

## Shrubland formations and associations in mediterranean-desert transitional zones of northwestern Baja California

M. Peinado<sup>1,\*</sup>, F. Alcaraz<sup>2</sup>, J. L. Aguirre<sup>1</sup>, J. Delgadillo<sup>3</sup> & I. Aguado<sup>1</sup>

<sup>1</sup>Departamento de Biología Vegetal, Universidad de Alcalá de Henares, E-28871 Alcalá de Henares, Madrid, Spain; <sup>2</sup>Departamento de Biología Vegetal, Universidad de Murcia, E-33600 Murcia, Spain; <sup>3</sup>Facultad de Ciencias, Universidad Autónoma de Baja California, Ensenada BC, Mexico

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### Abstract

The area between Ensenada and El Rosario (Baja California, Mexico) has long been considered as a transitional zone in which two great ecoclimatic regions (Mediterranean and Tropical-Desert) overlap. The floristic and biotypical diversity of this area was evaluated by analyzing its shrubland formations from a phytosociological point of view. This phytosociological study, carried out according to the Braun-Blanquet method and supported by cluster analysis, describes sixteen shrubland associations from Northwestern Baja California.

Floristic diversity of the transitional zone was evaluated using two indices, endemic value (EV) and endemic community value (ECV), which are related to the degree of endemism in the flora and plant associations. The phytosociological analysis showed that the high number of shrubland associations found in this area reflected its transitional character. The closer the associations are to the transitional zone, the higher their biotypical and floristic diversity.

**Abbreviations:** ADE – *Adenostoma fasciculatum*, AES – *Fraxinus trifoliata*-*Aesculus parryi*, BER – *Bergerocactus emoryi*-*Agave shawii*, DES – *Echinocereus engelmannii*-*Agave deserti*, ENC – *Viguiera deltoidea*-*Encelia asperifolia*, EUR – *Eurotia lanata*-*Yucca schidigera*, FOU – *Agave cerulata*-*Fouquieria columnaris*, FRA – *Atriplex julacea*-*Frankenia palmeri*, HYM – *Baccharis glutinosa*-*Hymenoclea monogyra*, KEC – *Clematis lasiantha*-*Keckiella antirrhinoides*, LAR – *Ambrosia chenopodifolia*-*Larrea tridentata*, LYC – *Ephedra californica*-*Lycium brevipes*, MAH – *Malosma laurina*-*Heteromeles arbutifolia*, MUN – *Salvia munzii*-*Artemisia californica*, ROS – *Rosa minutifolia*-*Aesculus parryi*, SAL – *Salvia apiana*-*Viguiera laciniata*.

### Introduction

The flora of Baja California is characterized by an unusually high rate of local endemics. The peninsula of Baja California has long been known to be an important area of biogeographical differentiation (Baird 1860; Cope 1873; Dice 1943). In addition, it is very rich in species and genera of native vascular plants; its richness is comparable with other areas of the North American Southwest, particularly with the Californian Floristic Province (Howell 1957; Thorne 1993) or Californian Phytogeographical Region (Peinado *et al.*

1994b). Most of the floristic diversity is concentrated in the northwest part of Baja California, that is, in what is called the 'transitional zone' (Shreve 1936). This Baja California area has about 1322 native vascular plants (Moran in Raven & Axelrod 1978), 902 of which are not usually found in the rest of the peninsula; besides, there are 633 genera, 292 of which do not exist elsewhere on the peninsula. Thus, this area, whose surface (24 500 km<sup>2</sup>) only constitutes 17% of the peninsular area, contains almost the half of the species (44%) and nearly three-fourth of the genera (71%). On the other hand, approximately 227 species in Northwestern Baja

California are not found within the borders of California (Moran in Raven 1988). The floristic richness of Baja California is fundamentally accumulated in the northwest of the peninsula.

The key to understanding this accumulation of diversity lies in the origin of the Baja Californian floristic elements. By using floristic analysis Peinado *et al.* (1994b) pointed out that this zone is a place of refuge as much as for taxa from the ancient Tertiary Geofloras (Madrean or Californian elements) as for taxa from the Sonoran Desert which found a magnificent refuge from the climatic oscillations of the Late Wisconsin glacial period on the Baja California coast. According to the terminology of Stebbins & Major (1965), this territory is an area with a high concentration of paleoendemics and neoendemics.

The vegetation of Northwestern Baja California has been considered a distinctive transitional type between the desertscrub of the south (Sonoran region) and the evergreen sclerophyllous scrub characteristic of the Mediterranean climate (Californian region) of the north (Shreve 1936; Epling & Lewis 1942; Mooney & Harrison 1972; Westman 1983; Walter 1985; Peinado & Delgadillo 1990; Peinado *et al.* 1994c).

Climatic stations within Southern California and Baja California reflect the existence of a gradient of aridity increasing towards the south of this area. As a consequence of this gradient, Northwestern Baja California may be regarded as a broad ecotonic zone in which a transition between Mediterranean and Tropical-Desert ecocomplexes (Polunin & Worthington 1990), ecoregions (Bailey 1991) or zoniobioses (Walter 1985; Peinado *et al.* 1994c) occurs. Dry-semiarid transitional areas in the southern Mediterranean Basin contain a high diversity of life forms, endemic plants and shrubland formations (Peinado *et al.* 1992). This article aims to explain the diversity of shrubland formations in Northwestern Baja California, a territory for which studies on plant communities are very scarce (Delgadillo *et al.* 1992). Some studies have analyzed the origin and distribution of the principal shrubland formations in the transitional zone (Epling & Lewis 1942; Axelrod 1978; Westman 1981, 1983; Pase & Brown 1982; Mooney 1988), but the differences in floristic structure, diversity, composition and habitat among these shrublands have not been detailed (Westman 1983) and only limited studies have as yet been published.

## Study area

Though the Baja California transitional zone extends south from Ensenada, 31 ° 52' N, to El Rosario, 30 ° N, (Mooney & Harrison 1972), adjacent zones were also analyzed, so that the area where the field study was done actually spreads from San Diego County (California) on the north to the Vizcaino Desert (Baja California) on the south. The main phytogeographical and climatic features of this territory were summarized by Peinado & Delgadillo (1990) and Peinado *et al.* (1994b, c).

Temperature and precipitation data from 40 weather stations existing in the area (Close *et al.* 1970; Reyes *et al.* 1990) indicate that there is a temperature gradient that increases southwards. Three main bioclimatic belts (Peinado *et al.* 1994c, d) can be recognized: Thermomediterranean, Inframediterranean and Mesotropical (Fig. 1).

