

## **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.

## Biogeographic regions and $\beta$ -diversity of woody dryland legumes in the Baja California peninsula

Garcillán, Pedro P.<sup>1\*</sup> & Ezcurra, Exequiel<sup>1</sup>

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

\* Corresponding author; E-mail pedrop@ine.gob.mx

**Abstract.** We analysed the floristic turnover, or  $\beta$ -diversity patterns, of woody legumes in Baja California, the 1300 km long peninsula in NW Mexico. From the specimen labels of nine herbaria, we digitized 4205 records from 78 species and projected them onto a grid of 205 cartographic cells (20' longitude  $\times$  15' latitude). We found that the E-W turnover from the Pacific coast to the Sea of Cortés was high (ca. 60% change from one cell to the next) and that it was 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 regionalizations, 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 1300 km long temperate-tropical climatic gradient and the dramatic E-W gradient running from the Pacific Ocean ca. 100 km across the mountain range into the Sea of Cortés.

**Keywords:** Desert; Distance decay; *Leguminosae*; Mexico; Similarity; Species turnover.

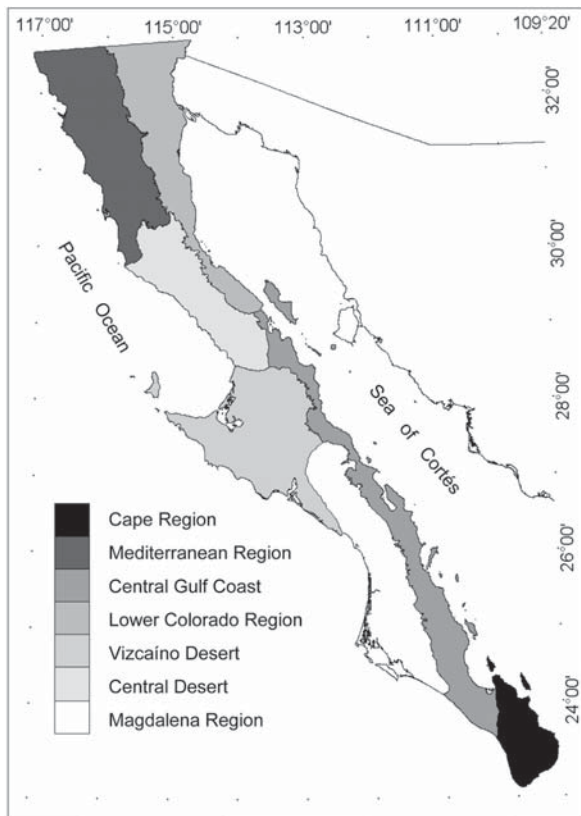
Nomenclature: Wiggins (1980), Hickman (1993), Skinner and Pavlik (1994), and International Legume Database & Information Service, [www.ildis.org/legumes.html](http://www.ildis.org/legumes.html).

### Introduction

The peninsula of Baja California, 1300 km long and from 40 to 200 km wide, covering 145 000 km<sup>2</sup>, contains a spectacular biological transition. Its northwestern part receives winter rains from Pacific storm fronts, and belongs to the California Floristic Province (Minnich & Franco-Vizcaíno 1998). Its southern tip receives late-summer cyclones called *chubascos* and is colonized 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 300 km long corridor 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, where the climate is controlled by 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 axes 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 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;



**Fig. 1.** Floristic regions of Baja California, modified from Shreve (1951), Wiggins (1980), León de la Luz et al. (2000), and Riemann (2001). Subdivisions: Cape Region (dry tropical scrubs and forests); Mediterranean Region (sclerophyllous scrubs); Central Gulf Coast (sarcocaulous desert); Lower Colorado Region (microphyllous desert); Vizcaíno Desert (sarcophyllous and sarcocaulous desert); Central Desert (Pacific coast, fog-fed sarcophyllous scrubs) and Magdalena Region (arborescent desert).

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 ca. 3000 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 ( $\beta$ -diversity) than to a high local species richness ( $\alpha$ -diversity). In this paper we intend to explore and test this statement using the woody legumes of the peninsula as a test group.

