

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.

Endemic regions of the vascular flora of the peninsula of Baja California, Mexico

Riemann, Hugo^{1*} & Ezcurra Exequiel²

¹El Colegio de la Frontera Norte, km 18.5 carretera escénica Tijuana – Ensenada, San Antonio del Mar, Tijuana, Baja California, México C.P. 22709; ²San Diego Natural History Museum, 1788 El Prado, San Diego CA 92101, USA;

*Corresponding author; E-mail riemann@colef.mx

Abstract

Question: Can we recognize areas of high endemism and high endemic richness, using data from collections, and what are the ecological variables that best explain these areas?

Location: Peninsula of Baja California, Mexico.

Methods: We analysed the distribution of 723 endemic vascular plants species along the peninsula of Baja California and neighbouring islands distributed in 218 cartographic cells 15' × 20' in size. By means of a residual analysis, we identified areas of significantly high endemic species richness, and we calculated the degree of endemism (or rarity) in each cell by giving to each species a weight factor inversely proportional to the land area it covers.

Results: Nine regions of high-endemism and/or high endemic species richness were found.

Discussion and conclusions: The analyses of rarity and endemic species richness showed two contrasting scenarios: High endemism values in oceanic and sky islands accounts for a high number of species with a restricted distribution, promoted most likely by genetic isolation and high environmental heterogeneity. High endemic richness along the peninsular coast is related to ecotonal transition along vegetation types. After correcting for collection effort (i.e. the number of specimens collected within a cell), we found the phytogeographic region and altitudinal heterogeneity to be the variables that best predicted endemic richness. Both high endemism and high endemic richness have distinct geographic patterns within our study region. The nine endemic regions provide elements for priority definitions in future conservation programs.

Keywords: California floristic province; Conservation; Endemism; Sonoran desert.

Abbreviation: GIS = Geographical information system.

Introduction

Areas of high endemism are of prime interest for conservation because of the concentration of unique species that are major conservation targets (Myers et al. 2000). The peninsula of Baja California flora contains no less than 3700 species of vascular plants, one fifth of which are endemic to this region. Although there are only 18 endemic genera and no endemic families, in Baja California endemism at the species and subspecies levels is found in 84 of its 155 native plant families, and is especially high in the Asteraceae, Cactaceae and Fabaceae, which jointly account for 40% of the regional endemism. The high number of endemic plant species in this region is possibly the result of landscape heterogeneity and isolation, two factors that favour biological speciation. Additionally, the presence of tertiary paleo-endemics may be the result of the long-term climatic stability of regions near to, and buffered by, the Pacific Ocean (Peinado et al. 1994). The peninsula forms an elongated land bridge that stretches almost 10° latitude from the Nearctic region in the north into the Neotropical region in the South.

The ecotonal nature of the region also contributes to the coexistence of species of different origin, and hence to its high biological diversity (Rzedowski 1978). The numerous landscapes, climates and landforms promote a mosaic of communities that traverse such extreme gradients as coastal scrubs to mountain coniferous forest to desert vegetation in less than 80 km of east-west distance. The sierras that stretch along the peninsula form 'sky island' refuges, where numerous Pleistocene relicts are found (Moran 1972, 1983; Axelrod 1979).

Although the flora throughout the peninsula has been collected for more than 150 years, the real number of vascular plants inhabiting it is still unknown, as the majority of the specimens in the herbaria come from sites near the main roads. In a recent, conservation oriented study we evaluated the extent to which endemic plant species are being protected in nature reserves within the Baja

California peninsula by using a Gap Analysis (Riemann & Ezcurra 2005). However, from the point of view of basic vegetation science, the geographic distribution of plant endemism in the peninsula still calls for a detailed analysis. The purpose of this investigation is (1) to make an analysis of the distribution of the vascular plant endemism in the peninsula of Baja California and nearby islands, (2) to relate the distribution patterns to vegetation types and other predictors, (3) to identify regions with greatest richness of endemics and (4) to identify regions with a high degree of micro-endemism.

The study region

Our region encompasses the Baja California peninsula, Cedros and Guadalupe and San Benito Islands in the Pacific, and all the islands that lie to the west of the deep sea rift of the Sea of Cortés. The peninsula is ca. 1300 km long and 45-250 km wide. The study region

represents an area of ca. 143 000 km², spanning almost 10° latitude from 22°53' N in the Cape Region to 32°46' N in the Mexico-US border.

The peninsula of Baja California was formed during the Tertiary (some 5-10 Myr ago), when a narrow section of Mexico's mainland was separated northwest by tectonic forces, giving rise to the Gulf of California, also known as the Sea of Cortés. A series of mountain ranges run in succession along the peninsula from north to south. This steep mountain backbone separates the ecosystems sloping east into the Gulf from those running west into the Pacific, and creates a complex landscape gradient with a large diversity of environments (Fig. 1).