However, the outstanding climatic characteristic of the area is its aridity gradient. From the north of the area southwards, a drop in the precipitation gradient is obvious. Annual rainfall ranges from 342 mm at El Cajon (San Diego Co.) to 125 mm at Chapala, which is situated at the southern extreme of the study area. Based on aridity and temperature the sampled meteorological stations can be placed into one of three groups: 1) Thermomediterranean: north of parallel 31 ° N (near Cabo Colonet) all stations show a more or less humid period between December and April; 2) Mesotropical: south of parallel 30 ° N (El Rosario) all stations show tropical desert climograms, i.e. they show year-long drought conditions; and 3) Inframediterranean: stations situated between these two parallels show intermediate features since the arid period lasts nine months and there is a short period (December, January and February) in which the rainfall line slightly exceeds the temperature line.

## Material and methods

The field work was undertaken during seven Spanish-Mexican botanical expeditions in North America between 1989 and 1993. With the aim of recording all the possible shrubland types, study sites were selected by means of field and aerial photography observations (1972 flight of the Mexican Dirección General de Geografía). Sites were selected on the basis of physiognomy, structure and species dominance. The selection of plots for our classification purposes was based on

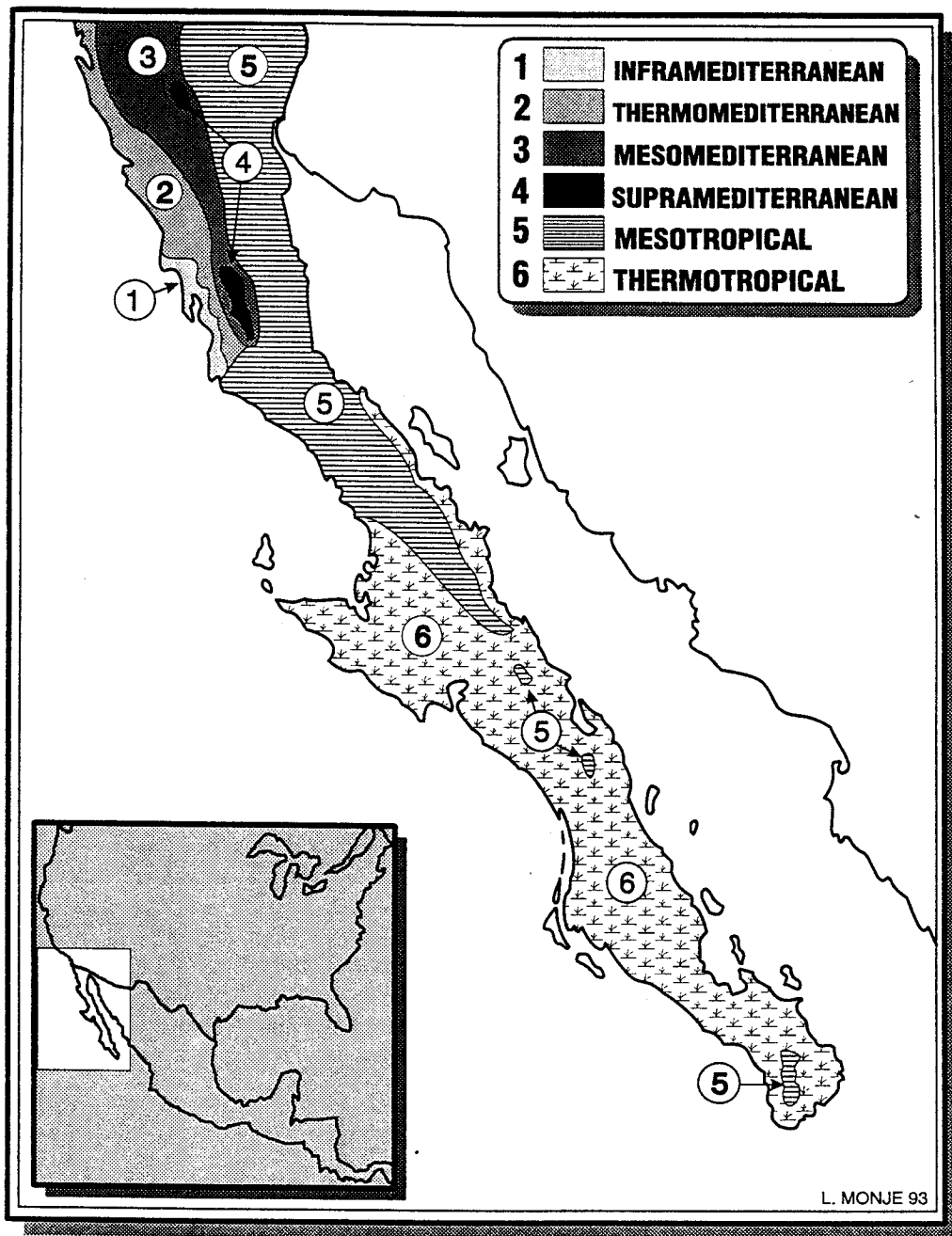


Fig. 1. Bioclimatic belts of Baja California (after Peinado *et al.* 1994b modified). Studied sites are included within belts 1, 2 and southwestern half of 5.

the concept of the minimum area of relatively uniform stands (Westhoff & van der Maarel 1973). The number of plots selected for each physiological type was variable, because some shrubland types spread over large areas whereas other show a very restricted loca-

tion. The location of the sites can be obtained from the senior author upon request.

The environmental data collected from each site consisted of its altitude in meters, slope, aspect and geological substratum. A phytosociological relevé was made in each plot; cover values for each plant canopy

were measured by the single combined estimation of cover-abundance scale (Braun-Blanquet 1979). Following the process described in Kent & Coker (1992), the relevés were arranged by means of tabular sorting and rearrangement of both relevés and species. In this way several primary or raw tables grouping homogeneous relevés were obtained.

As a new step, a synoptic table including all the relevés (165) and species (183) was elaborated. The relative importance of each species in this table was measured by its frequency and cover; this made it possible to compare relevés and characterize floristically homogeneous communities. Table 1 shows the frequency in percentage classes, noted in roman numerals, according to Braun-Blanquet's (1979) scale as modified by Géhu & Rivas-Martínez (1982). To limit the size of the table, only species belonging to classes III–V have been summarized. The cover (C) of each species in each community was calculated by the formula  $C = 100 Q/R$ , where Q is the amount of species average cover in each plot and R is the number of plots for each association. The sixteen associations appearing in the tables and figures were obtained using this initial approach.

A cluster analysis was made to improve this classification into associations. A matrix of Euclidean distance (Digby & Kempton 1989) among plots was calculated from coverage data. The technique for clustering was Average Linkage Clustering (Krebs 1989), and the diagram was obtained with the BMDP program (Dixon 1983). Rare taxa were removed; thus, the matrix only contained those taxa (160) that were present in at least 25% of the plots of any association.

