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Architecture and functional traits of semi-arid shrub species in Cabo de Gata Natural Park, SE Spain

Teresa Navarro, Virginia Pascual, Baltasar Cabezudo & Concepción Alados

Abstract

NAVARRO, T., V. PASCUAL, B. CABEZUDO & C. ALADOS (2009). Architecture and functional traits of Mediterranean semi-arid shrub species in Cabo de Gata Natural Park, SE Spain. *Candollea* 64: 69-84. In English, English and French abstracts.

The basic architectural features of 45 shrub species representing 12 families are described from a Mediterranean semi-arid shrubland in the location of Cabo de Gata (SE Spain). Six different architectural models were recognized: Scarrone, Rauh, Holtum, Leeuwenberg, Champagnat and Corner. The Tomlinson model was recognized as a variation with basitonic repetition of the Rauh, Corner, Leeuwenberg and Holtum models. The sympodic variant of the Scarrone model was the most common in our study area. Functional traits such as plant height, lateral spread and plant coverage were correlated with the architectural models. Small shrubs up to 0.6 m height with reduced lateral spread (0.1-0.25 m) and plant coverage (0.5-1 m²) were likely to have sympodic growth patterns, acrotonic dichasial branching and terminal inflorescences. Inversely, large shrubs up to 1-3 m in height, with large canopies (1-3 m²), and well developed lateral spread (> 0.25 m) were likely to have a determinate growth pattern with lateral inflorescences. The first group have species which grow following the sympodic variant of the Scarrone model, whereas the second group presents species following the Rauh model and includes thorny shrubs from the climax communities.

Key-words

Plant architecture – Functional traits – Cabo de Gata Natural Park – Spain – Semi-arid shrubs – Plant conservation – Mediterranean vegetation – Ecology

Résumé

NAVARRO, T., V. PASCUAL, B. CABEZUDO & C. ALADOS (2009). Caractéristiques architecturales et traits fonctionnels d'espèces arbustives en milieu semi-aride méditerranéen dans le parc national de Cabo de Gata, SE de l'Espagne. *Candollea* 64: 69-84. En anglais, résumés anglais et français.

Les caractéristiques architecturales basiques de 45 arbustes de 12 familles sont décrites dans un matorral semi-aride méditerranéen à Cabo de Gata (SE de l'Espagne). Six différents modèles architecturaux de croissance de plantes sont décrits: Scarrone, Rauh, Holtum, Leeuwenberg, Champagnat et Corner. Le modèle de Tomlinson a été considéré comme une variante à répétition basitone des modèles de Rauh, Corner, Leeuwenberg et Holtum. La variation sympodiale du modèle de Scarrone a été trouvée comme étant la plus commune dans la zone étudiée. Les caractères fonctionnels comme la hauteur de la plante, la croissance annuelle et la surface de recouvrement de la plante ont été corrélés avec les modèles architecturaux. Ainsi, des petits arbustes de taille inférieure à 0,6 m, avec une faible croissance annuelle (0,1-0,25 m) et une petite surface de recouvrement (0,5-1 m²), ont plutôt présenté un modèle de croissance sympodique, une ramification dichasiale acrotonique et des inflorescences terminales. Inversement, les grands arbustes d'une hauteur de 1-3 m, présentant une large surface de recouvrement (1-3 m²), une forte croissance de rameaux latéraux (> 0,25 m) ont montré un modèle de croissance déterminé portant des inflorescences latérales. Le premier de ces deux groupes comportent des espèces qui se développent suivant la variante sympodiale du modèle de Scarrone, tandis que le second groupe contient des espèces obéissant au modèle de Rauh et incluant des arbustes épineux des communautés climaxiques.

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Introduction

The plant architecture approach is a system for distinguishing and comparing organization (CREMERS & EDELIN, 1995) based on analysis of the overall plant structure and pattern of spatial occupation and to identify endogenous growth processes and reflect environmental conditions prevailing at a specific site (HALLÉ & OLDEMAN, 1970; HALLÉ & al., 1978).

Twenty-three architectural models have been described in nature (HALLÉ & OLDEMAN, 1970; HALLÉ & al., 1978; BELL, 1994; HALLÉ, 1995), and can be applied to temperate (EDELIN, 1981; CARAGLIO & EDELIN, 1990), tropical species (OLDEMAN, 1974, 1990) and herbaceous plants (JEANNODA-ROBINSON, 1977).

Architectural analysis has proved to be one of the most efficient means currently available for the study of plant form and structure (BARTHÉLÉMY & CARAGLIO, 2007). It is a useful tool for the study of shrub biology and ecology, and can contribute to plant systematics (SANOJA, 1992; VESTER, 1999) and plant taxonomy (KELLER, 1994). Plant architecture is also an important exploratory tool for investigating forest dynamics (OLDEMAN, 1974, 1990; VESTER, 1997; MILLET & al., 1998), plant succession (MILLET & al., 1998) and the structural complexity of ecosystems (VALLADARES, 1999).

Plant spatial occupation confers functional benefits to survive in the competitive and restrictive environments (TOMLINSON, 1982) such as the semi-arid ecosystems. However, very few studies have been carried out on plant architectural diversity and ecological significance in semi-arid communities.

Life forms, growth forms, plant height, plant coverage, lateral spread and clonality are functionally important (BELL & al., 1999; KLEYER, 1999; WEIHER & al., 1999) and are associated with plant structure and development (LANDSBERG & al., 1999), plant climate response, plant disturbance response and competitive strength (DIAZ & al., 1997; WEIHER & al., 1999; CORNELISSEN & al., 2003; KNEVEL & al., 2005; BALVANERA & al., 2006), as well as plant establishment and survival in disturbed habitats (MCINTYRE & al., 1999; DIAZ & al., 1992; NAVARRO & al., 2006). These features are easily measured. However, there exists little information on how they are associated with plant architectural features.

This study aims: (1) to describe the diversity of shrub architectural models (HALLÉ & OLDEMAN, 1970; HALLÉ & al., 1978; BELL, 1994) of a semi-arid Mediterranean ecosystem in order to characterize it by means of the models which make it up, and to determine the most ecologically dominant architectural model reflecting an adaptive function for these particular environmental conditions; (2) to analyse associated traits among plant architectural features and morphological functional traits (CORNELISSEN & al., 2003) in order to select the relevant morphological whole plant traits associated with the architectural

features that can be used as ecological and floristic indicators in a semi-arid ecosystem (LEISHMAN & WESTOBY, 1992; SCHULZE & MOONEY, 1993; GRIME, 1997; VALLADARES, 1999).

Material and Methods

Study area

Cabo de Gata Natural Park lies on the southeast coast of Spain in a volcanic mountain range (0-493 m). The climate is semi-arid Mediterranean characterized by mild summer temperatures with an average annual rainfall of 260 mm. The mean annual temperature is 17.7°C (figures for 1953-1991) (RIVAS MARTINEZ & RIVAS Y SÁENZ, 2008). In Cabo de Gata, the *Mayteno europaei-Periploceto angustifoliae* Rivas Goday & Esteve 1975 vegetation series develops and it is the climax-community (PEINADO & al., 1992). This community develops in humid sites exposed to the sea. Inland, where the aridity is greater, the association is replaced by the association *Chamaeropo humilis-Rhamnetum lycioidis* O. Bolòs 1957. The *Mayteno-Periplocetum* seral thyme-brushwood corresponds to the association *Siderito osteoxyllae-Teucrietum charidemi* Peinado & al. 1988 (PEINADO & al., 1992), formed basically by early successional species, it develops in the low and open formation in extreme arid conditions. In most abrupt and rocky sites, a formation of dwarf shrubs (*Phlomidia almeriensis-Ulce-tum canescentis* Rivas Goday & Rivas Martínez 1969), characteristic of middle successional stages, develops. The thermo Mediterranean broom fields formations dominated by *Retama spaherocarpa* (*Thymelaeo tartonrairae-Genistetum ramosissimae* Rivas Goday & Rivas Martínez 1969) colonise slight to strong disturbed slopes, while the open halophytic shrublands association (*Suaedo verae-Salsoletum oppositifoliae* O. Bolòs 1967) are scattered along the saline soils and disturbed areas. The phytosociological characterisation for each species is indicated (Table 1).

