd. ed. CRC Press, Boca Raton, FL, US.
- Ezcurra, E. & Rodrigues, J. 1986. Rainfall patterns in the Gran Desierto, Mexico. *J. Arid Environ.* 10: 13-28.
- Ezcurra, E., Peters, E., Búrquez, A. & Mellink, E. 2002. The Sonoran and Baja Californian deserts. In: Mittermeir, R.A., Goettsch-Mittermeir, C., Robles-Gil, P., Pilgrim, J., da Fonseca, G.A.B., Brooks, T. & Konstant, W.R. (eds.) *Wilderness: Earth's last wild places*. CEMEX-Conservation International, Washington, D.C. and Agrupación Sierra Madre, México, D.F., MX.
- Felger, R.S., Johnson, M.B. & Wilson, M.F. 2001. *The trees of Sonora, Mexico*. Oxford University Press, Oxford, UK.
- Flather, C.H. 1996. Fitting species-accumulation functions and assessing regional land use impacts on avian diversity. *J. Biogeogr.* 23: 155-168.
- Fowler, N. 1986. The role of competition in plant communities in arid and semiarid regions. *Annu. Rev. Ecol. Syst.* 17: 89-110.
- Franco, A.C. & Nobel, P.S. 1989. Effect of the nurse plant on the microhabitat and growth of cacti. *J. Ecol.* 77: 870-886.
- Franks, S.J. 1999. Plants need nurses too: The importance of nurse plant relationships for the dynamics of rare plant populations. *Plant Conserv.* 13: 1-8.
- García-Moya, E. & Mckell, C.M. 1970. Contribution of shrubs to the nitrogen economy of a desert wash plant community. *Ecology* 51: 81-88.
- Gaston, K.J. 1990. Patterns in the geographical ranges of species. *Biol. Rev.* 65: 105-129.
- Gentry, A.H. 1995. Diversity and floristic composition of neotropical dry forests. In: Bullock, S.H., Mooney, H.A. & Medina, E. (eds.) *Seasonally dry tropical forests*, pp. 146-194. Cambridge University Press, Cambridge, UK.
- Greig-Smith, P. 1984. *Quantitative plant ecology*. 3rd. ed. University of California Press, Berkeley, CA, US.

- Grismer, L.L. 2002. *Amphibians and reptiles of Baja California, including its Pacific islands and the islands in the Sea of Cortés*. The University of California Press, Berkeley, CA, US.
- Grismer, L.L. & McGuire, J.A. 1993. The oasis of central Baja California, Mexico. Part I. A preliminary account of the relict mesophilic herpetofauna and the status of the oases. *Bull. S. Calif. Acad. Sci.* 92: 2-24.
- Hastings, J.R. & Turner, R.M. 1965. Seasonal precipitation regimes in Baja California, Mexico. *Geogr. Ann.* 47 A 4: 204-223.
- Hayek, L.A. & Buzas, M.A. 1997. *Surveying natural populations*. Columbia University Press, New York, NY, US.
- Hickman, J.C. (ed.) 1993. *The Jepson Manual. Higher plants of California*. University of California Press, Berkeley, CA, US.
- Imbrie, J. & Imbrie, K. P. 1979. *Ice ages: solving the mystery*. Enslow, Hillside, NJ, US.
- Jones, C.G., Lawton, J. & Shachak, M. 1994. Organisms as ecosystem engineers. *Oikos* 69: 373-386.
- Lenz, W.L. 1992. *An annotated catalogue of the plants of the Cape Region, Baja California Sur, Mexico*. The Cape Press, Claremont, CA, US.
- León de la Luz, J.L. 2000. Vegetation of the lowlands of the Cape Region of Baja California Sur. In: White, P.S., Mucina, L. & Lepš, J. (eds.) *Vegetation science in retrospect and perspective*, pp. 154-157. Opulus Press, Uppsala, SE.
- León de la Luz, J.L. & Domínguez-Cadena, R. 1989. Flora of the Sierra de la Laguna, Baja California Sur, México. *Madroño* 36: 61-83.
- León de la Luz, J.L., Coria Benet, R.C. & Cansino, J. 1995. *Listados florísticos de México. XI. Reserva de la Biosfera El Vizcaíno, Baja California Sur*. Instituto de Biología, U.N.A.M., México, MX.
- MacArthur, R.H. & Wilson, E.O. 1967. *The theory of island biogeography*. Princeton University Press, Princeton, NJ, US.