Twenty different types of climates (as defined according to Köppen's classification of the world climates modified for Mexico by García 1988) cover the peninsula. Seven of these are arid, and are located mainly in the Cape region and in the slopes of the mountain ranges in the mid-peninsula, ten correspond to variants of the very arid climates, two are temperate and one is a cold

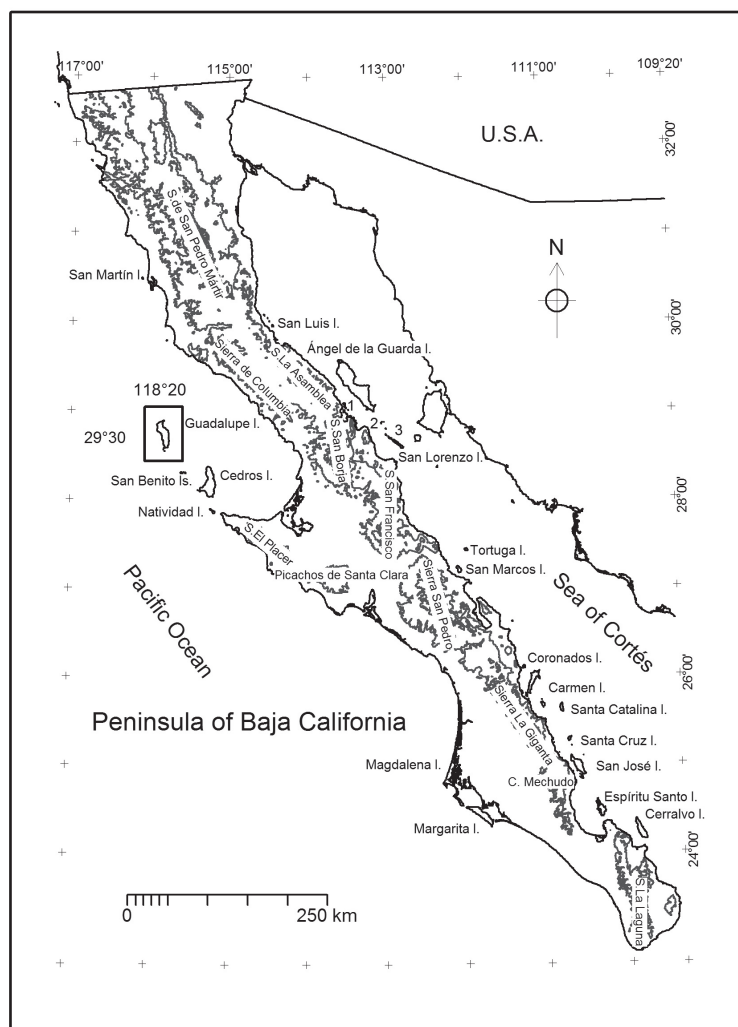


Fig. 1. Map of the Baja California peninsula and neighbouring islands. 1 = Bahía de Los Ángeles, 2 = Partida Norte island, 3 = Rasa island.

climate found in the high mountain zones of San Pedro Mártir. Most of the territory has mean annual temperatures above 18 °C and mean annual rainfall below 200 mm. The highest rainfall (500-700 mm) occur in the high parts of the sierras of San Pedro Mártir and La Laguna, in both extremes of the peninsula. The most extreme desert conditions occur along the coasts of the Gulf, in the northeast part of the territory, where the highest temperatures and lowest annual rainfall occur. The peninsular territory is occupied by a diverse array of plant communities that range from winter-rain mediterranean chaparrals, coastal sage scrubs and conifer forests in the northwest, to microphyllous scrub in the northeast, to tropical deciduous dry forests in the southern tip of the peninsula (the Cape Region), with a heterogeneous array of desert scrub communities in the central deserts, in which sarcocaulous (fleshy-stemmed) trees, giant columnar cacti and sarcophyllous (succulent-rossette) species prevail.

Methods

Geographic information

The information about endemic species was obtained from the literature and from herbaria. Following a previous paper (Riemann & Ezcurra 2005) and because of the obvious association between the biogeographic definition of the peninsula of Baja California and the political boundaries of the two Mexican States that lie within it, we arbitrarily defined endemic species as those that had their distribution restricted to our study region. Although this criterion may introduce some error in the case of species that occur along the northern border of the peninsula, which may be classified as non-endemic when in reality they may have a narrow biogeographic distribution, we were restricted in our project scope and funding to the Mexican territory.

The literature consulted was Gentry (1978), Wiggins (1980), Gould & Moran (1981), Perry (1991), Delgadillo (1992), Lenz (1992), León de la Luz & Coria (1992), Turner et al. (1995) and Moran (1996). The lists from these publications were compared with Beauchamp (1986), Hickman (1993) and Martin et al. (1998), in order to exclude those species that are present outside the study region. The consulted herbaria were San Diego Natural History Museum, Rancho Santa Ana at Claremont, University of California at Berkeley and California Academy of Sciences. From these sources of information it was possible to obtain location data for 723 of the 770 endemic taxa.

The information from the collections was geographically referenced by means of a topographic map, scale

1:250000 (Anon. 1982). This initial database consisted of a file of 12867 records related to 3925 field sites, representing 723 endemic taxa. With the original database we formed a species × sites data matrix of 723 endemic species and 218 cells, or cartographic units, that contained collection data. Each cell stretched 15' latitude by 20' longitude. We organized the matrix in two ways: On the one hand, we organized the matrix as a presence-absence dataset (matrix **A**), disregarding repeated collections of the same species for the same cell, totalling 5565 presence records. On the other hand, we also counted all collection records for each species in each cell, giving rise to a quantitative matrix (matrix **B**) describing the number of specimens collected for each species in each cartographic cell, totalling 12867 collection records.