Species data

Data were gathered for 45 major representative shrub species with the highest cover values (NAVARRO & al., 2006), which constitute a representation of the diversity of the study site's architecture. Botanical nomenclature follows CASTRO-VIEJO (1986-2007). The family and class affiliation of each species were added using the APG II (Angiosperm Phylogenetic Group) (2003).

The following basic features were considered (see HALLÉ & OLDEMAN, 1970; HALLÉ & al., 1978; BELL, 1994, for explanation of technical terms) and observed for each species included in the analysis: branching patterns (presence vs.

Table 1. – List of 45 shrub species from Cabo de Gata Natural Park (SE Spain) and their architectural models. The phytosociological characterisation is indicated for each species.

Family and APG II Groups affiliation	Architectural model	Morphological traits and life form
ARECACEAE (Commelinids)		
<i>Chamaerops humilis</i> L. (A)	CORNER **	Ph / Palmoid / Cl
ASTERACEAE (Euasterids II)		
<i>Helichrysum stoechas</i> (L.) Moench (B)	HOLTUM †	Ch / Small-shrub
<i>Artemisia herba-alba</i> Asso (E)	SCARRONE †	Ch / Small-shrub / Ax
<i>Launaea arborescens</i> (Batt.) Murb. (E)	LEEUEWENBERG †	Ch / Leafless shrub / Ax
<i>Phagnalon rupestre</i> (L.) DC. (B)	SCARRONE ***	Ch / Small-shrub / Ax
APOCYNACEAE (Euasterids I)		
<i>Periploca laevigata</i> Aiton (A)	RAUH *	Ph / Shrub
CISTACEAE (Eurosid II)		
<i>Cistus albidus</i> L. (C)	SCARRONE †	Ch / Dwarf-shrub
<i>C. clusii</i> Dunal (C)	SCARRONE †	Ch / Shrub
<i>C. ladanifer</i> L. (C)	SCARRONE †	Ph / Shrub
<i>C. salvifolius</i> L. (C)	SCARRONE ***	Ch / Small-shrub / Ax
<i>Fumana ericoides</i> (Cav.) Gand. (B)	SCARRONE ***	Ch / Small-shrub / Ax
<i>F. laevipes</i> (L.) Spach (B)	SCARRONE ***	Ch / Small-shrub / Ax
<i>F. thymifolia</i> (L.) Spach (B)	SCARRONE ***	Ch / Small-shrub
<i>Helianthemum almeriense</i> Pau (B)	SCARRONE ***	Ch / Small-shrub
<i>H. violaceum</i> (Cav.) Pers. (B)	SCARRONE ***	Ch / Small-shrub
<i>H. cinereum</i> (Cav.) Pers. (B)	SCARRONE ***	Ch / Small-shrub
FABACEAE (Eurosid I)		
<i>Genista umbellata</i> (L'Hér.) Poir. (C)	LEEUEWENBERG †	Ch / Leafless shrub / Tho
<i>Retama sphaerocarpa</i> (L.) Boiss. (D)	RAUH **	Ph / Leafless shrub / Tho
<i>Ulex baeticus</i> Pourr. (C)	CORNER †	Ph / Leafless shrub / Tho
<i>Anthyllis cytisoides</i> L. (C)	SCARRONE †	Ch / Small-shrub / Ax
FRANKENIACEAE (Core Eudicots)		
<i>Frankenia corymbosa</i> Desf. (E)	SCARRONE***	Ch / Small-shrub / Ax
LAMIACEAE (Euasterids I)		
<i>Phlomis purpurea</i> L. (C)	SCARRONE †	Ch / Dwarf-shrub / Ax
<i>Rosmarinus officinalis</i> L. (C)	SCARRONE †	Ch / Shrub / Ax
<i>Lavandula multifida</i> L. (B)	SCARRONE ***	Ch / Small-shrub
<i>L. stoechas</i> L. (B)	SCARRONE ***	Ch / Small-shrub / Ax
<i>Satureja intricata</i> Lange (B)	SCARRONE ***	Ch / Small-shrub / Ax
<i>Sideritis hirsuta</i> L. (B)	SCARRONE ***	Ch / Small-shrub / Ax
<i>S. oxeoxylla</i> (Pau) Rivas Godoy & Gómez García (B)	SCARRONE ***	Ch / Small-shrub / Ax (E)
<i>Teucrium capitatum</i> L. (B)	SCARRONE ***	Ch / Small-shrub / Ax
<i>T. charidemi</i> Sandwith (B)	SCARRONE ***	Ch / Small-shrub / Ax / (E)
<i>T. eriocephalum</i> Willk. (B)	SCARRONE ***	Ch / Small-shrub / Ax
<i>T. lusitanicum</i> Schreb. (B)	SCARRONE ***	Ch / Small-shrub / Ax
<i>T. pseudochamaepytis</i> L. (B)	SCARRONE ***	Ch / Small-shrub
<i>Thymus hyemalis</i> Lange (B)	SCARRONE ***	Ch / Small-shrub / Ax
<i>Marrubium vulgare</i> L. (B)	HOLTUM **	Ch / Small-shrub / Cl
<i>Phlomis lychnitis</i> L. (B)	HOLTUM **	Ch / Small-shrub / Cl
<i>Ballota hirsuta</i> Benth. (B)	HOLTUM †	Ch / Small-shrub / Cl

Table 1. – List of 45 shrub species from Cabo de Gata Natural Park (SE Spain) and their architectural models. The phytosociological characterisation is indicated for each species.

Family and APG II Groups affiliation	Architectural model	Morphological traits and life form
PLUMBAGINACEAE (Core Eudicots)		
<i>Limonium insigne</i> (Coss.) Kuntze (E)	LEEUEWENBERG †	Ch / Small-shrub / Cl
AMARANTHACEAE (Core Eudicots)		
<i>Salsola genistoides</i> Juss. (E)	SCARRONE +	Ph / Shrub
<i>S. vermiculada</i> L. (E)	SCARRONE +	Ph / Shrub
RHAMNACEAE (Eurosids I)		
<i>Rhamnus lycioides</i> L. (A)	RAUH *	Ph / Shrub / Tho
<i>Ziziphus lotus</i> (L.) Lam. (A)	RAUH *	Ph / Shrub / Sp
SOLANACEAE (Euasterids I)		
<i>Lycium intricatum</i> Boiss. (A)	CHAMPAGNAT †	Ph / Shrub / Tho / Cl
<i>Whitania frutescens</i> (L.) Pauquy (A)	RAUH *	Ph / Shrub / Tho
THYMELACEAE (Eurosids II)		
<i>Daphne gnidium</i> L. (A)	LEEUEWENBERG **	Ph / Dwarf-shrub

[Abbreviations for Family and APG II Groups affiliation: **A** = Species from the climax communities association *Mayteno europaei-Periploceto angustifoliae* Rivas Goday & Esteve 1975 and *Chamaeropo humilis-Rhamnetum lycioidis* O. Bolòs 1957; **B** = Early successional species from the seral thyme-brushwood (*Siderito osteoxyllae-Teucrietum charidemi* Peinado & al. 1988); **C** = Species from the middle successional vegetation stages from the rocky sites (*Phlomidia almeriensis-Ulicetum canescens* Rivas Goday & Rivas Martínez 1969); **D** = Species from the thermo-Mediterranean broom fields colonizing disturbed slight slopes (*Thymelaeo tartonrairae-Genistetum ramosissimae* Rivas Goday & Rivas Martínez 1969); **E** = Species from open halophytic shrublands (*Suaeda verae-Salsoletum oppositifoliae* O. Bolòs 1967) scattered along the saline soils].