In a previous paper we analysed the distribution patterns and hotspots of species richness within the peninsula (Garcillán et al. 2003). For this second paper, we investigated the means through which high species turnover can maintain an elevated regional diversity despite low local richness. For this purpose, we tested the following simple hypotheses: 1. The peninsula has a high  $\beta$ -diversity relative to other, more homogeneous, regions; 2. 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; 3. 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 mountains 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 data set used, can be found in Garcillán et al. (2003) and references therein.

We worked with 4205 geo-referenced records from the 78 species of woody legumes of Baja California, belonging to 32 genera within the three legume sub-families and digitized from herbarium labels from nine herbaria. Following Riemann (2001), we divided the Peninsula of Baja California into 228 cartographic cells, each ca. 20' in longitude and 15' in latitude; 23 cells contained no collection records and were not included in the analysis, which thus consisted only of 205 cells.

Based on herbaria and geographic information, we constructed a presence-absence or incidence matrix (78 species  $\times$  205 cells). If the species had been collected in that cell the score '1' was entered, otherwise the score was '0'. The elements of the matrix totalled 1284 presences. By adding all the elements for each column (i.e. geographic cell) of the matrix, we could estimate the species richness ( $\alpha_i$ ) 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 analysed species turnover along E-W transects, from one coast to the other. For this, we used the simple model proposed by Schluter & Ricklefs (1993), which is in turn related to Whittaker's (1960) and Harrison et al. (1992) models:

$$\gamma = n \cdot \beta \cdot \bar{\alpha} \quad (1)$$

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

To test whether  $\beta$ -diversity is related to landscape heterogeneity, we calculated a series of estimates of topographic variation for each transect. For this purpose, we measured the maximum altitude and the altitude of six points distributed regularly within each 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  $\beta$ -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:

$$\beta = \gamma / (n \cdot \bar{\alpha}) \quad (2)$$

where  $\gamma$  is the total richness of both transects together,  $\bar{\alpha}$  is the mean species richness of the pair of transects,  $\beta$  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  $\beta$ -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*

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 of 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  $\beta$ -diversity, has also been 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 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 (Preston 1962; Whittaker 1972; Okubo & Levin 1989; Nekola & White 1999):

$$S_d = S_0 \cdot e^{-kd} \quad (3)$$

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 data set, 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 data sets.

*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. In 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*

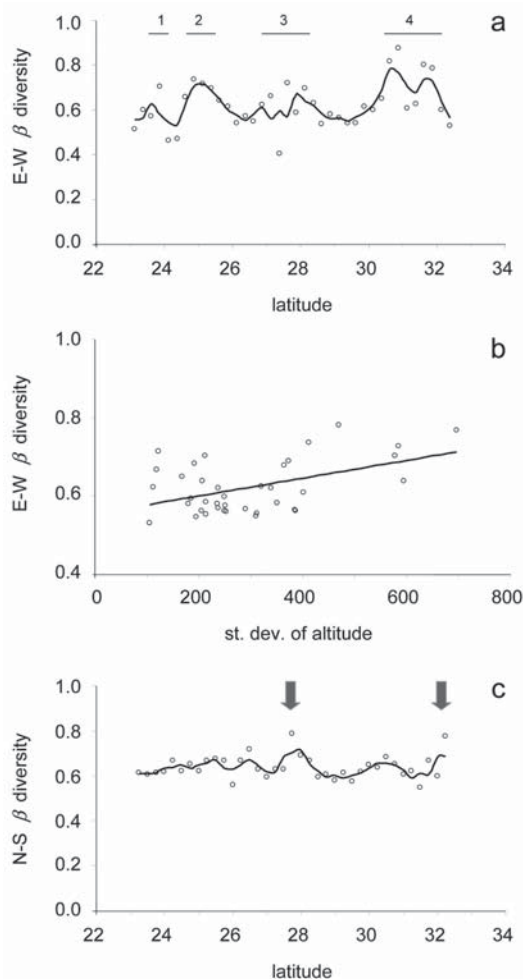
$\beta$ -diversity within E-W transects varied between 0.40 and 0.82, with a mean value of 0.62 (Fig. 2a). That is, within a transect more than 60% of all species are replaced from one cell to the next. Latitudinally, we found no significant trend in within-transect turnover. However, four regions of 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° 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  $\beta$ -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)*