To relate the physical geography of the region to the database matrix and to the location of natural vegetation areas (i.e. ecological regions), we used a geographic information system (GIS), and carried out the following procedures: 1. We digitized the land area, coastlines, and islands of the peninsula, with isolines every 100m from contour maps published by Mexico's National Institute of Statistics, Geography and Informatics (INEGI, scale 1:1 000 000). From this map we generated a peninsular divide map with two categories: Pacific slope and Gulf slope. 2. We constructed for the study region a polygon map consisting of the 218 cartographic cells described above. 3. We used a map of the five major phytogeographic regions of the peninsula (see Riemann & Ezcurra 2005 for details), derived primarily from Shreve (1951) and Brown & Lowe (1980), and modified according to later works (León de la Luz et al. 2000 for the southern part of the Peninsula; Peinado et al. 1997 and Delgadillo 2005 for the northern section; See Fig. 2). Thus, the GIS consisted of four maps and corresponding databases: the physical topographic map, the topographic-divide map, the cartographic-cells map and the phytogeographic regions.

For our geographic analysis, all maps were transformed to a raster format with a 150-m pixel resolution. All the spatial information was transformed to the Lambert conformal conic projection (Pearson 1990), which is commonly used in large-scale maps in Mexico. For each cell we calculated, (1) the land area, i.e. the area of the cell minus the area within the cell occupied by water or falling outside our study region; (2) the altitude values (minimum, maximum, mean and standard deviation of the mean); (3) the divide to which the cell belongs (Pacific or Gulf) and (4) the types of phytogeographic regions in the interior of each cell.

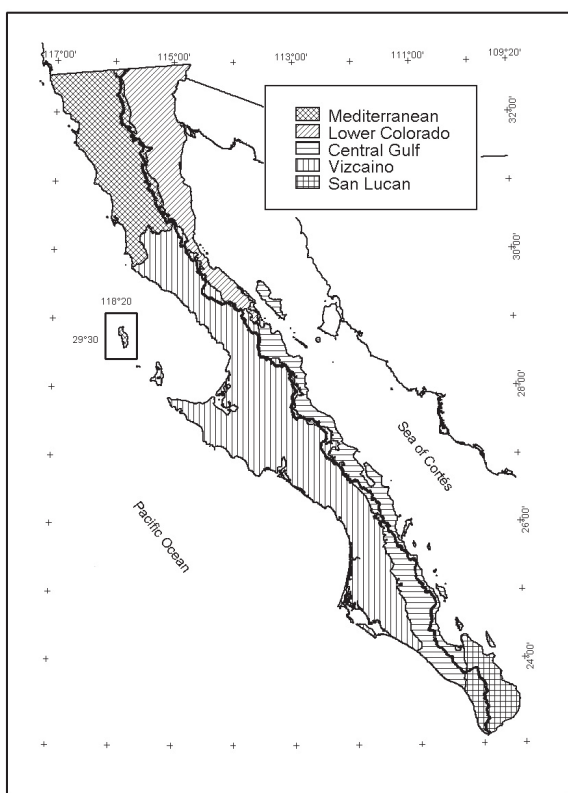


Fig. 2. Phytogeographic regions of the Peninsula of Baja California and neighbouring islands. See text for explanation. The thick line along the peninsular backbone shows the topographic divide (modified from Riemann & Ezcurra 2005).

Mapping of endemism, and collection effort

Endemicity

We calculated the level of endemism (e) in each cell, by giving to each species a weight factor (w) inversely proportional to the land area covered by the cells occupied by the species. That is, the weight factor for species i was simply calculated as $w_i = 1 / \text{area}(i)$. The factor, an estimate of the geographic rarity of each species, was then used to weight the species richness count for each cell. That is,

$$e_j = \sum_i^s a_{ij} \cdot w_i \quad (1)$$

where the a_{ij} values correspond to the presence-absence records in matrix **A**. Quite obviously, the value of the endemicity measure (e) reflects the presence of species with highly restricted distributions within the endemic flora of the peninsula. In the rest of this paper we will refer to these species as 'rare species' or 'micro-endemics'.

Collection effort

Finally, we calculated for each cell the collection effort, represented by the number of specimens collected in that cell. These were obtained from the cell or column totals of the quantitative matrix (matrix **B**) describing all collection records for each species in each cell. As with the other parameters, the collection effort values were plotted in the corresponding map cells.

Testing hypotheses on endemic species richness patterns

The variation in species richness observed between cells was tested statistically to see whether the observed patterns can be attributed to random variation (our null hypothesis), or if they should be ascribed to non-random causes (i.e. 'hotspots' of biodiversity concentration). In order to do this, we first corrected the number of species observed in any given cell by the land area of the cell, using the method described in Garcillán et al. (2003), which corrects observed species richness values with Preston's 'power function' model ($s = cA^z$, where s is the number of species present in an area of size A , z a power exponent and c a scale factor that depends on the unit used to measure area; see Arrhenius 1921; Preston 1960). The value of the power exponent (z) was estimated following Dunn & Loehle (1988, see also Garcillán et al. 2003 for details) by resampling our cartographic cells at different scales, and estimating the parameter using log-log regression. The value for z was 0.5, very similar to the value (0.498) reported by Garcillán et al. (2003) for woody legumes in Baja California. With this method, the species richness values in the larger cells was corrected down, while the smaller than average cells were corrected up, bringing all species counts to a comparable and standard cell size.