[Abbreviations for life form: **Ph** = Phanerophyte, **Ch** = Chamaephyte, **Cl** = Clonality, **Tho** = Thorns, **Sp** = Spines, **Ax** = Axis splitting, **E** = Endemic from Cabo de Gata Natural Park. (**)].

[Abbreviations for architectural model: (†) Species conforming to the variant with basitonic repetition of the Holttum, Corner, Leeuwenberg and Rauh models; (*) Species conforming to the sympodic variant of the Rauh model with mixed axes; (**) Species conforming to the variant with basitonic repetition of the Holttum, Corner, Leeuwenberg and Rauh models; (***) Species conforming to the sympodic variant of the Scarrone model, but may conform to the Leeuwenberg model in sunniest sites; (+) Species conforming to the sympodic variant of the Scarrone model.

absence, terminal vs. lateral, monopodial vs sympodial); growth direction of differentiated axes (orthotropy vs. plagiotropy); preferential development of lateral axes on a vertical parent axis or shoot; (acrotonic, for the distal position of the largest lateral branch, vs. basitonic, when the proximal branches grow larger than the distal ones; and the position of reproductive structures (terminal vs. lateral). Each architectural model was defined by a particular combination of these features. Approximately 50 individual plants of different ages and development stages for each species were studied. Each seasonal developmental stage was described for representative aged individuals. The basic architectural descriptions were completed with additional characteristics such as phyllotaxis and phenological traits: main growing and flowering seasons, leaf phenology (ORSHAN, 1982), and inflorescence typology (which follows mainly KUBITZKY, 1990/2004). The two last characters were used to differentiate species sets within the same architectural model. The basitonic repetition of the Holttum, Corner, Leeuwenberg and Rauh models was considered such as variations of the Tomlinson model (CREMERS & EDELIN, 1995).

Plant functional traits used in the study correspond to morphological whole plant traits (Table 2). Field observations were made from June 2005 to June 2007, visiting the study sites regularly every 4-6 weeks. Observations and measurements were taken on at least 20-25 adult plants growing in full sunlight (CORNELISSEN & al., 2003). Voucher specimens of the species studied are kept in the MGC Herbarium.

Statistical analysis

The relations between architectural models and plant traits were tested. The relationships between ordinal morphological plant traits and architectural models were assessed by means of a Kruskal-Wallis test. The association between nominal morphological traits and basic architectural features was determined with the Pearson Chi-square test-statistic. Statistical analyses were performed using SPSS 14.0 software (SPSS Inc.). The original data matrices are available on request.

Table 2. – Functional traits recorded on the 45 shrub species in Cabo de Gata Natural Park (SE Spain).

Trait	Description	Description of classes in matrix	Associated plant functions (CORNELISSEN & al., 2003; MCINTYRE & al., 1999; WEIHER & al., 1999)
Life form (RAUNKIAER, 1934)	Position of dormant buds	1: Phanerophyte; 2: Chamaephyte	Disturbance and climate tolerance. Competitive ability. Response to soil resources.
Growth forms (CORNELISSEN & al., 2003)		1: Shrub; 2: Dwarf-shrub; 3: Small-shrub; 4: Palmoid; 5: Leafless shrub	Plant defence / protection. Disturbance and climate tolerance. Competitive ability. Response to soil resources and land use. Herbivory avoidance.
Plant height (CORNELISSEN & al., 2003)	The shortest distance between the upper boundary of the main photosynthetic tissues on a plant and the base of the plant	1: 0.11-0.29 m; 2: 0.3-0.59 m; 3: 0.6-0.99 m; 4: 1-3 m	Competitive ability. Response to land use. Plant defence / protection. Disturbance and climate tolerance. Response to soil resources. Herbivory avoidance. Whole plant fecundity.
Plant coverage (CORNELISSEN & al., 2003)		1: 0.5-1 m ² ; 2: 1-3 m ² ; 3: > 3m ²	Disturbance and climate tolerance. Space occupancy.
Lateral spread (CORNELISSEN & al., 2003, MCINTYRE & al., 1999)	The distance covered by lateral spread in one year	1: < 0.1 m; 2: 0.1-0.25 m; 3: > 0.25 m	Space occupancy. Plant defence/protection.
Clonality (CORNELISSEN & al., 2003)	Presence of clonal stems	1: Absence; 2: Presence	Space acquisition. Competitive vigour. Persistence after environmental disturbances. Ability to exploit patches rich in key resources. Responses to soil resources. Disturbance and climate tolerance.
Axis splitting (SCHENK, 1999)	Axis splitting is a clonal survival strategy common in the shrubs of arid environments; it can be considered a defining characteristics of this growth form	1: Absence; 2: Presence	Response to disturbance. Tolerance to drought stress. Persistence after environmental disturbances.
Spinescence (CORNELISSEN & al., 2003)	Presence of spines, thorns or prickles	1: Absence; 2: Presence	Reduces drought stress. Defence against herbivores. Tolerance to drought stress. Plant defence / protection. Competitive strength.

Results

Basic architectural descriptions

1. Species conforming to the Scarrone model

Shrubs with a main stem (growth beginning with an orthotropic phase resulting in a relatively stout, erect trunk) and sympodial branching (2- or rarely 3-tiered arrangement) a single subtending branch appears occasionally (Fig. 1A, 1B). The new branches develop from renewal buds located below the inflorescence apices of previous season's branches or from an elongation from part of the partial lateral brachyblasts. Brachyblasts develop in the axils of the leaves of renewal branches or on lower part of previous season's branches. They grow practically the entire year and the elongation to the new branches occurs in May. In the case of the evergreen shrubs, branches grow practically throughout the year, starting in March-April, with intra-annual growth stopping in autumn-winter; rapid elongation is resumed and the terminal inflorescence (Fig. 1A, 1B) develop in the following spring (June). The phyllotaxis is opposite-decussate.

Cistus ladanifer, *C. clusii* and *C. salvifolius*

Evergreen shrubs with branches ending in a simple cyme.

Cistus albidus

Semi-deciduous shrubs with branches ending in a simple cyme (Fig. 1A).

Phlomis purpurea

Semi-deciduous shrubs with branches ending in a well developed spiciform thyse of distant many-flowered verticillasters.

Rosmarinus officinalis

Evergreen shrubs with branches ending in a short raceme (a simple thyse of axillary flowers) (Fig. 1B).

2. Species conforming to the sympodic variant of the Scarrone model

Salsola vermiculata and *S. genistoides*

Evergreen many-branched shrubs consisting of a sympodium of orthotropic stems with acrotonic sympodial branching. Dichasial or 3-tiered arrangement (*S. vermiculata*) and dichasial or sometimes only a single subtending branch (*S. genistoides*). The new branches with opposite-decussate phyllotaxis develop in February-May from renewal buds located on the upper part of previous season's branches and ending in "flower-bearing branches", which develop at the end of June. Branching architecture of the plant tends to be variable in development between individuals. A common growth form modification occasionally occurs when the outer main branches, originally growing vertically, declinate in part or entirely to the horizontal or arch downwards, the renewal branches with vertical growth are formed on the highest part of this arch.

The following species conform to the sympodic variant of the Scarrone model, but they can conform to the Leeuwenberg model in the places with the strongest light intensity such as rocky slopes facing the sea.