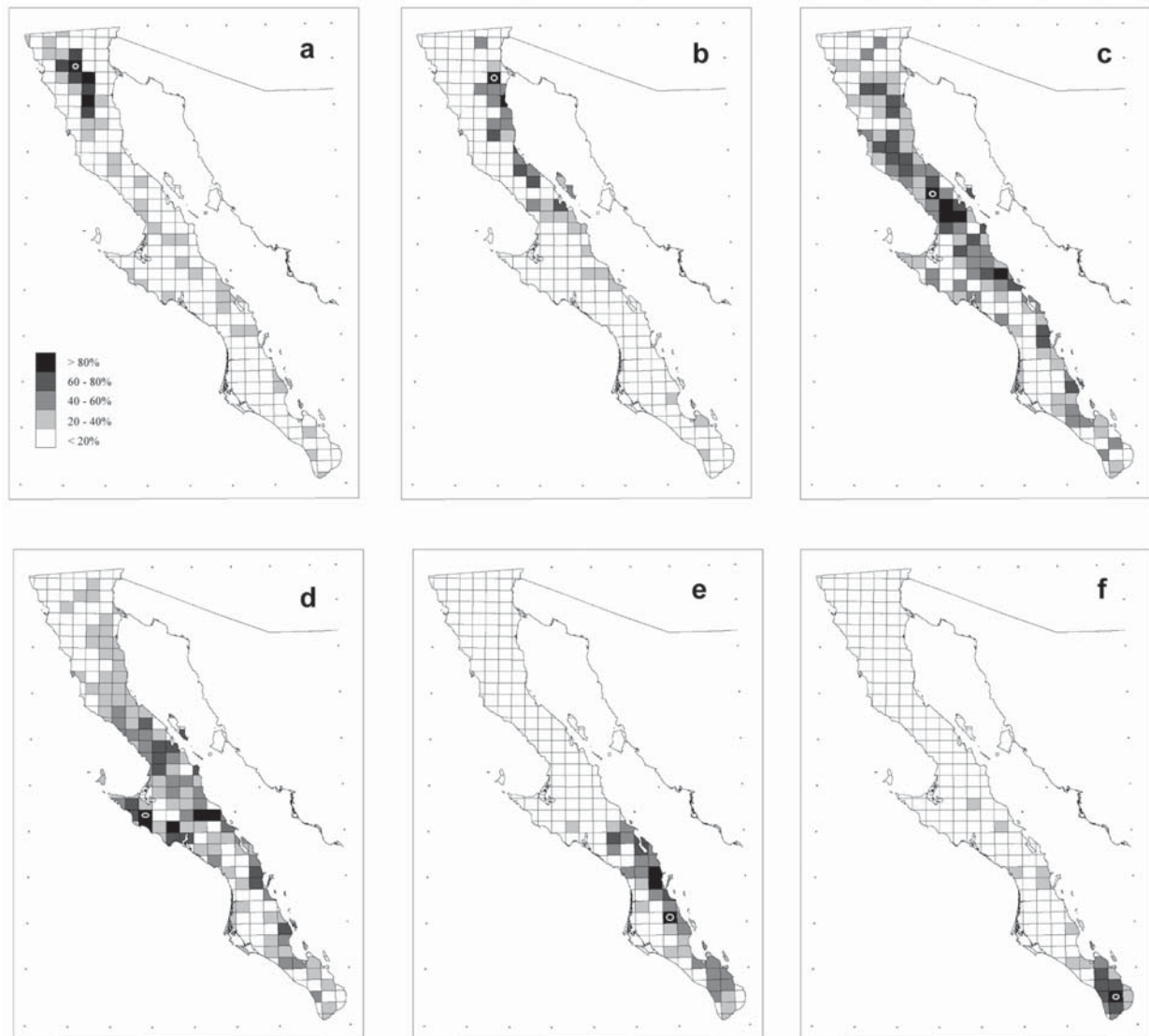
N-S turnover between adjacent transects varied less than E-W turnover, and had values ranging between 0.55 and 0.79, with a mean value of 0.64 (Fig. 2c). That is, from one transect to the next more than 60% of all species are replaced. We found no significant latitudinal trend in between-transect turnover; 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, a second region was identified at 33° N, near the border between Mexico and the USA.