- Magurran, A.E. 1988. *Ecological diversity and its measurement*. Princeton University Press, Princeton, NJ, US.
- May, R.M. 1975. Patterns of species abundance and diversity. In: Cody, M.L. & Diamond, J.M. (eds.) *Ecology and evolution of communities*, pp. 81-120. Belknap Press, Cambridge, MA.
- McAuliffe, J. 1984. Sahuaro nurse tree associations in the Sonora Desert: Competitive effect of sahuaro. *Oecologia* 64: 319-321.
- McAuliffe, J. 1990. Paloverdes, pocket mice, and bruchid beetles-interrelationships of seeds, dispersers and seed predators. *Southw. Nat.* 35: 329-337.
- Montaña, C., Ezcurra, E., Carrillo, A. & Delhoume, J.P. 1988. The decomposition of litter in grasslands of northern Mexico: a comparison between arid and non-arid environments. *J. Arid Environ.* 13: 551-556.
- Moreno, C.E. & Halffter, G. 2000. Assessing the completeness of bat biodiversity inventories using species accumulation curves. *J. Appl. Ecol.* 37: 149-158.
- Mourelle, C. & Ezcurra, E. 1996. Species richness of Argentine cacti: A test of some biogeographic hypotheses. *J. Veg. Sci.* 7: 667-680.
- Mourelle, C. & Ezcurra, E. 1997. Rapoport's rule: A comparative analysis between South and North American columnar cacti. *Am. Nat.* 150: 131-142.
- Murphy, R.W. 1983. Paleobiogeography and genetic differentiation of the Baja California Herpetofauna. *Occas. Pap. Calif. Acad. Sci.* 137: 1-48.
- Nabhan, G.P. 2000. *Desert ironwood primer: biodiversity and uses associated with ancient legume and cactus forests in the Sonoran Desert*. Research Report, Arizona-Sonora Desert Museum, Tucson, AZ, US.
- Nobel, P.S. 1989. Temperature, water availability, and nutrient levels at various soil depths: consequences for shallow-rooted desert succulents, including nurse plant effects. *Am. J. Bot.* 76: 1486-1492.
- Nobel, P.S. & Geller, G.N. 1987. Temperature modelling of wet and dry desert soils. *Ecology* 75: 247-258.
- Peinado, M., Alcaraz, F., Delgado, J., & Aguado, I. 1994. Fitogeografía de la península de Baja California, México. *Anal. Jardín Bot. Madrid* 51: 255-276.
- Pianka, E. R. 1966. Latitudinal gradients in species diversity: A review of concepts. *Am. Nat.* 100: 33-45.
- Pielou, E.C. 1975. *Ecological diversity*. John Wiley & Sons, New York, NY, US.
- Preston, F.W. 1960. Time and space and the variation of species. *Ecology* 41: 611-627.
- Preston, F.W. 1962. The canonical distribution of commonness and rarity. *Ecology* 43: 185-215, and 410-432.
- Preston, F.W. 1980. Noncanonical distributions of commonness and rarity. *Ecology* 61: 88-97.
- Rapoport, E.H. 1975. *Areografía. Estrategias geográficas de las especies*. Fondo de Cultura Económica, México, MX.
- Riddle, B. & Honeycutt, R.L. 1990. Historical biogeography in North American arid regions: an approach using mitochondrial-dna phylogeny in grasshopper mice (genus *Onychomys*). *Evolution* 44: 1-15.
- Riddle, B.R., Hafner, D.J., Alexander, L.F. & Jaeger, J.R. 2000. Cryptic vicariance in the historical assembly of a Baja California peninsular desert biota. *Proc. Nat. Acad. Sci.* 97(26): 14438-14443.
- Rohde, K. 1998. Latitudinal gradients in species diversity. Area matter, but how much? *Oikos* 82: 184-190.
- Romney, E.M., Wallace, A., Kaaz, H. & Hale, V.Q. 1980. The role of shrubs on redistribution of mineral nutrients in soil in the Mojave Desert. *Great Basin Nat. Mem.* 4: 124-133.
- Rosenzweig, M.L. 1992. Species diversity gradients: we know more and less than we thought. *J. Mamm.* 73: 715-730.
- Shreve, F. 1931. Physical conditions in sun and shade. *Ecology* 12: 96-104.
- Shreve, F. 1951. *Vegetation of the Sonoran Desert*. Carnegie Institution of Washington Publication no. 591. Washington, DC, US.