Species with dichasial or, less frequently, 3-tiered subligneous branching ending in a terminal inflorescence. Exceptionally, the branching patterns may tend to be monochasial in the upper parts of the plants. The new branches develop from renewal buds located below the inflorescences or from the elongation of some of the partial lateral brachyblasts located on previous season's branches. Branches start to grow in February and elongate until April-May when the inflorescences develop. The phyllotaxis is opposite-decussate.

Lavandula stoechas

Evergreen shrubs with branches ending in a pedunculate spiciform thyse.

Thymus hyemalis and *Frankenia thymifolia*

Summer deciduous shrubs with branches ending in a terminal head (inflorescence of condensed cymes).

Fumana ericoides, *F. thymifolia* and *F. laevipes*

Summer deciduous shrubs with branches ending in a cymose inflorescence (Fig. 1C).

Teucrium charidemi, *T. lusitanicum*, *T. capitatum* and *T. eriocephalum*

Summer semi-deciduous shrubs with branches ending in a well developed paniculiform or spiciform raceme of condensed cymes (Fig. 1D).

Helianthemum almeriense, *H. violaceum*, *H. cinereum*.

Summer semi-deciduous shrubs with branches ending in a short thyse.

Phagnalon rupestre

Summer deciduous shrubs with branches ending in a capitulum.

Sideritis oxiteoxylla, *S. hirsuta*, *Satureja intricata* and *Teucrium pseudochamaeipyitis*.

Summer deciduous shrubs with branches ending in a spiciform thyse of distant 2 to many-flowered verticillasters. When young the renewal branching is mainly basitonic.

Lavandula multifida

Winter deciduous shrub with stems ending in a slender simple or compound dense thyse. The main stems of the *Teucrium pseudochamaeipyitis* and *Lavandula multifida* may conform to the Holttum model. The new stems are developed from the renewal buds located in the lower part of the lignified stems and grow from February to May.



Fig. 1. – The Scarrone model. **a.** Terminal inflorescences; **b.** Sympodial branching (2-or 3-tiered arrangement).
A. *Cistus albidus* L.; **B.** *Rosmarinus officinalis* L.; **C.** *Fumana ericoides* L.; **D.** *Teucrium lusitanicum* Schreb.

3. Species conforming to the Leeuwenberg model

Launaea arborescens

Spinescent shrub consisting of a sympodium of orthotropic unpaired zigzag branches with 2-tiered arrangement. They elongate in March-April from lateral axillary buds located in the upper part of previous season's branches and end in a solitary capitulum with flowering in June-July.

Genista umbellata

Thorny shrubs consisting of a sympodium of orthotropic branches with dichasial or 3-tiered, rarely 4-tiered arrangement. The new branches elongate in January-February from the lateral buds located in the upper part of previous season's branches, which end in a slender solitary umbel with flowering in March.

Limonium insigne

Shrubs with lignified underground stems with dichasial branching. The aerial stem is monopodial and develops from a small rosette. This stem develops (June) a paniculate inflorescence (sinflorescence of cincinnes). The plant conforms to the Leeuwenberg model with underground stems and the aerial green stems conform to the Holtum model.

4. Species conforming to the sympodic variant of the Rauh model

Rhamnus lycioides

Evergreen thorny shrubs. The main long spiny stem is orthotropic. The lateral thorny branchlets are side branches of the spiny long ones. They have a horizontal growth direction and alternate phyllotaxis, while the non-thorny leafy branches (brachyblasts) show spiral phyllotaxis and short growth (March-April). At its base, the axillary umbelliform cymes appear in April-June. The new branches develop in March-May from renewal buds located at the apex and on the upper part of previous season's branches. Lateral branchlets will develop on these new seasonal branches, remaining as thorns. Along the stem, the branches are arranged radially.

Ziziphus lotus

Evergreen thorny shrubs. The main long zigzag stem is orthotropic. The lateral unpaired thorn zigzag branchlets have horizontal growth direction and develop in April-June. The spiny short floral twigs forming a cincinnal cymoid system (axillary corymb-like cymes) develop in June at the base of the old dried spiny branchlets and also at the base of the new renewal branches. The new branches develop in April-June from renewal buds located at the apex of previous season's branches. The leaves and the branchlets are alternate-distichous.

Withania frutescens

Summer-deciduous thorny shrubs. The principal stem is orthotropic with spiral phyllotaxis. The lateral thorny twigs, with horizontal growth direction, are side branches of the long

shoots. The partial non-thorny leaf brachyblasts develop on the upper parts of the branches. The new branches develop in September-January from partial brachyblasts located in the upper parts of the branches. Along the stem, the branches are arranged radially. Lateral solitary flowers are formed in June on the old and new season's branches.

Periploca laevigata

Evergreen thorny shrubs. The main stem is orthotropic with opposite-distichous phyllotaxis. The renewal branches develop from the lower part of the plant with rapid elongation in May. They are initially orthotropic, but which become tendrils attached to the main old branches until the end of the elongation. In some cases, basal plagiotropic (plagiotropy by apposition) sprouter branches develop on the lower part of the plant. Lateral short simple racemes (with 2-4 flowers) are developed in the axils of leaves on the same season's branches (June).

The architectural model of *Ziziphus lotus*, *Withania frutescens* and *Periploca laevigata* is closely similar to the Massart model on the basis of the horizontal growth direction of their lateral branches.

5. Species conforming to variants with basitonic repetition of the Holtum, Corner, Leeuwenberg and Rauh models

Phlomis lychnitis, *Marrubium vulgare* and *Ballota hirsuta*

Winter semi-deciduous shrubs in which only the lower base of the stems is lignified and perennial. The monopodial main stem conforms to the Holtum model, shows opposite-decussate phyllotaxis and a terminal inflorescence that develops in June-July consisting of a slender spiciform thyrses with distant many-flowered verticillasters.

Chamaerops humilis

Evergreen palmoid shrub in which the monopodial main stems conform to the Corner model with spiral phyllotaxis.

Daphne gnidium

Evergreen shrub in which the main stems conforms to the Leeuwenberg model with sympodial 2- or 3-tiered branching and spiral phyllotaxis ending in an umbel inflorescence. The new branches elongate in January-March from the upper part of the previous season's branches until flowering in July.

Retama sphaerocarpa

Evergreen large shrub in which the main stems conform to the Rauh model. The main stems have acrotonic pseudo-monopodial branching and lateral inflorescences formed of single racemes and flowering in May-June. The terminal renewal branches develop in June-July after flowering.

6. Species conforming to the Holttum, Corner and Scarrone models as regards the upright part

Helichrysum stoechas

Summer semi-deciduous shrubs. The upright parts (outer parts) conform to the Holttum model. The renewal branches develop in March-April from lateral buds located in the apex of main stems or from elongation of lateral brachyblasts located on previous season's branches, each branch ending in a corymbose inflorescence composed of a small capitulum.

Ulex baeticus

Evergreen spiny shrubs with the outer upright parts conforming to the Corner model. Monopodial branches with lateral spines develop in December-January and flower in February-March from the upper part of the previous season's branches. Lateral single flowers are axillary to the spines.

Anthyllis cytisoides and *Artemisia herba-alba*

Summer semi-deciduous shrubs. The upright parts of these plants conform to sympodic variant of the Scarrone model. Branching of the outer stems has a 2-tiered arrangement or only a single subtending branch with spiral phyllotaxis. Brachyblasts develop in (May-)June-July in the axils of the leaves of renewal branches. Some brachyblasts located on the middle part of the old branches may last more than one year or eventually elongate to the new branches during the following season's growth. In *Anthyllis cytisoides* the branches ending in a single raceme and the renewal branches develop in February-May. In *Artemisia herba-alba* the branches ending in a paniculate raceme of capitula and the renewal branches develop in May-June.