### *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. 3 a-f.



**Fig. 2.** Relationship between  $\beta$ -diversity along E-W transects and (a) latitude, (b) standard deviation of altitude. (c) Relationship between  $\beta$ -diversity between N-S transects and latitude. The continuous lines in (a) and (c) show the moving-mean 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  $\beta$ -diversity: the Vizcaíno Desert and the Sierra de Juárez.



**Fig. 3.** Floristic affinities of woody legumes among different 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.

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 calls 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 intrude into the mediterranean ecosystems), with relatively high similarities down to 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 had 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 had 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, with relatively

high similarities up to 27° N, i.e. the beginning of the more transitional Vizcaíno region. Southwards, however, this area has high affinities with the Cape Region.

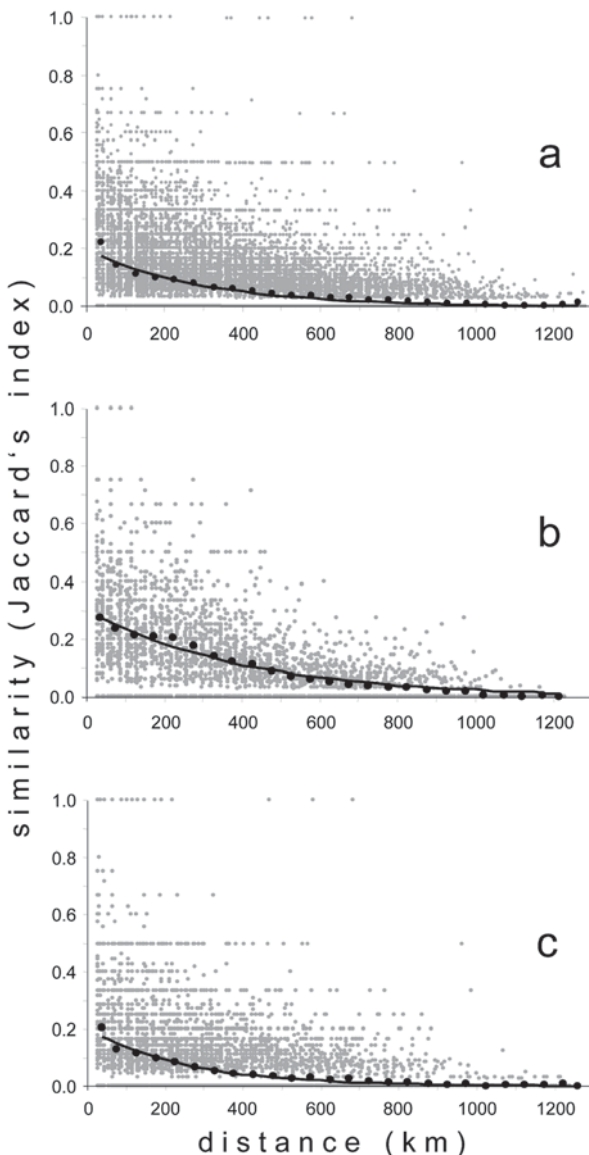
(f) *Cape Region*. The Cape Region, an area of very high endemism and species richness within the peninsula (Garcillán et al. 2003), has a well defined boundary that runs along the La Paz geologic fault, with a low proportion of its species shared with the Central Gulf Coast.