Once the cells were corrected for area, the richness values of each cell were regressed against a series of predictor variables, following the method described in Mourelle & Ezcurra (1996). Because species richness values are frequency counts, our null model for the distribution of regression errors was the Poisson distribution and, for this reason, we performed a Poisson regression (also known as log-linear regression) on our data sets using the GLIM package (Crawley 1993; Francis et al. 1993). Our dependent variable was the area corrected species richness, and our predictor variables were (1) collection effort (estimated from the species:specimens ratio in each cell; see Garcillán et al. 2003 for methodological details), (2) latitude of the cell, (3) floristic province, (4) slope of the peninsular divide (Pacific or Gulf), (5) the different altitude values (minimum, maximum, and mean altitude and standard deviation of altitude within each cell) and (6) a set of climatic variables (mean annual

temperature, precipitation and water deficit).

Once we had fitted the best model, we plotted the residual values on a map. A property of random frequency counts (i.e. the Poisson distribution) is that the mean equals the variance, and this property can be used to test for those cells where species richness is higher than could be expected by random variation alone, i.e. to identify diversity 'hotspots'. Once we had an expected value of species richness for each cell calculated from the regression model, we calculated the Pearson residual difference between the observed and the expected value ($r_j = (o_j - e_j) / \sqrt{e_j}$). Because e_j is the expected value, then it follows that, if the data is randomly (Poisson) distributed, $\sqrt{e_j}$ is the standard deviation. Hence, under the null hypothesis of random variation of the model residuals, the values of the Pearson residuals should behave as normalized deviates and their probability of occurrence can be calculated from the Normal distribution. Any residual departing significantly from the normal distribution would indicate that the species richness observed in that cell is not satisfactorily explained by the regression model, and that in all likelihood other causes are also intervening in the concentration of endemic species there (see Mourelle & Ezcurra 1997).

To make our test statistically conservative, and taking into account that species distributions are normally autocorrelated in space (Lyons & Willig 1999), we used a Bonferroni correction for our test on the normalized residuals, establishing a rejection threshold for each cell at $P = 0.0002$ and $P = 0.00004$, in order to obtain a global probability of a type-I error in 218 non-independent simultaneous tests of $P = 0.05$ and $P = 0.01$, respectively.

Results

Endemic species richness and distributional areas

Species richness

Each cartographic cell had a mean of 25.6 recorded endemic species. The distribution of endemic species was, however, extremely clumped: the variance of the species richness was 555.4, and hence the variance to mean ratio was 21.7, a value significantly ($P < 0.0001$) higher than the expected ratio of 1, under the assumption of random Poisson variation. In short, the observed variations in endemic species richness in space cannot be attributed to random factors but are indicative of non-random causes.

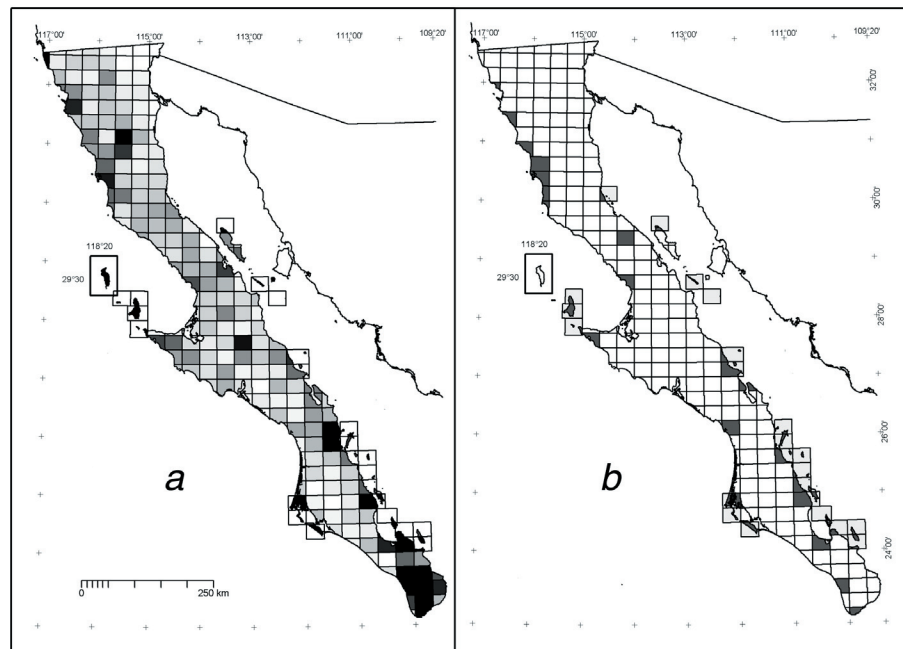
Species distributions

Each species occupied ca. 7.7 cells. The distribution of these spatial occupancies was highly skewed: While most species occupied less than six cells, a few widely distributed endemics occupied a large proportion of Baja California. In this case, however, the pattern did fit to a statistical distribution model: As discussed and predicted by Rapoport (1975) the distribution of species in the cells did not differ significantly from the lognormal.