The term association as used here refers to a type of plant community defined by grouping together various sample relevés that have a certain number of taxa in common. According to the Braun-Blanquet approach, any association is defined by its combination of characteristic species including character- and differential-species. Character-species are taxa that are relatively restricted to a given plant community. These taxa characterize the community and indicate its environment. Differential taxa define associations on the basis of the distributional boundaries of taxa, without regard to fidelity to the association in question. The concept of character-species and differential-species is a long-standing problem in the Braun-Blanquet approach. The difference between both categories becomes clear only when the floristic-phytosociological system is well-developed in the study region, which is not the case

here. Consequently, we have used the values of frequency, cover and biotypical composition to define associations. These also have outstanding floristic features, but these associations have not been typified according to the rules in the Code of Phytosociological Nomenclature (Barkman *et al.* 1986) because that is not the aim of this paper.

For floristic and endemic analysis (Table 3) every recorded taxon was placed into one of four endemic types: E1 Californian, that is, taxa belonging to the Californian Province (Thorne 1993); E2 Southern Californian (Raven 1988), also called the Peninsular floristic element (McLaughlin 1989); E3 Vizcaino Desert (Turner & Brown 1982; Peinado *et al.* 1994b); and E4 Northwestern Baja California, that is endemics found in the area lying between the international border and El Rosario, using the crest of the San Pedro Mártir and Juárez Sierras as its eastern limit. Every endemic type received an endemic value (EV), which was calculated by the formula  $EV = 100\,000/S$ , where S is the area of each endemic region. The resultant data were: E1 ( $S = 411\,000\text{ km}^2$ ;  $EV = 0.24$ ); E2 (45 000; 2.22); E3 (35 500; 2.82); E4 (16 800; 5.95).

EV values were used to weight the endemic values of different sampled associations (ECV) by the formula:  $ECV = (EV1 \times P1) + (EV2 \times P2) + (EV3 \times P3) + (EV4 \times P4)$ , where P is the percentage of each endemic type in each association.

For the purposes of analysis, biotypes or growth forms were grouped into five classes (Table 2): 1, low trees and high shrubs (LT); 2, subligneous or drought deciduous shrubs (SLG); 3, succulents (SUC); 4, climbing plants (CLI) and 5, other plants (OT). Plant nomenclature follows Munz (1973) and Beauchamp (1986) for Californian plants and Wiggins (1980) for Baja Californian taxa.

## Results

Floristic composition of the recorded associations is shown in Table 1; taking into account their biotypical structure (Table 2) and endemic variation (Table 3; Figs 2, 3), these associations can be grouped into five types.

The first type includes the associations *Malosma laurina-Heteromeles arbutifolia* (MAH), *Fraxinus trifoliata-Aesculus parryi* (AES), *Adenostoma fasciculatum* (ADE) and *Clematis lasiantha-Keckiella antirrhinoides* (KEC). These associations show some common features such as the predominance of low trees,



Table 1 continued. Frequency (Roman numerals) and cover (Arabic numerals) of taxa in the different sampled associations (columns). Frequency is shown in percentage classes: V = species occurring in 81–100% of the plots, IV = 61–80%, III = 41–60%. Cover is shown as C = 100QR (see text). E1–E4: endemic types. NE: non-endemic type

Association	MAH	AES	ADE	KEC	SAL	MUN	BER	ROS	ENC	FOU	LAR	EUR	DES	LYC	FRA	HYM
No. of relevés	9	13	23	8	70	13	10	4	6	14	9	5	10	9	8	7
Species average	11	11	8	13	9	10	16	6	7	16	11	11	12	5	3	6
<i>Ribes tortuosum</i> , E4	.	.	.	.	.	.	.	III.250	.	.	.	.	.	.	.	.
<i>Opuntia littoralis</i> , E2	.	.	.	.	.	.	.	III.150	.	.	.	.	.	.	.	.
<i>Encelia californica</i>	.	.	.	.	.	.	.	.	V.2700	.	.	.	.	.	.	.
var. <i>asperifolia</i> , E3	.	.	.	.	.	.	.	.	IV.467	III.93	IV.133	V.1460	V.1060	.	.	.
<i>Ambrosia dumosa</i> , NE	.	.	.	.	.	.	.	.	.	V.308	.	.	.	.	.	.
<i>Fouquieria columnaris</i> , E3	.	.	.	.	.	.	.	.	.	V.179	.	.	.	.	.	.
<i>Pachycereus pringlei</i> , E3	.	.	.	.	.	.	.	.	.	IV.164	III.144	.	.	.	.	.
<i>Lophocereus schottii</i> , NE	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>Larrea divaricata</i>	.	.	.	.	.	.	.	.	.	IV.136	V.2011	V.980	III.490	.	.	.
ssp. <i>tridentata</i> , NE	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>Ferocactus acanthodes</i>	.	.	.	.	.	.	.	.	.	IV.129	.	V.180	III.410	.	.	.
var. <i>acanthodes</i> , NE	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>Agave cerulata</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
spp. <i>cerulata</i> , E3	.	.	.	.	.	.	.	.	.	IV.186	III.356	III.220	.	.	.	.
<i>Eriogonum flavoviride</i> , NE	.	.	.	.	.	.	.	.	.	IV.171	V.444	V.420	.	.	.	.
<i>Pachycormus discolor</i> , E3	.	.	.	.	.	.	.	.	.	III.129	.	.	.	.	.	.
<i>Fouquieria splendens</i> , NE	.	.	.	.	.	.	.	.	.	III.100	IV.611	III.540	IV.260	.	.	.
<i>Opuntia cholla</i> , NE	.	.	.	.	.	.	.	.	.	III.100	.	.	.	.	.	.
<i>Yucca schidigera</i> , NE	.	.	.	.	.	.	.	.	.	.	III.944	IV.240	.	.	.	.
<i>Asclepias subulata</i> , NE	.	.	.	.	.	.	.	.	.	.	III.178	.	.	.	.	.
<i>Opuntia echinocarpa</i> , NE	.	.	.	.	.	.	.	.	.	.	IV.389	.	.	.	.	.
<i>Opuntia prolifera</i> , E2	.	.	.	.	.	.	.	.	.	.	IV.289	.	.	.	.	.
<i>Ferocactus gracilis</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
var. <i>gracilis</i> , E3	.	.	.	.	.	.	.	.	.	.	III.56	.	.	.	.	.
<i>Eurotia lanata</i> , NE	.	.	.	.	.	.	.	.	.	.	.	V.500	.	.	.	.
<i>Coldenia canescens</i> , NE	.	.	.	.	.	.	.	.	.	.	.	III.300	.	.	.	.
<i>Opuntia tesajo</i> , E3	.	.	.	.	.	.	.	.	.	.	.	III.140	.	.	.	.
<i>Agave deserti</i> , NE	.	.	.	.	.	.	.	.	.	.	.	.	V.1540	.	.	.
<i>Encelia farinosa</i> , NE	.	.	.	.	.	.	.	.	.	.	.	.	III.1300	.	.	.
<i>Echinocereus engelmannii</i> , NE	.	.	.	.	.	.	.	.	.	.	.	.	V.330	.	.	.
<i>Lycium brevipes</i> , NE	.	.	.	.	.	.	.	.	.	.	.	.	.	V.2767	.	.
<i>Atriplex canescens</i> , NE	.	.	.	.	.	.	.	.	.	.	.	.	.	.	III.170	.