#### Floristic similarity and geographic distance

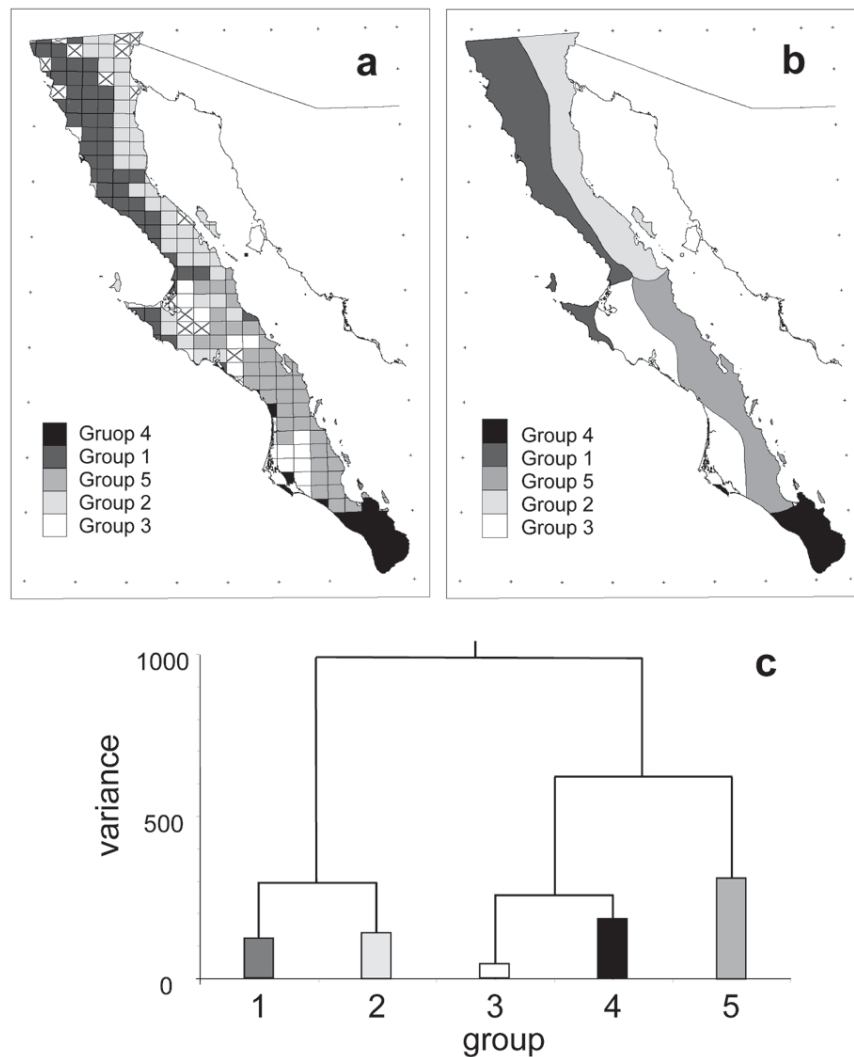
The parameters of Whittaker's exponential model differed significantly from one slope to the other (Fig. 4a-c). For the whole peninsula, the intersect value was  $S_0 = 0.199 (\pm 0.006)$  and the exponent value was  $k = 0.0033 (\pm 0.0001)$ . In the Pacific slope, the intersect was  $S_0 = 0.196 (\pm 0.005)$ , and the exponent was  $k = 0.0039 (\pm 0.0001)$ . In the Gulf slope, the intersect was  $S_0 = 0.303 (\pm 0.007)$  and the exponent was  $k = 0.0025 (\pm 0.0001)$ . The intersect did not differ significantly between the whole peninsula and the Pacific slope, but it was significantly higher ( $P < 0.00001$ ) for the Gulf slope. The exponent was somewhat higher for the Pacific slope compared to the whole data set ( $P = 0.0006$ ) and very low for the Gulf corridor compared to the other two data sets ( $P < 0.00001$ ). In short, both parameters differed significantly from one slope to the other. The Gulf slope had higher expected similarity between neighbouring cells ( $S_0$ ) and a lower turnover rate ( $k$ ) implying that, for any geographic distance, it is expected to find higher between-cell similarities on the Gulf than on 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; in the Pacific slope it is 0.56, while on the Gulf it is 0.36.

#### Floristic classification

The divisive classification procedure was continued until five groups were identified (Fig. 5 a-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 ca. 28° N. Subsequent divisions chiefly separated the cells according to the peninsular divide. Group 1, in the north, corresponds very closely to 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 on the southern Pacific slope of the



**Fig. 4.** Similarity between pairs of cells as a function of distance between the cells: (a) whole peninsula (205 cells;  $n = 20910$  cross-comparisons); (b) Gulf slope (78 cells;  $n = 3003$ ) and (c) Pacific slope (127 cells;  $n = 8001$ ). 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) geographic 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.

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 *S. atomaria* and (Group 5)

*Cercidium microphyllum* and *Prosopis articulata*. A full list of indicator species and their indicator values is provided in App. 1.