Patterns of endemism

The highest values of endemism (Fig. 3a) were found in the Pacific islands, especially in San Benito. High levels of micro-endemics were also found in the Sierra San Pedro Mártir towards the north of Baja California,

Fig. 3. (a) Endemism values in the peninsula for the 218 cartographic cells: The shades of black indicate intensity of endemism; darker cells represent high-endemism areas, (b) Regression residuals for the species-richness regression model: Grey cells show 'hotspot' areas of significantly high ($P < 0.05$) concentration of species.



the Sierra San Francisco in the Vizcaíno Desert near the peninsular centre, the Sierra de La Giganta in the lower Gulf coast, the islands of Bahía Magdalena and the Cape Region, at the extreme south of the peninsula. In general, the cells rich in rare species (high endemicity values) were associated with high biological isolation: sky islands, highly distinctive local floras and oceanic islands (Fig. 3a).

Endemic species richness patterns

The regression model that best explained species richness included as predictors variables the ecoregion, collection redundancy and standard deviation of the altitude (i.e. landscape heterogeneity; Table 1). An increment in the values of the last two variables is associated with an increase in species richness. If ecoregions were not included in the analysis, then the second best predictor was simply latitude, as is expected in most continental biodiversity gradients. Precipitation is directly associated with species richness. Water deficit and temperature presented a significant negative association to endemic species richness but, as with latitude, their predictive capacity was lower than that of ecoregions, and was not get added into the final stepwise regression model. The residuals in 38 cells departed significantly from the expected values, and reflect areas of high endemic richness even after controlling for the explanatory variables collection effort, ecoregion and variance in elevation (Fig. 3b). Although the pattern of high endemic richness hotspots resembles, in many aspects, the distribution of high endemicity cells (Fig. 3a) some notable differences were apparent. Guadalupe Island, for example, an area that harbours some extremely restricted micro-endemics, did not show as a hotspot because its total endemic species richness (considering both micro and macro-endemics) is not very high. A similar trend was found in most sky islands, e.g. San Pedro Mártir and San Francisco, where a large proportion of the flora is micro-endemic, but their total endemic species richness is not significantly higher than neighbouring areas.

Table 1. Best predictors of richness of endemic species in the Baja California peninsula. All effects were highly significant ($P < 0.00001$).

Source of variation	X ²	d.f.	r ²
Complete model	2424.3	6	0.604
Collection effort	1107.4	1	0.276
Ecoregion	1155.2	4	0.288
Altitudinal variation	161.7	1	0.040
Residuals	1591.4	211	
Total	4015.7	217	

High-endemicity/high-endemic richness regions

Combining our results, nine regions of high endemicity, high endemic species richness, or both, can be identified in the peninsula, characterized by either an unusual concentration of rare plants and/or by a high richness of regional plants independently of their rarity (Fig. 4).

Region 1. This mediterranean corridor located along the northwest coast between 29°45' and 32°00' latitude in coastal scrub and chaparral, harbours 106 endemics. *Adenothamnus validus* (Asteraceae), *Selaginella cinerascens* (Selaginellaceae), *Sphaeralcea fulva* (Malvaceae), *Amorpha apiculata* (Fabaceae) are examples of rare, narrowly distributed endemics. *Cneoridium dumosum* (Rutaceae), *Bergerocactus emoryi* and *Cylindropuntia prolifera* (Cactaceae), *Ribes viburnifolium* (Grossulariaceae) and *Phacelia ixodes* (Hydrophyllaceae) are also characteristic taxa, which barely cross the political border into California. The coastal corridor of mediterranean scrub, which shows the highest values of endemicity, also coincides with the part of the region facing the large development and urbanization pressures (Fig. 4).

Region 2. Located in the San Pedro Mártir range above 1200 m a.s.l. in oak and conifer forests, this sky island harbours no less than 66 endemics. *Amorpha apiculata* (Fabaceae), *Ophiocephalus angustifolius* (Scrophulariaceae), *Dudleya pauciflora* (Crassulaceae), *Ambrosia flexuosa*, *Stenotus pulvinatus*, *Cirsium trachylomum*, *Stephanomeria monocephala* and *Sphaeromeria martinensis* (Asteraceae) and *Echinocereus mombergerianus* (Cactaceae) are some of the micro-endemics found in this region.

Region 3. East of the peninsula, between 28°35' and 30°15' N, several high-endemicity and high-richness areas are found. The coastal area in San Luis harbours 41 species, including *Gilia palmeri* ssp. *spectabilis* (Polemoniaceae), *Nicotiana greeneana* (Solanaceae), *Hazardia odontolepis* and *Hofmeisteria fasciculata* (Asteraceae) among its rare taxa. In contrast with other high-endemicity sky islands, Sierra La Asamblea shows low levels of endemicity but high endemic species richness, with 42 relatively widespread taxa, such as the cacti *Cylindropuntia tesajo*, *Stenocereus gummosus* and *C. cholla*, or the legume *Errazurizia megacarpa*. Bahía de Los Ángeles and the Midriff Gulf Island archipelago that extend from Ángel de la Guarda Island in the north to San Pedro Mártir Island in the south including San Lorenzo, Rasa and Partida Norte islands harbour no less than 76 endemics. Ángel de la Guarda harbours at least 31 endemic taxa, including some rare species such

as *Hofmeisteria filifolia* (Asteraceae), *Lyrocarpa linearifolia* (Brassicaceae), *Ferocactus johnstonianus* and *Mammillaria angelensis* (Cactaceae). Another extremely rare species, *Pelucha trifida* (Asteraceae), is found in San Pedro Mártir Island.