Table 1 continued. Frequency (Roman numerals) and cover (Arabic numerals) of taxa in the different sampled associations (columns). Frequency is shown in percentage classes: V = species occurring in 81–100% of the plots, IV = 61–80%, III = 41–60%. Cover is shown as C = 100Q/R (see text). E1–E4: endemic types. NE: non-endemic type

Association	MAH	AES	ADE	KEC	SAL	MUN	BER	ROS	ENC	FOU	LAR	EUR	DES	LYC	FRA	HYM
No. of relevés	9	13	23	8	7	13	10	4	6	14	9	5	10	9	8	7
Species average	11	11	8	13	9	10	16	6	7	16	11	11	12	5	3	6
<i>Helianthus niveus</i> , NE	.	.	.	.	.	.	.	.	.	.	.	.	.	III.622	.	.
<i>Haploappus furfuraceus</i> , E2	.	.	.	.	.	.	.	.	.	.	.	.	.	III.311	.	.
<i>Frankenia palmeri</i> , NE	.	.	.	.	.	.	.	.	.	.	.	.	.	.	V.1700	.
<i>Atriplex julacea</i> , E4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	IV.675	.
<i>Hymenoclea monogyra</i> , NE	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	V.3157
<i>Baccharis glutinosa</i> , NE	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	V.1343
<i>Tamarix pentandra</i> , NE	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	IV.300
<i>Baccharis sarothroides</i> , NE	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	III.329
<i>Nicotiana glauca</i> , NE	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	III.214

*lus parryi*); a very low percentage of succulents and the complete absence of Vizcainan elements (E3); on the other hand, the endemic component in the first type is closely related to the Californian elements E1 and E2.

The second type includes the associations *Salvia apiana* – *Viguiera laciniata* (SAL) and *Salvia munzii*–*Artemisia californica* (MUN). Like in the first group, E3 elements are completely lacking, the percentage of succulent plants is also very low and the endemic elements belong to the E1 and E2 groups. Unlike the first group, nearly 90% of the cover consists of subligneous plants.

The third type groups the associations *Bergerocactus emoryi*–*Agave shawii* (BER) and *Rosa minutifolia*–*Aesculus parryi* (ROS), which – besides several typical features that are discussed below – have in common the highest percentages of northwestern endemics (E4). Taking into account its biotypical structure, in which both subligneous and succulent taxa are predominant, this type may be regarded as intermediate between the second and fourth types.

In the fourth type, in which the associations *Agave cerulata*–*Fouquieria columnaris* (FOU), *Ambrosia chenopodifolia*–*Larrea tridentata* (LAR), *Eurotia lanata*–*Yucca schidigera* (EUR) and *Echinocereus engelmannii*–*Agave deserti* (DES) are included, biotypical and endemic compositions are completely opposite the two former types: the low tree component is smaller, there is a higher percentage of both succulents and E3 elements, while the Californian endemics E1 and E2 are nearly lacking.

*Viguiera deltoidea*–*Encelia asperifolia* (ENC), *Ephedra californica*–*Lycium brevipes* (LYC), *Atriplex julacea*–*Frankenia palmeri* (FRA) and *Baccharis glutinosa*–*Hymenoclea monogyra* (HYM), constitute the fifth and heterogeneous group. However, they are all azonal communities, that is distributed in both Mediterranean and Desert zones, inhabiting very specific biotopes. As is discussed below, these facts explain the variability in this group.

## Discussion of results

Physiognomically, four broad shrubland formations had been recognized in the sampled area: chaparral, Californian coastal scrub, coastal succulent scrub and Sonoran desert scrub (Mooney and Harrison 1972; Westman 1983; Turner and Brown 1982). Our first four types are comparable to these four formations.

most of which are sclerophyllous (*Malosma laurina*, *Heteromeles arbutifolia*, *Rhus integrifolia*, *Xylococcus bicolor*) or deciduous (*Fraxinus trifoliata*, *Aescu-*

Table 2. Biotypical composition (%) in the different sampled associations. Columns: Freq. = Percent frequencies for each biotype (LT = low trees, SLG = subligneous, SUC = succulents, CLI = climbing plants, OT = other biotypes). Cov. = Percentages of cover for each biotype

Associations	LT		SLG		SUC		CLI		OT	
	Freq.	Cov.	Freq.	Cov.	Freq.	Cov.	Freq.	Cov.	Freq.	Cov.
MAH	66.7	87.3	11.1	6.6	0	0	16.7	5.3	5.5	0.8
AES	66.7	93.4	13.3	2.7	0	0	6.7	1	13.3	2.9
ADE	42.9	86	42.8	11.7	14.3	2.2	0	0	0	0
KEC	47	64.9	23.5	26.6	0	0	23.5	8.3	6	0.2
SAL	15.4	1.8	69.2	96.3	7.7	0.9	0	0	7.7	0.9
MUN	15.4	6.9	69.2	90.7	0	0	7.7	0.4	7.7	2
BER	12.5	16.8	45.8	46.9	41.7	36.3	0	0	0	0
ROS	44.4	44	22.2	33.6	22.2	19.2	0	0	11.2	3.1
ENC	0	0	100	100	0	0	0	0	0	0
FOU	3.4	2.9	48.3	43.6	44.8	52.7	0	0	3.5	0.7
LAR	5.8	1.1	47.1	64	47	35	0	0	0	0
EUR	7.1	3.7	50	74.9	35.7	16.6	0	0	7.2	5.5
DES	6.7	5.5	60	58.6	33.3	35.8	0	0	0	0
LYC	18.1	3.9	54.5	90.6	27.4	5.4	0	0	0	0
FRA	0	0	75	95.1	25	4.9	0	0	0	0
HYM	42.8	11.8	42.9	86.7	0	0	14.3	1.5	0	0