7. Species conforming to the Champagnat model

Lycium intricatum

Summer deciduous thorny shrubs. The main long stems are initially orthotropic, but gradually change their orientation and become pendulous (arched) under their own weight, which creates a plagiotropic appearance. In the distal portion, the pseudomonopodial branches develop in September-January by superposition of lateral shoots. If these branches touch the soil they may produce adventitious shoots. Along the stem, the branches are arranged radially. The lateral thorny twigs with horizontal growth direction are side branches of the long spiny shoots. The partial non-thorny leafy brachyblasts develop on the upper parts of the plant. Lateral solitary flowers are formed mainly from autumn to spring over the upper thorny twigs.

Architectural diversity

The most characteristic Mediterranean semi-arid shrub species from Cabo de Gata Natural Park conform to six architectural models (Table 1; Fig. 2): Scarrone (29), Rauh (5), Holttum (4) Leeuwenberg (4), Corner (2) and Champagnat (1). The Scarrone and Rauh models were also represented by sym-

podic variants and the Leeuwenberg model also by its underground stem variant. Species conforming to the Scarrone model have brachyblasts with short term determinate growth; species conforming to the Rauh model have three axes types: long spiny stems, lateral thorny twigs and non-thorny leafy brachyblasts. The highest percentage of species (46.9%) conforms to a sympodic variant of the Scarrone model and to the Leeuwenberg model often on sunny rocky slopes facing to the sea (42.6%). Six species conform to the variant with basitonic repetition of the Holttum, Corner, Leeuwenberg and Rauh models (Table 1). A total of 67.4% of species were axis splitting which was especially frequent within the species conforming to the Scarrone model.

Architectural models and systematic position

Architectural models were not independent of taxonomic affiliation (Table 1, e.g. 100% *Rhamnaceae* in the Rauh model; 100% *Cistaceae* and 86.6% *Labiatae* in the Scarrone model), whereas the representation of different families was much more even in other cases (*Fabaceae*).

There was a significant relationship between architectural models and the taxonomic groups affiliation of families (APG II) ($\chi^2 = 111.1$; $df = 55$; $P < 0.001$; Fig. 3). Families conforming to the Scarrone model were over-represented in *Eurosids* II and *Euasterids* I, whereas families conforming to the Rauh model were over-represented in the *Eurosids* I and *Euasterids* I, and families conforming to the Holttum model were restricted to *Euasterids* I and II.

Relationship among architectural models and morphological functional traits

There was a significant relationship between architectural model and plant coverage ($H = 36.8$; $P < 0.001$; Fig. 4A), lateral spread ($H = 32.2$; $P < 0.001$; Fig. 4B) and plant height ($H = 32$; $P < 0.001$; Fig. 4C). In our study area, the species conforming to the sympodic variant of the Scarrone model tend to have a reduced plant coverage, a reduced lateral spread and low plant height. Whereas, the species conforming to the sympodic variant of the Rauh model tend to have large plant coverage, a well developed lateral spread and high plant height. The species conforming to the Scarrone model tend to have medium lateral spread. While species conforming to the Holttum model tend to have a low plant height.

Life form was significant associated with position of reproductive structures ($\chi^2 = 21.5$, $df = 1$, $P = 0.006$; Fig. 5). All chamaephyte species have terminal inflorescences, but the phanerophytes species have fewer inflorescences that are terminal (6) than lateral (8).

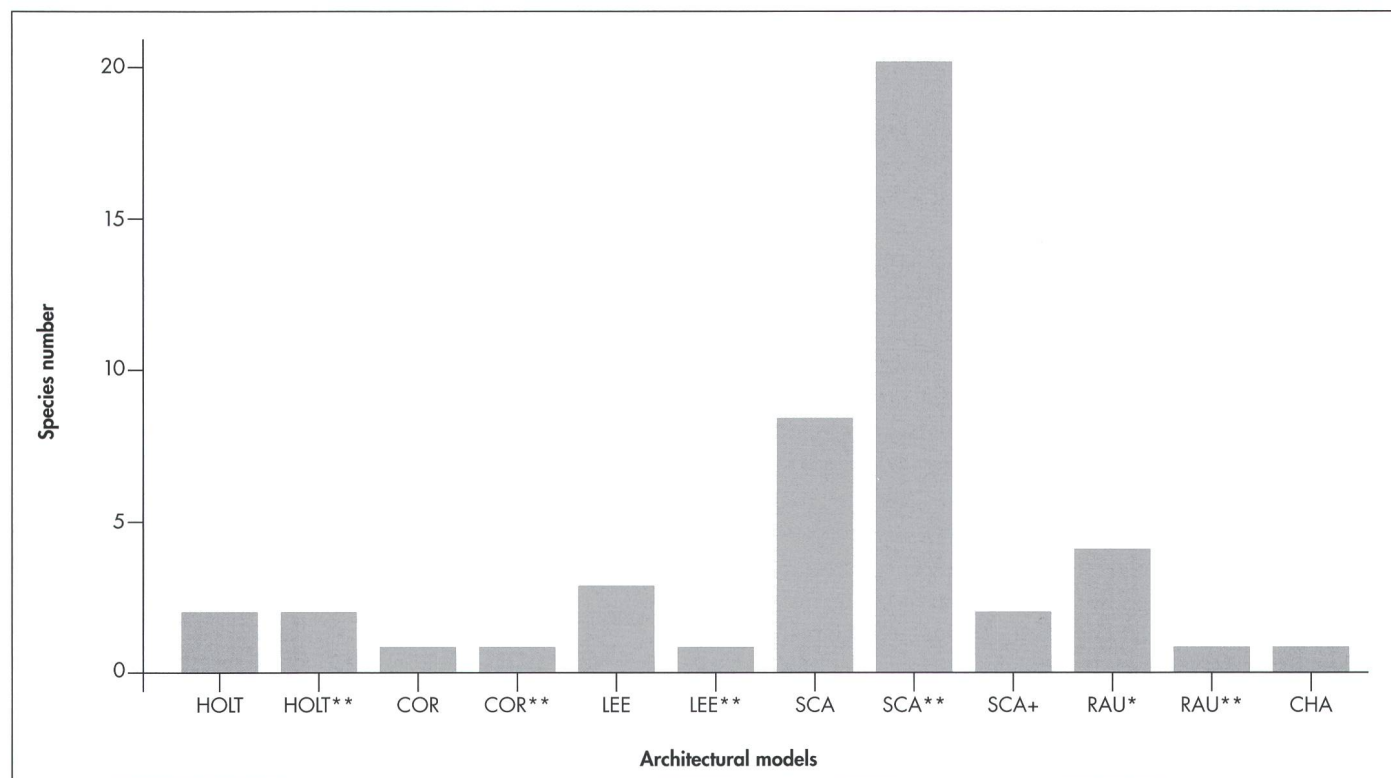


Fig. 2. – Frequency distribution of architectural models of 45 shrub species from Cabo de Gata Natural Park (SE Spain). SCA: Scarrone; RAU: Rauh; HOLT: Holttum; COR: Corner; LEE: Leeuwenberg; CHA: Champagnat. (**) Species conforming to the variant with basitonic repetition of the Holttum, Corner, Leeuwenberg and Rauh models. (*) Species conforming to the sympodic variant of the Rauh model with mixed axes. (***) Species conforming to the sympodic variant of the Scarrone model, but may conform to the Leeuwenberg model in sunnier sites. (+) Species conforming to the sympodic variant of the Scarrone model.