### Discussion and Conclusions

The species turnover of woody legumes in Baja California is high: 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 the 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 had 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 with 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  $\beta$ -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 regionalization is coherent with the analyses of  $\beta$ -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 centre, 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 regionalizations 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 described for the peninsula in a previous paper (Garcillán et al. 2003), 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: 1. Baja California has an extremely high  $\beta$ -diversity of woody legumes, mostly as a result of its abrupt topography and contrasting influence of the two surrounding seas. 2. Because the peninsula lies chiefly in a N-S direction along a central mountainous 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. 3. The ecological regions of woody legumes in the peninsula clearly reflect the two main environmental forces that act on it, namely the temperate-tropical 1300 km long climatic gradient and the dramatic E-W gradient that runs from the Pacific Ocean across the mountain divide into the Sea of Cortés along a distance of 100 km or less.

**Acknowledgements.** We are grateful to Dr. H. Riemann for his invaluable help in the use of the Geographic Information System and to the curators of all the herbaria we visited for their assistance and hospitality. We are especially indebted to José Luis León de la Luz and José Delgadillo, for generously sharing the rich database of CIBNOR's and UABC's herbaria. We also thank Charlotte González and the Huerta-González family for their assistance in checking the herbaria. 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.

## References

- Arriaga, I., Aguilar, C., Espinosa, D. & Jiménez, R. (eds.) 1997. *Regionalización ecológica y biogeográfica de México*. CONABIO, México D.F., MX.
- Arriaga, L. & Rodríguez-Estrella, R. (eds.) 1997. *Los oasis de la península de Baja California*. SIMAC, CIBNOR, La Paz, MX.
- 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. *Occas. Pap. Calif. Acad. Sci.* 132. San Francisco, CA, US.
- Condit, R., Pitman, N., Leigh Jr., E., Chave, J., Terborgh, J., Foster, R.B., Nuñez, P., Aguilar, S., Valencia, R., Villa, G., Muller-Landau, H.C., Losos, E. & Hubbell, S.P. 2002. Beta-diversity in tropical forest trees. *Science* 295: 666-669.
- Crosswhite, F.S. & Crosswhite, C.D. 1982. The Sonoran Desert. In: Bender, G.L. (ed.) *Reference book of the deserts of North America*, pp. 163-320, Greenwood Press, CT, 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, Tucson, AZ, US.
- Ezcurra, E. 1987. A comparison of reciprocal averaging and non-centred Principal Component Analysis. *Vegetatio* 71(1): 41-48.
- Ezcurra, E. 2001. Desert and Sea. In: Robles-Gil, P., Ezcurra, E. & Mellink, E. (eds.) *The Gulf of California. A world apart*, pp. 37-61. Agrupación Sierra Madre, México D.F., MX.
- Ezcurra, E. & Rodrigues, V. 1986. Rainfall patterns in the Gran Desierto, Sonora, Mexico. *J. Arid Environ.* 10: 13-28.
- Ezcurra, E., Peters, E., Búrquez, A. & Mellink, E. 2002. The Sonoran and Baja Californian Deserts. In: Mittermeier, R.A., Mittermeier, C.G., Robles-Gil, P., Pilgrim, J., da Fonseca, G.A.B., Brooks, T. & Konstant, W.R. (eds.) *Wilderness. Earth's last wild places*, pp. 315-333. CEMEX (Monterrey), Conservation International (Washington, D.C.) and Agrupación Sierra Madre, México D.F., MX.
- Garcillán, P.P., Ezcurra, E. & Riemann, H. 2003. Distribution and species richness of woody dryland legumes in Baja California, México. *J. Veg. Sci.* 14: 475-486.
- 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.
- Harrison, S., Ross, S.J. & Lawton, J.H. 1992. Beta diversity on geographic gradients in Britain. *J. Anim. Ecol.* 61: 151-158.
- Hastings, J.R. & Turner, R.M. 1965. Seasonal precipitation regimes in Baja California, Mexico. *Geogr. Ann.* 47 A 4: 204-223.
- Hengeveld, R. 1990. *Dynamic biogeography*. Cambridge University Press, Cambridge, UK.
- Hill, M.O. 1979. *TWINSPAN – a FORTRAN program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes*. New Cornell University, New York, NY, US.
- Jackson, D.A. 1993. Principal Component Analysis: how many components are nontrivial and interpretable? *Ecology* 74: 2204-2214.
- 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., 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 D.F., MX.
- León de la Luz, J.L., Pérez Navarro, J.J., Domínguez M. & Domínguez, R. 1999. *Flora de la Región de El Cabo, Baja California Sur, México*. Serie Listados Florísticos de México, Instituto de Biología, U.N.A.M., México D.F., MX.
- León de la Luz, J.L., Pérez Navarro, J.J. & Breceda, A. 2000. Vegetation of the lowlands of the Cape Region of Baja California Sur: a transitional xerophytic tropical plant community. *J. Veg. Sci.* 11: 547-555.
- Martin, P.S., Yetman, D.A., Fishbein, M.E., Jenkins, P.D., Van Devender, T.R. & Wilson, R. (eds.) 1999. *Gentry's rio Mayo plants: The tropical deciduous forest and environs of Northwest Mexico*. Southwest Center Series, University of Arizona Press, Tucson, AZ, US.
- McAuliffe, J. 1990. Paloverdes, pocket mice, and bruchid beetles – interrelationships of seeds, dispersers and seed predators. *Southw. Nat.* 35: 329-337.
- Minnich, R.A. & Franco-Vizcaíno, E. 1998. *Land of chamise and pines. Historical counts and current status of Northern Baja California's vegetation*. U.C. Publications in Botany no. 80, University of California Press, Berkeley, CA, US.
- Mourelle, C. & Ezcurra, E. 1996. Species richness of Argentine cacti: A test of biogeographic hypotheses. *J. Veg. Sci.* 7: 667-680.
- Murphy, R.W. 1983. Paleobiogeography and genetic differentiation of the Baja California herpetofauna. *Occas. Pap. Calif. Acad. Sci.* 137: 1-48.
- Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B. & Kent, J. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403: 853-858.
- Nekola, J.C. & White, P.S. 1999. The distance decay of similarity in biogeography and ecology. *J. Biogeogr.* 26: 867-878.
- Noy-Meir, I. 1973. Divisive polythetic classification of vegetation data by optimized divisions on ordination components. *J. Ecol.* 61: 753-760.
- Okubo, A. & Levin, S.A. 1989. A theoretical framework for data analysis of wind dispersal of seeds and pollen. *Ecology* 70: 329-338.
- Peinado, M., Alcaraz, F., Delgadillo, J. & Aguado, I. 1994. *Fitogeografía de la península de Baja California, México*. *An. Jard. Bot. Madr.* 51: 255-277.
- Preston, F.W. 1962. The canonical distribution of commonness and rarity: parts I and II. *Ecology* 43: 185-215, 410-432.