Table 3. Endemic composition (%) in the different sampled associations. Columns: Freq. = percent frequencies. Cov. = Percentages of cover (E = total of endemisms; E1, E2, E3, E4 = for every endemic type; NE = for non-endemic plants). AS = species average in each association. ECV = endemic value for each association

Associations	AS	E		E4		E3		E2		E1		NE		ECV
		Freq.	Cov.	Freq.	Cov.	Freq.	Cov.	Freq.	Cov.	Freq.	Cov.	Freq.	Cov.	
MAH	11.3	94.4	92.2	11.1	26.9	0	0	55.5	40	27.8	25.3	5.6	7	196
AES	11.2	100	97.1	26.7	41.5	0	0	40	35.4	33.3	20.2	0	0	254
ADE	8	85.7	97.7	0	0	0	0	71.4	29	14.3	68.6	14.3	2.2	162
KEC	13.1	82.3	95.2	11.8	23	0	0	41.2	17	29.4	55.2	17.7	4.8	168
SAL	8.7	61.5	96.6	15.4	23	0	0	23.1	45.6	23.1	28	38.5	3.4	148
MUN	9.9	76.9	88.7	23.1	44.6	0	0	30.7	18.3	23.1	25.8	23.1	11.2	210
BER	16	79.2	70	41.7	51.7	8.3	4.7	12.5	9.6	16.7	39	20.8	29.9	302
ROS	6	100	98.1	77.8	94.7	0	0	22.2	3.3	0	0	0	0	511
ENC	7.1	80	90.5	40	17.8	40	72.7	0	0	0	0	20	9.4	351
FOU	16.4	51.7	57.1	17.2	19.1	34.5	38	0	0	0	0	58.3	37.2	199
LAR	10.7	29.4	16.4	5.9	6.7	17.6	6	5.9	3.7	0	0	70.6	87.3	97
EUR	12.2	21.4	8.8	7.1	2.2	14.3	6.5	0	0	0	0	78.6	91.3	74
DES	12.2	20	22	0	0	13.3	3.1	6.7	18.9	0	0	80	78	52
LYC	5.4	63.6	31.2	27.3	2.8	0	0	18.2	7.7	18.2	20.6	36.4	68.8	207
FRA	3.1	50	31	25	26.2	25	4.8	0	0	0	0	50	68.9	219
HYM	5.7	0	0	0	0	0	0	0	0	0	0	100	100	0



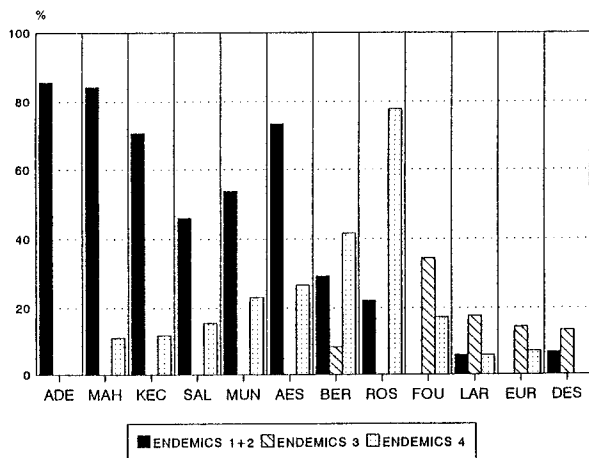


Fig. 2. Endemic composition of twelve shrubland associations from Northwestern Baja California.

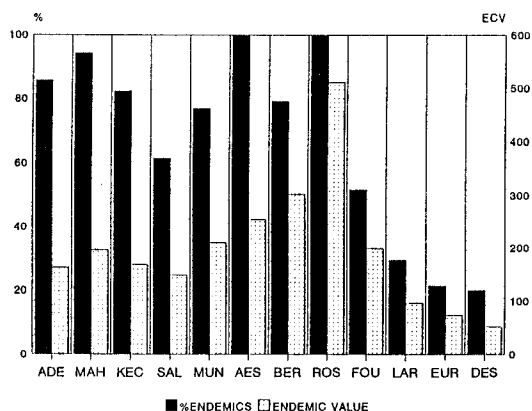


Fig. 3. Percentages of endemics and endemic values of twelve shrubland associations. ECV = Endemic Community Value (absolute values).

### Group 1, Chaparral formation

Chaparral includes four different plant communities in this area; two of them (*Malosma laurina*-*Heteromeles arbutifolia* and *Fraxinus trifoliata*-*Aesculus parryi*) are closely related; both are dominated by shrubs and low trees (66.7% of the species) and both include a high number of endemics (94.4 and 100%, respectively). However, they differ in endemic type; in the *Malosma laurina*-*Heteromeles arbutifolia* association, found as far north as Point Conception (34.5 °N), the dominant elements are E2 taxa, such as *Malosma laurina*, *Rhus integrifolia*, *Marah macrocarpus*, *Ceanothus leucodermis*, and *Ceanothus oliganthus*; in the *Fraxinus trifoliata*-*Aesculus parryi* association, found only in Baja California, the percentage of E4 endemics (*Aes-*

*culus parryi*, *Fraxinus trifoliata*, *Ptelea aptera*, *Xylococcus bicolor*) is nearly three times higher (26.7% vs. 11.1%). *Malosma laurina*-*Heteromeles arbutifolia* is the climax association in the thermomediterranean belt in both southern California and Baja California (Southern Californian and Martirensis phytogeographical provinces, after Peinado *et al.* 1994b), while the *Fraxinus trifoliata*-*Aesculus parryi* association also occurs within the Baja California thermomediterranean belt, but only near the coast where there are no spring frosts.

The cluster analysis (Fig. 4) did not distinguish MAH from AES. They were grouped together because they share several taxa. *Aesculus parryi* is the best differential factor for separating the *Fraxinus trifoliata*-*Aesculus parryi* association from the *Malosma laurina*-*Heteromeles arbutifolia* association, but because this endemic plant is more or less frequent in other associations (*Berberocactus emoryi*-*Agave shawii*, *Rosa minutifolia*-*Aesculus parryi* and *Salvia munzii*-*Artemisia californica*) found in the zone, its presence is not enough to separate the two chaparral associations by clustering. However, since the *Fraxinus trifoliata*-*Aesculus parryi* association has a specific distribution area and a precise bioclimatic fringe, we consider it to be a well-differentiated association.