Region 4. Between 27°20' and 28°55' N in the Pacific side of the peninsula three high-endemic species richness and high-endemicity subregions are found, containing 158 species. Towards the north, in the region of Santa Rosalita, 63 endemic species are located, including some rare plants such as *Encelia ventorum*, *Greenella ramulosa* and *Verbesina hastata* (Asteraceae) and *Cochemia maritima* (Cactaceae). Offshore, in the southwest part of this region, high-endemicity and high-richness coincide in Cedros and the three San Benito Islands, including rare plants such as *Agave sebastiana* (Agavaceae), *Encelia cedrosensis* and *Senecio cedrosensis* (Asteraceae). South of Cedros Island, the peninsula of Vizcaíno in the western 'horn' of Baja has evolved in relative floristic isolation, separated from the rest of the peninsula by a belt of halophytic scrubs. Most of the endemics found in this area are located in the west tip and at the Sierras El Placer and Santa Clara. Some of the distinctive species in this area are *Agave vizcainoensis* (Agavaceae), *Astragalus piscinus* (Fabaceae), *Camissonia sceptrostigma* (Onagraceae) and *Eriogonum encelioides* (Polygonaceae).

Region 5. The high-endemicity sky island of Sierra San Francisco, located in the middle of the peninsula, harbours 77 endemic taxa. *Serjania californica* (Sapindaceae), *Abutilon carterae* (Malvaceae) and *Brickellia brandegeei* (Asteraceae) are among the rarest micro-endemics of these ranges.

Region 6. The coastal corridor formed by the Sierra La Giganta and southern Gulf islands is unusually speciose, giving refuge to 302 endemic taxa. Although many of these have a broad distribution within the peninsula there are some very restricted rarities such as *Galium mechudoense* (Rubiaceae) at Cerro Mechudo, *Ferocactus diguetii* (Cactaceae), a strict island endemic, or *Mammillaria cerralboa* (Cactaceae) at Cerralvo Island. Inside this region, an area located in the north part of Sierra La Giganta stands out as a high-endemicity area, sheltering micro-endemics such as *Agave gigantensis* (Agavaceae) and *Galium carterae* (Rubiaceae).

Region 7. A high-richness area is found towards the north of the Magdalena plains, sheltering at least 49 relatively common Baja California endemic species, such as *Sarcostemma arenarium* (Asclepiadaceae), *Amauria brandegeana*, *Ambrosia bryantii*, *Encelia palmeri* and

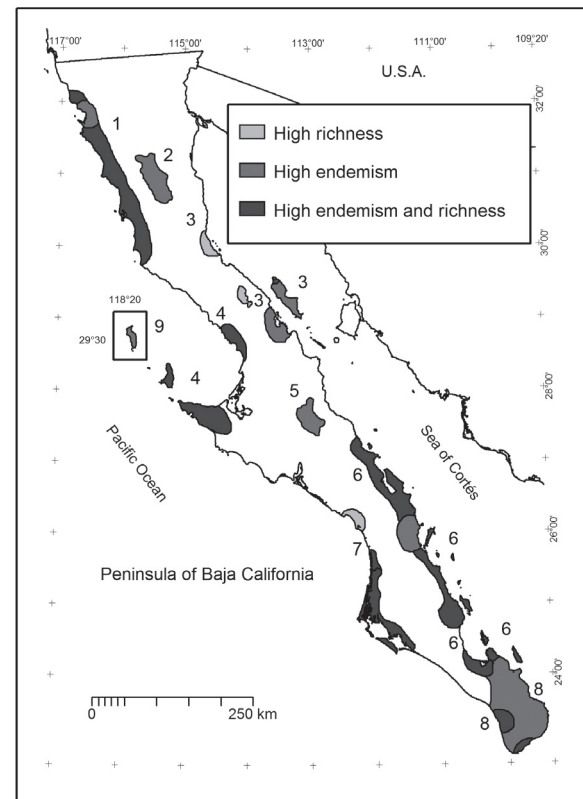


Fig. 4. Endemic regions of the peninsula of Baja California and neighbouring islands (see text for a description of numbered areas).

Nicoletia trifida (Asteraceae), *Sibara laxa* (Brassicaceae), *Cylindropuntia cholla* and *Stenocereus eruca* (Cactaceae). Southwards, the rocky landmasses of Magdalena and Margarita islands enclosing Magdalena Bay show not only high endemic species richness but also high levels of micro-endemism, sheltering some rare species such as *Cochemia halei* (Cactaceae), *Abronia carterae* (Nyctaginaceae), *Agave margaritae* (Agavaceae) and *Asclepias masonii* (Asclepiadaceae).

Region 8. The Cape Region, in the extreme south of the peninsula harbours a unique sequence of rare tropical dry ecosystems including xeric scrubs in the lowlands, tropical dry forest in the lower slopes of the Sierra de La Laguna, and pine-oak forests in the upper reaches. Isolated from the tropical ecosystems of the Mexican mainland, this region provides refuge for a rich mosaic of high-endemicity and high-richness areas, with some distinctive micro-endemic species such as *Pinus lagunae* (Pinaceae), *Cyrtocarpa edulis* (Anacardiaceae), *Dyssodia speciosa*, *Hofmeisteria fasciculata xantii*,

Viguiera tomentosa, (Asteraceae), *Lyrocarpa xantii* (Brassicaceae), *Cylindropuntia alcahes* var. *burrageana* and *Mammillaria peninsularis* (Cactaceae).