- Shreve, F. & Wiggins, I.L. 1964. *Vegetation and flora of the Sonoran Desert*, Vols. 1 and 2. Stanford University Press, Stanford, CA, US.
- Skinner, M.W. & Pavlik, B.M. (eds.) 1994. *Inventory of rare and endangered vascular plants of California*. Special Publication No. 1. 5th. ed. The California Native Plant

- Society, Sacramento, CA, US.
- Smith, S.D., Monson, R.K. & Anderson, J.E. 1997. *Physiological ecology of North American desert plants*. Springer-Verlag, Berlin, DE.
- Soberón, J. & Llorente, J. 1993. The use of species accumulation functions for the prediction of species richness. *Conserv. Biol.* 7: 480-488.
- Sokal, R.R. & Rohlf, F.J. 1995. *Biometry*. 3rd. ed. Freeman & Company, New York, NY, US.
- Steenbergh, W.H. & Lowe, C.H. 1977. *Ecology of the sahuaro II: Reproduction, germination, establishment, growth and survival of the young plant*. National Park Service, Scientific Monographs Series no. 8, U.S. Government Printing Office, Washington DC, US.
- Stevens, G.C. 1989. The latitudinal gradient in geographical range: How many species coexist in the tropics. *Am. Nat.* 133: 240-256.
- Suzán, H., Nabhan, G.P. & Patten, D.T. 1996. The importance of *Olneya tesota* as a nurse plant in the Sonoran Desert. *J. Veg. Sci.* 7: 635-644.
- Suzán, H., Patten, D.T. & Nabhan, G.P. 1999. Effects of exploitation and park boundaries on legume trees in the Sonoran Desert. *Conserv. Biol.* 13: 1497-1501.
- Taylor, R.J. & Regal, P.J. 1978. The peninsular effect on species diversity and the biogeography of Baja California. *Am. Nat.* 112: 583-593.
- Turner, R.M., Alcorn, S.M., Olin, G. & Booth, J.A. 1966. The influence of shade, soil, and water on saguaro seedling establishment. *Bot. Gaz.* 127: 95-102.
- Turner, R.M., Bowers, J.E. & Burgess, T.L. 1995. *Sonoran desert plants: An ecological atlas*. University of Arizona Press, Tucson, AZ, US.
- Upton, D.E. & Murphy, R.W. 1997. Phylogeny of the Side-Blotched lizards (Phrynosomatidae: *Uta*) based on mt-DNA sequences: support for a midpeninsular seaway in Baja California. *Molec. Phylogen. Evol.* 8: 104-113.
- Valiente-Banuet, A. & Ezcurra, E. 1991. Shade as a cause of the association between the cactus *Neobuxbaumia tetetzo* and the nurse plant *Mimosa luisana* in the Tehuacán Valley, Mexico. *J. Ecol.* 76: 961-971.
- Valiente-Banuet, A., Vite, F. & Zavala, A. 1991. Interaction between the cactus *Neobuxbaumia tetetzo* and the nurse shrub *Mimosa luisiana*. *J. Veg. Sci.* 2: 11-14.
- Van Devender, T.R. 1990. Late Quaternary vegetation and climate of the Sonoran Desert, United States and Mexico. In: Betancourt, J.L., Van Devender, T.R. & Martin, P.S. (eds.) *Packrat middens: the last 40,000 years of biotic change*, pp. 134-164. University of Arizona Press, Tucson, AZ, US.
- Van Devender, T.R. & Burgess, T.L. 1985. Late Pleistocene woodlands in the Bolson de Mapimi: a refugium for the Chihuahuan Desert biota. *Quart. Res.* 24: 346-353.
- Wiggins, I.L. 1980. *Flora of Baja California*. Stanford University Press, Stanford, CA, US.
- Williams, S.C. 1980. Scorpions of Baja California, Mexico, and adjacent islands. *Occas. Pap. Calif. Acad. Sci.* 135: 1-127.
- Willis, J.C. 1922. *Age and area*. Cambridge University Press, Cambridge, UK.
- Yeaton, I.R. & Romero-Manzanares, A. 1986. Organization of vegetation mosaics in the *Acacia shaffneri*-*Opuntia streptocantha* association southern Chihuahuan Desert, Mexico. *J. Ecol.* 74: 211-217.

Received 9 November 2002;
 Revision received 27 January 2003;
 Accepted 4 February 2003.
 Co-ordinating Editor: J. Franklin.

For App. 1, see JVS/AVS Electronic Archives;
www.opuluspress.se/pub/archives/index.htm