Sclerophyllous and deciduous species dominating these climax associations (MAH and AES) are adapted to tolerate burning but show no selective preadaptation to fire (Zedler & Zammit 1989); seedling recruitment in these species seems to depend on a long fire-free period (Keeley *et al.* 1989). In contrast, the response to fire by chamise chaparral of the *Adenostoma fasciculatum* association is very different. Its reproductive cycle is clearly adapted (Keeley *et al.* 1989; Stohlgren *et al.* 1989) and periodic fires appear to be essential to maintaining this association in a vigorous condition (Pase 1982; Hanes 1988). Its floristic composition reflects this fact: the *Adenostoma fasciculatum* association is a community in which nearly 70% of the cover consists of the postfire pioneer *Adenostoma fasciculatum*. The rest of the taxa inhabit areas which have not been burned in a long time, and they represent the slow regeneration of the sclerophyllous climax, particularly on north-facing slopes (Hanes 1971). In contrast with other sclerophyllous chaparrals, the ECV of the *Adenostoma fasciculatum* association is lower, as would be expected of the most widespread Californian chaparral (Hanes 1988).

In the cluster analysis ADE was separated into two relatively distant groups. This can be explained by its

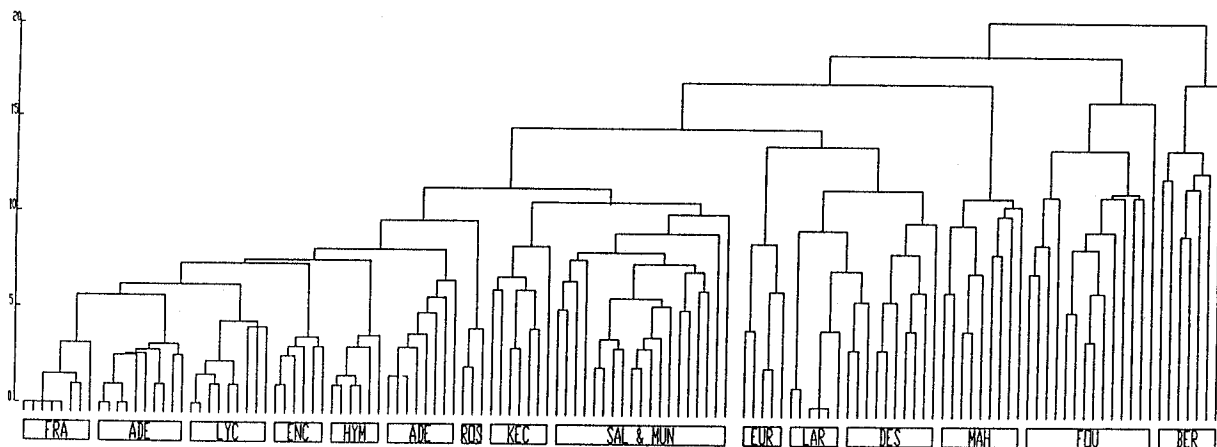


Fig. 4. Cluster classification of 165 plots, using 160 taxa occurring in at least 25% of the plots of any association.

different floristic composition; recently burned areas are very poor in floristic richness, and *Adenostoma fasciculatum* is the only dominant plant. The presence of *Agave shawii* in one of its plots, and the existence of that plant in the *Atriplex julacea*-*Frankenia palmeri* association (another association which is floristically poor), grouped both closely. On the other hand, mature stands of the *Adenostoma fasciculatum* association, living in areas that have long been fire-free, are richer in species and were separated from the former group in the cluster analysis.

#### Group 2, Coastal sage scrub formation

Most studies of Californian chaparral have considered its evolution from a point of view closely associated with postfire succession. Less studied has been secondary succession on lands that have been disturbed or cleared for agriculture or other purposes (Zedler & Zammit 1989). Anthropozoogenic degradation is phytosociologically well known in European sclerophyllous ecosystems; there are some communities in Europe that are dominated by subligneous plants, most of which are aromatic species belonging to the *Ononido-Rosmarinetea*, *Cytisetea scopario-striati* and *Cisto-Lavanduletea* phytosociological classes. In southern California and Baja California mediterranean climate areas, when a site is cleared for forestry or agricultural purposes, it is mostly invaded by *Eriogonum fasciculatum*, *Artemisia californica*, *Lotus scoparius*, *Salvia* sp. div., *Gutierrezia californica*, etc. These plants form communities like the already mentioned European shrublands and are called coastal sage scrub or soft chaparral in California, 'batha' in Israel, 'tomil-

lares' in Spain, 'phrygana' in Greece or 'matorral' in Chile.

Although these communities represent a successional or retrogressive vegetation type in disturbed sites, they are also a permanent-type vegetation (subclimax) in many habitats: drier sites, steep southern slopes, shallow stony soils and others (Axelrod 1978). Pure coastal sage scrub can therefore maintain an extensive permanent cover in areas which have not been disturbed or grazed in many decades (Bradbury 1978; Kirkpatrick & Hutchinson 1980).

Unlike evergreen sclerophyllous chaparral, however, the dominant species of coastal sage scrub are malacophyllous subshrubs whose leaves abscise during summer drought and are replaced by a lower number of smaller leaves. Our analysis points out the existence of three types of successional stages: the *Clematis lasiantha*-*Keckiella antirrhinoides*, *Salvia apiana*-*Viguiera laciniata* and *Salvia munzii*-*Artemisia californica* associations. The first includes seral stages of chaparral, in which the degradation of both soil and the original chaparral structure has been less intense than in the other two associations; consequently, climax regeneration is relatively possible from this community. Unlike the *Salvia apiana*-*Viguiera laciniata* and *Salvia munzii*-*Artemisia californica* associations, the cover of trees and high shrubs (most being sclerophyllous taxa) is much greater (64.9% versus 1.8 and 6.9), and there are climbing plants (23.5% of species); the frequency of these biotypes reflects the maturity of the *Clematis lasiantha*-*Keckiella antirrhinoides* association and allows its inclusion in the first type. In European sclerophyllous ecosystems the associations of the

*Cytisetea scopario-striati* phytosociological class play a similar ecological role.

In contrast, the *Salvia apiana-Viguiera laciniata* and *Salvia munzii-Artemisia californica* associations are more advanced degradative stages of the chaparral climatic climax; the former is seral to the *Malosma laurina-Heteromeles arbutifolia* association, whereas the latter is seral to associations dominated by *Aesculus parryi* (*Fraxinus trifoliata-Aesculus parryi* and *Rosa minutifolia-Aesculus parryi*). In both associations subligneous plants constitute 70% of the cover, climbing plants are absent and the only phanerophytes are *Fraxinus trifoliata* and the xerophytic opportunist *Simmondsia chinensis*. The ECV of these associations is strikingly high, being higher in *Salvia munzii-Artemisia californica* (210.4) than in *Salvia apiana-Viguiera laciniata* (148.45), as would correspond to a typical association exclusive to Northwestern Baja California in which the endemic component is richer. In fact, a similar relation occurs when the ECVs of their respective climax chaparrals are compared (*Fraxinus trifoliata-Aesculus parryi*: 254.4; *Malosma laurina-Heteromeles arbutifolia*: 195.9).