Region 9. Guadalupe Island, Mexico's westernmost oceanic island, shares phylogeographic characteristics with the mediterranean corridor. A total of 40 regional species are found here, including some strict island endemics such as *Castilleja guadalupensis* (Scrophulariaceae), *Triteleia guadalupensis* (Liliaceae), *Brahea edulis* (Arecaceae), *Cupressus guadalupensis* (Cupressaceae) and *Perityle incana* (Asteraceae).

Discussion

Some areas of Baja California show high levels of micro-endemicity and/or significantly high endemic species richness, even after the effects of ecoregions, collection effort and altitudinal heterogeneity were accounted for. These high-richness/high-endemicity spots may be the result of the combination of several factors. Firstly, the presence of Pleistocene relictual temperate forests may account for an important fraction of the paleo-endemisms. Secondly, modern desert and mediterranean scrubs appeared in the peninsula only after the last glaciation, adding diversity to the pre-existing vegetation matrix (Axelrod 1978, 1979). Thirdly, the dramatic diversity in climates, soils and landscapes induced by the pronounced peninsular topography promotes the presence of relatively fragmented communities and, consequently, of biological speciation, as has been described for other parts of the California floristic region (Stebbins & Major 1965; Richerson & Lum 1980). Lastly, short distance gradients from mesic to arid environments generate abrupt ecotones that allow the survival of transitional species and that promote speciation (Shreve 1936; Stebbins 1952).

In spite of the clear patterns observed, there are a few caveats to our study that should be considered. On the one hand, as we are working with herbarium records, the species distributions may reflect historic patterns and not necessarily current presence. This is particularly true for recently developed urban/tourism areas where large scale vegetation clearing has taken place. In contrast, there also some potential false absences as our database is necessarily based on the known flora, which is unavoidably less than the actual flora. Finally, the species-area correction may have some methodological limitations too, as it assumes that floristic richness throughout the peninsula follows Preston's model with a power exponent $z = 0.5$ in all ecoregions (Preston 1960). In an area as large as this one, this is likely to be an oversimplification.

Consequences for conservation

Most of the high-richness or high-endemicity areas identified in this study correspond to coastal corridors. This is especially important, as coastal areas and nearby islands are at immediate risk due to the increasing land-use change and growing development pressures, especially from urbanization, tourism and industry.

Although correlated to some degree, species rarity and richness do not always coincide in the peninsula; this seems to call for different conservation strategies. While the value of high-species-richness areas is simply the unusual concentration of species, it is clear that those species can also be found – and hence protected – in other parts of the peninsula. On the other hand, high-endemicity areas harbour rare, micro-endemic species that are not found elsewhere. Hence, their inclusion in a system of protected areas is less open to alternatives.

Thus, high-endemicity areas face much more localized threats and need very specific protection strategies. For example, one of the main threats in the oceanic islands of the region is the presence of goats and other domestic animals, as in Guadalupe and Cedros islands in the Pacific and several islands in the Sea of Cortés that urgently need effective eradication programs of invasive species. On the other hand, the main threats to the micro-endemic species located in the region's sky islands are mining, logging and cattle ranching. These pressures, however, do not seem to be as important as those on the oceanic islands. In some ranges resource extraction has been maintained near its current levels for the last 300 years with relatively low impact; mining has been done at a small scale and cattle are usually herded at lower altitudes. Indeed, some of these sky islands are among the less explored and most unaltered regions of the peninsula.

Conclusion

Two important points are derived from this research. Firstly, the results allowed us to identify areas with high levels of micro-endemism and high endemic species richness, information that is important to plan and prioritize new conservation policies in the peninsula. Secondly, the study highlighted the importance of the coastal peninsular corridors as biological hotspots, an important finding in relation to the increasing pressure of urbanization and tourism along the coasts of the Baja California peninsula.

Acknowledgements. Susan Wiser, Irma Trejo, Aaron Moody and one anonymous reviewer provided useful comments that greatly improved this manuscript.