Discussion

An overview of architectural studies in temperate regions (KAHN, 1975; EDELIN, 1977; RAMAROSON-RAMPARANY, 1978) indicates that the Rauh model is the most frequent followed by the Leeuwenberg model, with the Scarrone model being the least frequent (FOURNIER, 1979). The presence of these three models in Cabo de Gata Natural Park in addition to the Corner, Holttum and Champagnat models, reflects a certain diversity of architectural models in this semi-arid ecosystem. This structural complexity is coherent with the functional complexity observed (NAVARRO & al., 2006, 2009).

The relative abundance of a particular architectural model in an ecosystem is related with their competitiveness. The overall ability of a model to adapt itself to the environment is associated with its success (FOURNIER, 1979) and with their systematic importance which will be greater if the model is adopted by a relatively high number of species belonging to different families (KAHN, 1975). Although in temperate regions the Scarrone model is rare (KAHN, 1975), its sympodic variant is the most common

architectural model, apparently showing an overall ability to adapt itself to the Mediterranean semi-arid shrubland of Cabo de Gata Natural Park. The mid xeric successional species from *Lamiaceae* such as *Phlomis purpurea*, *Rosmarinus officinalis* and *Cistaceae* such as *Cistus spp.*, conform to this model. The sympodic variant of the Scarrone model is represented by (1) halo-nitrophylous species colonising abandoned cultures and grazing sites such as *Salsola spp.*, and (2) the early successional species with axis splitting belonging mainly to *Lamiaceae* such as *Thymus spp.*, *Teucrium spp.*, *Sideritis spp.*, *Lavandula spp.* and *Cistaceae* such as *Helianthemum spp.*, and *Fumana spp.*, which form patches in scattered seral-thyme brushwood. These species may conform to the Leeuwenberg model in most sunniest places such as rocky slopes facing the sea. The architectural models with a high bifurcation ratio such as the Leeuwenberg model are theoretically more efficient for leaf light interception (LEOPOLD, 1971), which seems to be an advantageous strategy in response to climatic factors and disturbance when light is excessive (VALLADARES & PUGNAIRE, 1999). Among them, endemic or rare species, such as *Teucrium charidemi*, *Sideritis*

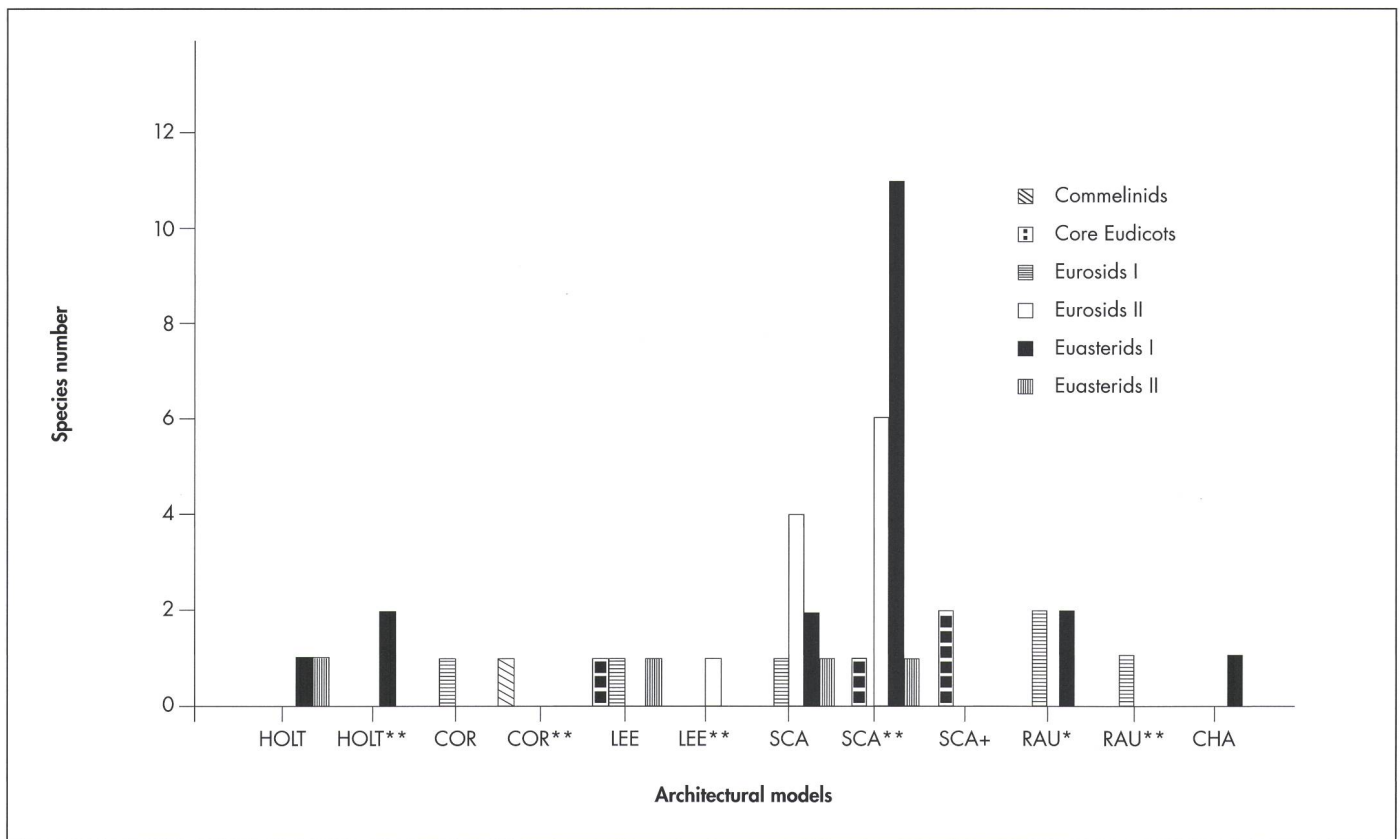


Fig. 3. – Number of species in each APG II taxonomic groups affiliation of families (Angiosperm Phylogenetic Group) (2003) as functions of the architectural models. (See Fig. 2 for abbreviations).

osteoxylla and *Frankenia corymbosa*, are not significantly different from their largely distributed co-occurring congeners present in the same community.

The Rauh model is the most widely distributed in temperate and tropical regions (KAHN, 1975; FOURNIER, 1979; HALLÉ & al., 1978; MILLET & al., 1998). Its success probably lies in the capacity for regrowth of all its meristems that permit this model to regenerate after traumatism. Axis differentiation related to the presence of spines or thorns is highly specialized in species conforming to this model, particularly in our study area, where the Rauh model is associated with thorny species in remnants of native vegetation (PEINADO, 1992), such as *Periploca laevigata*, *Ziziphus lotus*, *Withania frutescens* and *Rhamnus lycioides*. *Lycium iontricum* and other climatic local species are represented by the Champagnat model, which is typical of dry regions which have high axis differentiation with almost three different axis types.

HALLÉ & al. (1978) attempted to link architectural models to *r*- and *k*-selected strategies. However, it has been demonstrated that only the Holttum model is adapted for an *r*-strategy. This model is associated with repetition of the Tomlinson model

(KAHN, 1975) and is possibly pre-adapted to the traumatisms of grazing or fire (FOURNIER, 1979). In our study area, nitrophilous and most pioneer species, such as *Marrubium vulgare* and *Ballota hirsuta*, which are highly favoured by grazing pressure (ALADOS & al., 2006), conform to this model in agreement with previous results.

Species conforming to the Tomlinson model (recognized as a variation with basitonic repetition of the Rauh and Leeuwenberg models) such as *Retama sphaerocarpa* and *Daphne gnidium* are well adapted to semi-arid open environments through their open crown and terminal active buds which facilitate adaptation to excessive light (KAHN, 1975). In the case of *Retama sphaerocarpa*, VALLADARES & PUGNAIRE (1999) demonstrates how the open crown is associated with a higher photosynthetic photon flux density (PPFD) interception during the critical dry season.