### Group 3, Coastal succulent scrub formation

The *Berberocactus emoryi-Agave shawii* and *Rosa minutifolia-Aesculus parryi* associations belong to the coastal succulent scrub described by Mooney & Harrison (1972) and Mooney (1988) at the base of Sierra de San Pedro Mártir in Baja California. Both associations occur only in the transitional area, so that their floristic and endemic compositions show a combination of mediterranean and desertic elements. Both also share some common numerical trends: a) their ECVs are among the highest; b) their frequencies of low trees and succulents are both higher than in any other association; c) as with the tropical desert associations, climbing plants are completely absent. However, clear differences in frequencies of endemics and biotypes (Fig. 5) show the *Berberocactus emoryi-Agave shawii* association to be the clearest representative of a transitional community. However, these associations also have clear floristic, ecological and biotypical differences, which were pointed out by Peinado *et al.* (1994b, c).

The *Berberocactus emoryi-Agave shawii* association includes all the endemic types expected in a widespread community that can appear in both mediterranean and tropical desert climatic areas. It is a xeric shrubland type that extends continuous-

ly from the northern Vizcaino Desert – where it is the dominant association (Turner & Brown 1982) – through the mediterranean climate area, to Torrey Pines State Reserve in San Diego County, a northern limit that is only reached by some of its plants (Beauchamp 1986). From this site southwards, the association settles on a coastal fringe of the thermomediterranean belt, where it alternates with the *Fraxinus trifoliata-Aesculus parryi* association; this coastal fringe spreads in the inframediterranean belt south of Cabo Colonet, penetrating inland across the Sierra de San Pedro Mártir to northern Vizcaino (mesotropical belt), where the association shows its highest floristical richness.

Thus, the *Berberocactus emoryi-Agave shawii* association is the best example of the penetration of tropical desert vegetation into the mediterranean climate area; its actual existence and its continuous distribution area can be explained on the base of paleoclimatic data and taking into account the fact that associations of species in modern communities are primarily manifestations of past and recent climatic changes. The palynological and paleontological studies done in the North American Southwest have shown that during the late Wisconsin glacial period, forest and woodland grew as much as 1200 m lower than today, and replaced tropical desert scrub communities over most of the elevational gradient (Martin & Mehringer 1965; Van Devender *et al.* 1987). Late Wisconsin glacial climates also provoked substantial vegetational changes in the present Baja Californian desert area (Van Devender 1990), as woodland and forest trees expanded widely into lowlands the dominant desert scrub retreated. During periods favourable to forests, the desert vegetation could take refuge in two habitats: 1) in the driest parts of the desert core: the Lower Colorado River Valley below 300 m (Cole 1986) and the Amargosa Desert in the Sierra Nevada rainshadow (Spaulding 1990); and, 2) on the driest sites such as steep southern slopes, rocky areas, exposed sea bluffs, etc., that is to say the habitats where the *Berberocactus emoryi-Agave shawii* occurs today.

Northwestern Baja California has been regarded as an important survival area in which many isolated endemics can be found (Axelrod 1978); if one also considers that ‘conservation territories’ are areas where the endemic richness is due to the survival of many Tertiary relicts, which have been expelled from their original areas by paleoclimatic fluctuations (Favarger 1964; Contandriopoulos & Favarger 1974), it is reasonable to think that coastal succulent scrub constituted

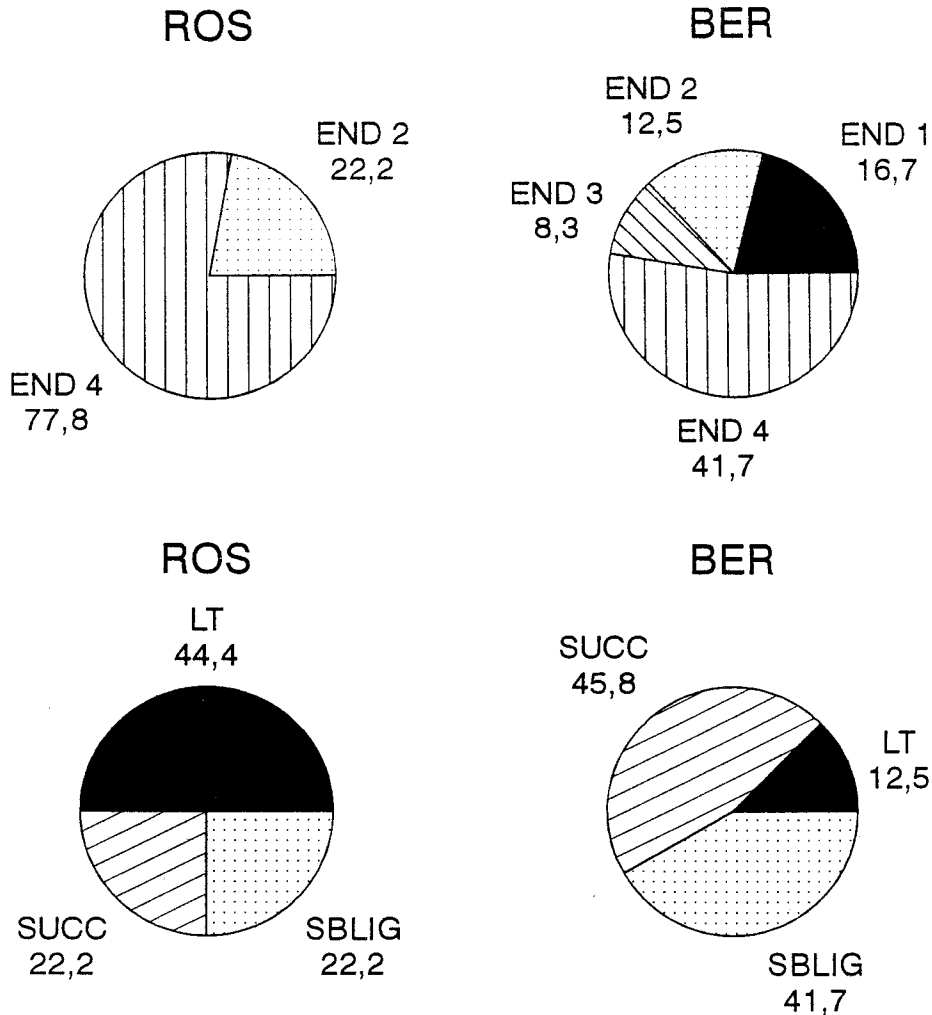


Fig. 5. Endemic (above) and biotypal (beneath) differences between the associations *Bergerocactus emoryi-Agave shawii* (BER) and *Rosa minutifolia-Aesculus parryi* (ROS). END (1–4) = percentages of each endemic type. The percentages of each biotype are shown as LT = lower trees, SBLIG = subligneous, SUCC = succulents.