- Rapoport, E.H. 1975. *Areografía*. FCE, México D.F., MX.
- Rapoport, E.H. & Ezcurra, E. 1979. Natural and man-made biogeography in Africa: a comparison between birds and phytopathogens. *J. Biogeogr.* 6: 341-348.
- 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.
- Riemann, H. 2001. *Flora vascular endémica de la península de Baja California, patrones de distribución y escenarios de conservación*. Ph.D. Thesis. U.N.A.M., México D.F., MX.
- Robichaux, R.H. & Yetman, D.A. (eds.) 2000. *The tropical deciduous forest of Alamos. Biodiversity of a threatened ecosystem in Mexico*. University of Arizona Press, Tucson, AZ, US.
- Schluter, D. & Ricklefs, R.E. 1993. Species diversity, an introduction to the problem. In: Ricklefs, R.E. & Schluter, D. (eds.), *Species diversity in ecological communities: historical and geographical perspectives*, pp. 1-10. The University of Chicago Press, Chicago, IL, US.
- 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.
- Smith, S.D., Monson, R.K. & Anderson, J.E. 1997. *Physiological ecology of North American desert plants*. Springer-Verlag, Berlin, DE.
- 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.
- Whittaker, R.H. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. *Ecol. Monogr.* 30: 279-338.
- Whittaker, R.H. 1972. Evolution and measurement of species diversity. *Taxon* 21: 213-251.
- Wiggins, I.L. 1980. *Flora of Baja California*. Stanford University Press, Stanford, CA, US.

Received 12 March 2003;

Revision received 22 May 2003;

Accepted 23 May 2003.

Co-ordinating Editor: J. Franklin.

For App. 1, see *JVS/AVS Electronic Archives*;  
[www.opuluspress.se/pub/archives/index.htm](http://www.opuluspress.se/pub/archives/index.htm)