Chamaerops humilis and *Ulex baeticus*, both species with large canopies that conform to the Corner model, are well distributed in rocky slopes and show good regeneration after fire according to FOURNIER (1979).

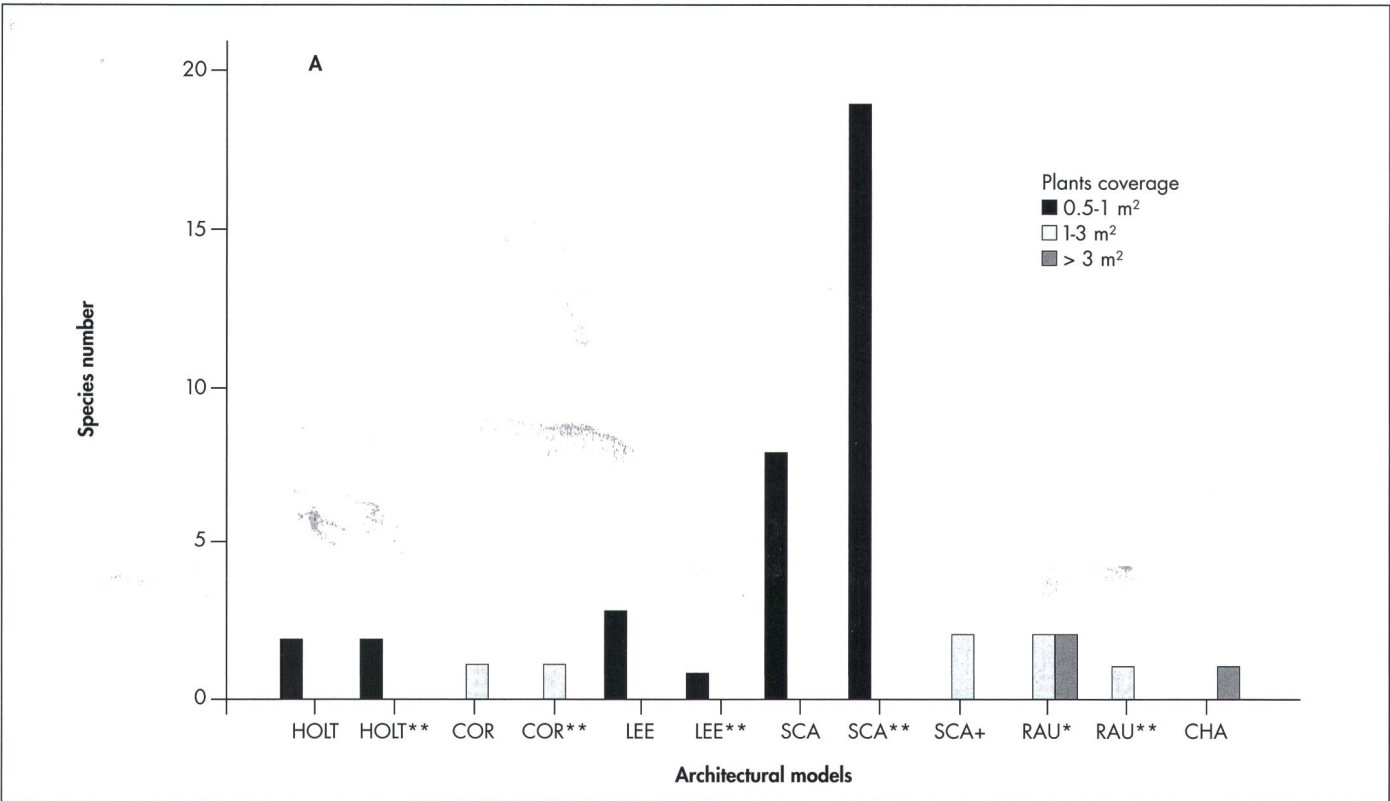


Fig. 4. – Architectural model and morphological functional traits. A. Architectural model and plant coverage.

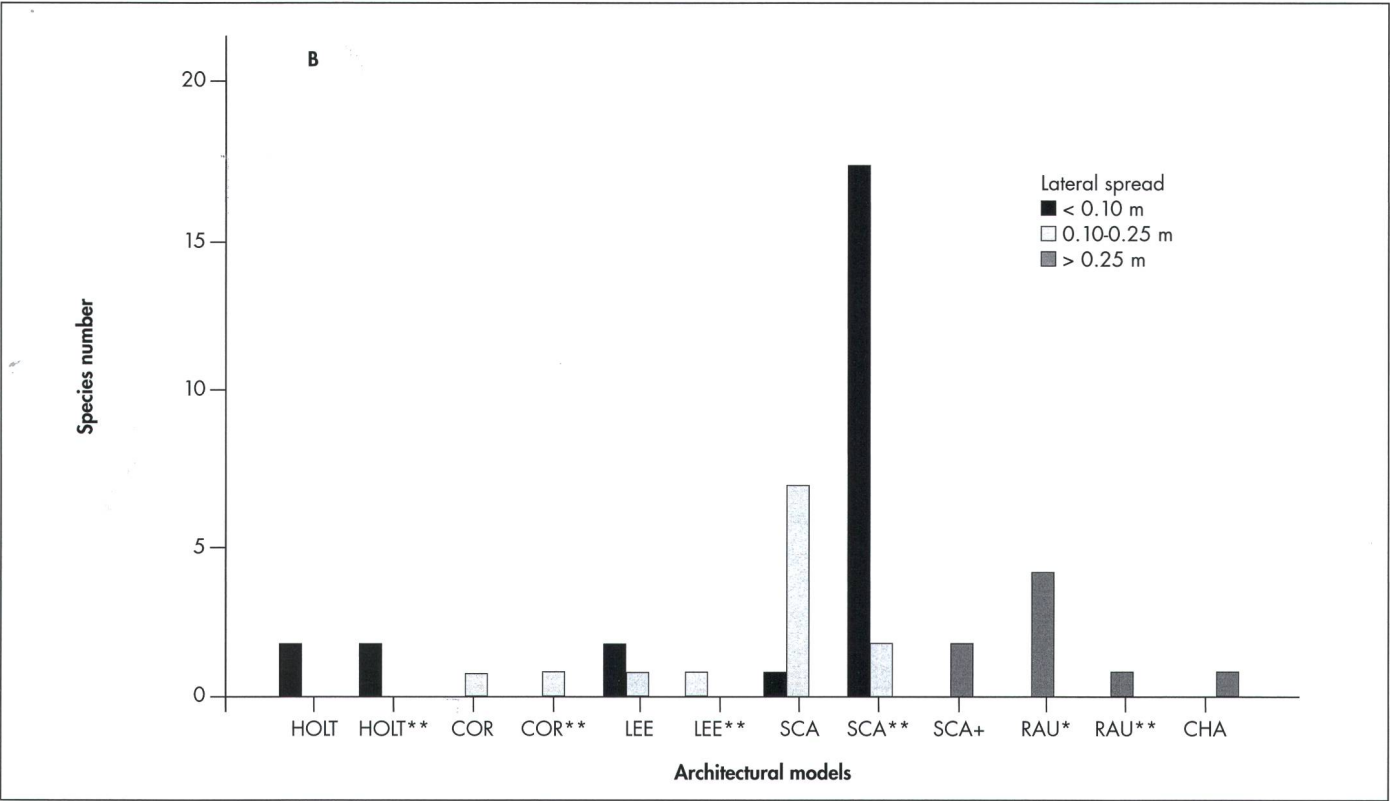


Fig. 4. – Architectural model and morphological functional traits. B. Architectural model and plant lateral spread.