the survival refuge for the Sonoran taxa turned out of their original habitat by the humid Late Wisconsin climates. Thus, the floristic composition of the *Bergerocactus emoryi-Agave shawii* association, even in the most northern areas, is very similar to coastal Vizcaino desert shrublands. For similar reasons, this Baja California area has been considered a refuge for ancient Miocene and Pliocene taxa, such as *Fraxinus trifoliata*, *Ptelea aptera*, *Malosma laurina*, *Rhus integrifolia*, *Aesculus parryi* and *Rosa minutifolia* (Lewis & Epling 1942; Axelrod 1978; Raven & Axelrod 1978), which live nowadays in another transitional shrubland (*Rosa minutifolia-Aesculus parryi* association).

#### Group 4, Tropical desert formations

Desert associations, which are included in the mesotropical belt, show the lowest ECVs; this is due to the great expanse of the Sonoran Desert, which has no major biogeographic barriers. Nevertheless, in the Vizcaino Desert there are some endemics, such as *Agave cerulata* ssp. *cerulata*, *Opuntia tesajo*, *Ferocactus gracilis* ssp. *gracilis*, *Viguiera deltoidea* var. *chenopodina*, *Fouquieria columnaris* and others), that raise the ECV of both of the endemic Vizcainan associations (*Agave cerulata-Fouquieria columnaris*, on granitic and basaltic rocky hills and upper bajadas;

*Ambrosia chenopodifolia*-*Larrea tridentata*, on lower bajadas).

The same is not true of the *Eurotia lanata*-*Yucca schidigera* and *Echinocereus engelmannii*-*Agave deserti* associations, two widespread communities that reach the northern border of the Mojave Desert. In the Vizcaino Desert, *Eurotia lanata*, the dominant plant in the first association, lives exclusively on the scarce calcareous outcrops of the San Agustín area. The *Echinocereus engelmannii*-*Agave deserti* association, a community that is dominated by *Agave deserti*, grows in all the Sonoran rocky hills situated between desert lowlands and highlands.

#### Group 5, Heterogeneous formations

The *Viguiera deltoidea*-*Encelia asperifolia* association must also be considered as a typical community of the transitional area; although our samples were only collected in the northern Vizcaino, it is an opportunist association whose main elements (*Encelia asperifolia*, *Viguiera deltoidea*, *Ambrosia chenopodifolia*) regularly occur in new open areas, such as steep stripped slopes, road cuts and abandoned clearings in the entire transitional area. Its ECV is very high because, of the six plants that are the most common, two are E4 endemics and two are E3 endemics.

*Ephedra californica*-*Lycium brevipes* and *Atriplex julacea*-*Frankenia palmeri* are two edaphic associations; the first is a thorny shrubland that thrives in coastal dunes in which there is a more or less direct salt spray influence. In Baja California this association extends from Punta Banda (Ensenada) to the Vizcaino Desert, i.e. it is another transitional association with a high ECV (207). *Atriplex julacea*-*Frankenia palmeri* is a peculiar association of the deflocculated alkaline soils (Solonetz) that originate from the formation of sodium carbonate through the alkalization of the usually saline soils or solonchak (Peinado *et al.* 1994a). The environmental conditions that give rise to the alkalization process occur mainly in coastal flats under extremely arid climates.

Finally, the *Baccharis glutinosa*-*Hymenoclea monogyra* association is outstanding because its ECV is zero; this widespread association inhabits washes, desert run-offs and the banks of dry stream beds and rivers, in mediterranean as well as in transitional and desert areas. During run-off events, this position allows easy seed-dispersion in every ecoclimatic zone.

## Conclusions

1. The phytosociological analysis has shown high diversity in Northwestern Baja California reflected by the high number of shrubland associations, a phenomenon that is also found in other mediterranean climate transitional zones around the world. The high number of associations is linked to the aridity gradient which provokes two climates: Mediterranean and Tropical Desert. These two climates, which respectively occupy the northern and southern parts of this territory, intermix between parallels 30 and 31, laying a rich plant associations mosaic.
2. This climatic gradient of aridity increasing southwards is closely related with the increase in floristic diversity as evaluated by the indices for plant endemic value (EV) and endemic community value (ECV) as well as in the increase in biotype diversity. The vegetational trends accompanying this gradient include a descent in the average number of low trees and high shrubs, an increase in succulent biotypes, an increase in the EV and ECV, and a change from predominantly evergreen to predominantly drought-deciduous elements.
3. In the thermomediterranean belt situated north of parallel 31, climax vegetation corresponds to sclerophyllous chaparral (*Malosma laurina*-*Heteromeles arbutifolia* and *Fraxinus trifoliata*-*Aesculus parryi* associations), which, under fire or human disturbance, are substituted by chaparrals (*Adenostoma fasciculatum* and *Clematis lasiantha*-*Keckiella antirrhinoides* associations) or coastal sage scrubs (*Salvia apiana*-*Viguiera laciniata* and *Salvia munzii*-*Artemisia californica* associations).
4. In the mesotropical belt situated south of parallel 30, the Sonoran vegetation constitutes the potential vegetation of the area. Succulent biotypes dominate the associations of this area in contrast to the sclerophyllous, evergreen shrubs (chaparrals) and partially drought deciduous and seasonally dimorphic shrubs (coastal sage scrub), which dominate the mediterranean areas.
5. The area between parallels 30 and 31 appears as a climatic transitional zone or ecotone between northern mediterranean and southern desert climates. Both vegetational types mediterranean and sonoran-alternate in the transitional zones, relic chaparrals with some succulents (*Rosa minutifolia*-*Aesculus parryi* association) living in topographically wetter places, and typical succulent scrubs

(*Bergerocactus emoryi*-*Agave shawii* association) regularly inhabiting the driest sites and even penetrating into thermomediterranean areas in xeric microclimates.

This transitional zone, where precipitation falls between values for mediterranean and desertic climates, is the area with the greatest floristic and biotypical diversity. The closer the associations are to the transition zone, the higher their biotypical and floristic diversity. Thus, the true transitional associations (*Rosa minutifolia*-*Aesculus parryi*, *Bergerocactus emoryi*-*Agave shawii*, *Viguiera deltoidea*-*Encelia asperifolia* and *Ephedra californica*-*Lycium brevipes*) show the highest ECVs.

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