References

- Anon. 1982. *Carta de México. Topográfica. Escala 1:2500000*. Instituto Nacional de Estadística Geografía e Informática (INEGI), México, MX.
- Arrhenius, O. 1921. Species and area. *J. Ecol.* 14: 95-99.
- Axelrod, D.I. 1978. The origin of coastal sage vegetation, Alta and Baja California. *Am. J. Bot.* 65: 1117-1131.
- Axelrod, D.I. 1979. Age and origin of the Sonoran desert vegetation. *Occasional Papers, California Academy of Sciences*, No. 132, San Francisco, CA, US.
- Beauchamp, R.M. 1986. *A Flora of San Diego County*. Sweetwater River Press, National City, CA, US.
- Brown, D. E. & Lowe, C. H. 1980. *Biotic communities of the Southwest*. USDA Forest Service. Rocky Mountains Forest and Range Experimental Station. General Technical Report RM 78. Fort Collins, CO, US.
- Crawley, M.J. 1993. *GLIM for ecologists*. Blackwell, Oxford, UK.
- Delgadillo, J. 1992. *Florística y ecología del Norte de Baja California*. Universidad Autónoma de Baja California. Ensenada, México, MX.
- Delgadillo, J. 2005. *El bosque de coníferas de la sierra de San Pedro Mártir, Baja California, México*. Instituto Nacional de Ecología, México, D.F., MX.
- Dunn, C.R. & Loehle, C. 1988. Species-area parameter estimation: testing the null model of lack of relationship. *J. Biogeogr.* 15: 721-728.
- Francis, B., Green, M. & Payne, C. (eds.) 1993. *The GLIM system: Release manual 4*. Clarendon Press, Oxford, UK.
- García, E. 1988. *Modificaciones al sistema de clasificación climática de Köppen*. Universidad Nacional Autónoma de México, México, MX.
- Garcillán, P.P., Ezcurra, E. & Riemann, H. 2003. Distribution and species richness of woody dryland legumes in Baja California, Mexico. *J. Veg. Sci.* 14: 475-486.
- Gentry, H.S. 1978. *The agaves of Baja California*. Occasional Papers of the California Academy of Sciences. No. 130, San Francisco, CA, US.
- Gould, F.W. & Moran, R. 1981. *The grasses of Baja California, Mexico*. San Diego Society of Natural History. Memoir 12. San Diego, CA, US.
- Hickman, J.C. (ed.) 1993. *The Jepson manual. Higher plants of California*. University of California Press. Berkeley, CA, US.
- Lenz, L.W. 1992. *An annotated list of the plants of the Cape Region, Baja California Sur Mexico*. Cape Press, Claremont, CA, US.
- León de la Luz, J.L. & Rocío Coria, B. 1992. *Flora iconográfica de Baja California Sur*. Publicación No. 3. Centro de Investigaciones Biológicas de Baja California Sur. La Paz, México, MX.
- León de la Luz, J.L., Pérez Navarro, J.J. & Breceda, A. 2000. A transitional xerophytic tropical plant community of the Cape Region, Baja California. *J. Veg. Sci.* 11: 555-564.
- Lyons, S.K. & Willig, M.R. 1999. A hemispheric assessment of scale dependence in latitudinal gradients of species richness. *Ecology* 80: 2483-2491.
- Martin, P.S., Yetman, D., Fishbein, M., Jenkins, P., Van Devender, T.R. & Wilson, R.K. (eds.) 1998. *Gentry's Río Mayo Plants. The Tropical Deciduous Forest & Environs of Northwest Mexico*. The University of Arizona Press. Tucson, AZ, US.
- Moran, R. 1972. Plant notes from the Sierra Juarez of Baja California, Mexico. *Phytologia* 35: 205-214.
- Moran, R. 1983. Relictual northern plants on peninsular mountaintops. In: Case, T.J. & Cody, M.L. (eds.) *Island Biogeography of the Sea of Cortéz*, pp. 408-410. University of California Press, Berkeley, CA, US.
- Moran, R. 1996. *The Flora of Guadalupe Island, Mexico*. California Academy of Sciences. Memoir No. 19. San Francisco, CA, US.
- Mourelle, C. & Ezcurra, E. 1996. Species richness of Argentine cacti: A test of biogeography hypotheses. *J. Veg. Sci.* 7: 667-680.
- Mourelle, C. & Ezcurra, E. 1997. Differentiation diversity of Argentine cacti and its relationship to environmental factors. *J. Veg. Sci.* 8: 547-558.
- Myers, N., Mittermeier, R. A., Mittermeier, C.G., da Fonseca, G.A.B. & Kent, J. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403: 854-858.
- Pearson, F. 1990. *Map Projections: Theory and applications*. CRC Press Inc. Boca Raton FL, US.
- Peinado, M., Alcaraz, F., Delgadillo, J. & Aguado, I. 1994. Fitogeografía de la Península de Baja California, México. *Ann. Jard. Bot. Madrid* 51: 255-277.
- Peinado, M., Aguirre, J.L. & Delgadillo, J. 1997. Phytosociological, bioclimatic and biogeographical classification of woody climax communities of western North America. *J. Veg. Sci.* 8: 505-528.
- Perry, J.P. 1991. *The Pines of Mexico and Central America*. Timber Press, Portland, OR, US.
- Preston, F.W. 1960. Time and space and the variation of species. *Ecology* 41: 785-790.
- Rapoport, E.H. 1975. *Aerografía. Estrategias Geográficas de las Especies*. Fondo de Cultura Económica, México, MX.
- Richerson, P.J. & Lum, K.L. 1980. Patterns of plant species diversity in California: relation to weather and topography. *Am. Nat.* 116: 504-536.
- Riemann, H. & Ezcurra, E. 2005. Plant Endemisms and Natural Protected Areas in The Peninsula of Baja California, Mexico. *Biol. Conserv.* 122:141-150.
- Rzedowski, J. 1978. *Vegetación de México*. Editorial Limusa, México, MX.
- Shreve, F. 1936. The transition from desert to chaparral in Baja California. *Madroño* 3: 257-264.
- Shreve, F. 1951. *Vegetation of the Sonoran Desert*. Pub-

- lication No. 591, Carnegie Institution of Washington, Washington, DC, US.
- Stebbins, G.L. 1952. Aridity as a stimulus to plant evolution. *Am. Nat.* 86: 33-44.
- Stebbins, G.L. & Major, J. 1965. Endemism and speciation in the California flora. *Ecol. Monogr.* 35: 1-35.
- Turner, M.R., Bowers, J.E. & Burgess, T.L. 1995. *Sonoran Desert Plants. An Ecological Atlas*. University of Arizona Press, Tucson, AZ, US.
- Wiggins, I.L. 1980. *Flora of Baja California*. Stanford University Press, Stanford, CA, US.

Received 24 February 2006;
Accepted 15 January 2006;
Co-ordinating Editor: S. Wisser.