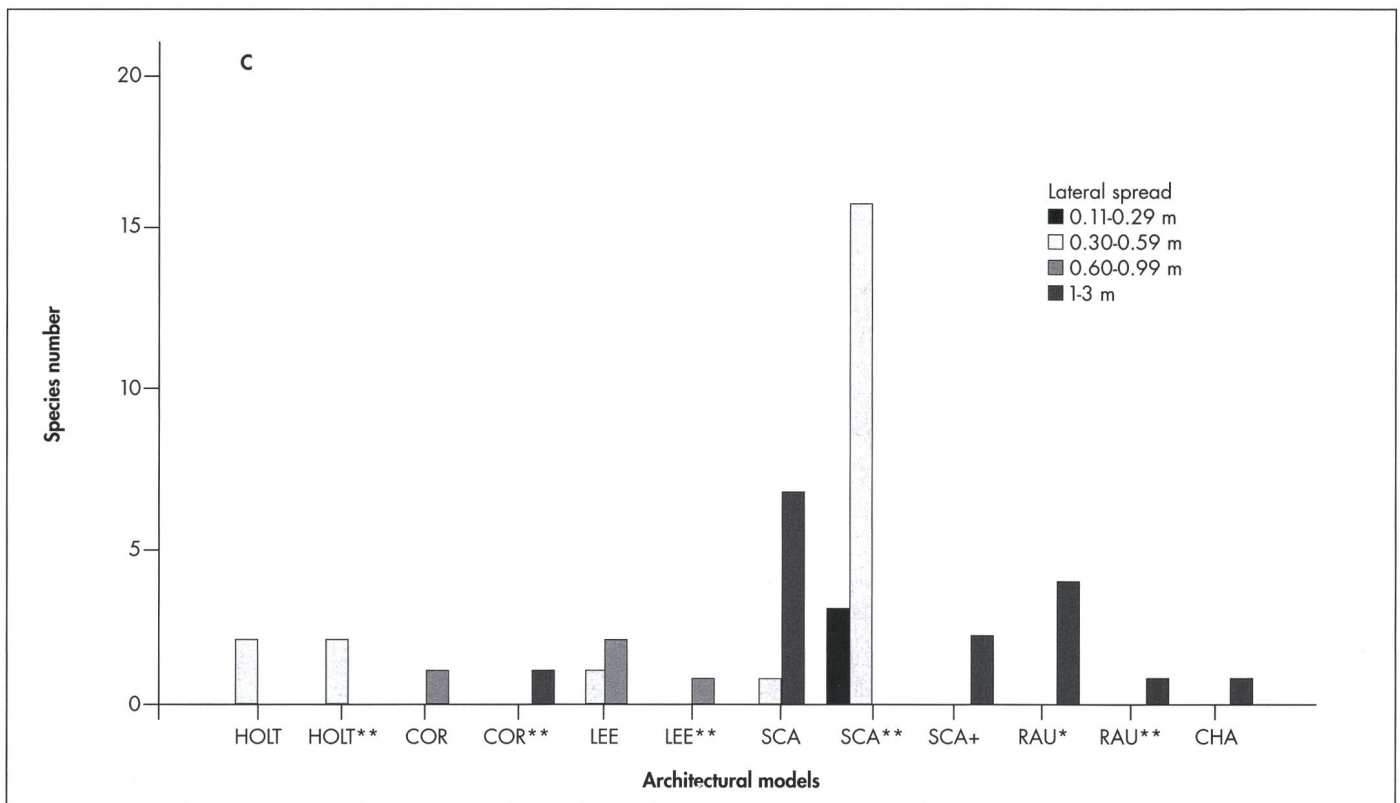


Fig. 4. – Architectural model and morphological functional traits. C. Architectural model and plant height. (See Fig. 2 for abbreviations).

We can therefore recognize some clear associations between certain architectural features and environmental conditions. Sympodial and orthotropic growth patterns and the terminal position of reproductive structures, are the basic architectural features identifying the Scarrone model. This is the most common architectural model in the Cabo Gata Natural Park and seems to be the most advantageous facing up to drought and disturbance according to FOURNIER (1979), SCHULZE & al. (1986), CARLQUIST (1988) and VALLADARES & PUGNAIRE (1999).

Species conforming to the Rauh model (e.g., *Ziziphus lotus*, *Whitania frutescens*, *Periploca laevigata*, *Rhamnus lycioides*) and the Champagnat model (*Lycium intricatum*) were thorny phanerophytes with large canopies and developed lateral spread forming part of climax communities (PEINADO & al., 1992; NAVARRO & al., 2006, 2008). Thorns provided a competitive advantage (SCHULZE & al., 1986). Conversely, early successional species conforming to sympodic variants of the Scarrone model (e.g. *Teucrium* spp., *Sideritis* spp., *Thymus hymalis*, *Frankenia corimbosa*, *Phagnalon saxatile*) were chamaephytes with medium canopies

and reduced lateral spread forming part of the seral thyme-brushwood (NAVARRO & al., 2006, 2008). This last trend was consistent with evidence from previous studies, where it was assumed that adaptation to disturbance involves small stature, low space occupation and reduced lateral spread (DIAZ & CABIDO, 1992; LAVOREL & al., 1997; WESTOBY, 1998; WEIHER & al., 1999; MCINTYRE & al., 1999; GRIME & al., 1998; GRIME, 2001).

The exploration of trait environmental associations (LEISHMAN & WESTOBY, 1992; SCHULZE & MOONEY, 1993; GRIME & al., 1998) is of great use in assessing ecosystem function and in the case of architectural models, they can be used as ecological indicators. The Scarrone model can be used as an indicator of middle successional stages from the most abrupt and rocky sites, where the formation of dwarf shrubs (*Phlomidia almeriensis*-*Ulicetum canescentis*) develops. And, the sympodic variant of Scarrone model can be used as an ecological indicator of early successional stages from long-term degradation thyme-brushwood that resists disturbances (JAUFFRET & LAVOREL, 2003; NAVARRO & al., 2006). Species

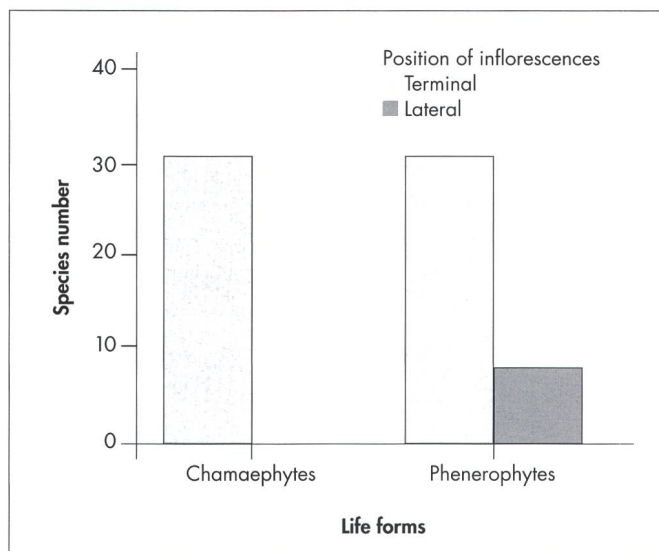


Fig. 5. – Life forms and position of reproductive structures (inflorescences).

conforming to the Rauh and Champagnat models are the species from the climax communities which facilitate plant persistence and establishment (NAVARRO & al., 2006), enhance ecosystem functioning (MAESTRE & CORTINA, 2004) and provide resilience against disturbances (TRABAUD, 1991), so that they can be used for restoration programs. Similarly the Holttum model is an indicator of perturbation, often under grazing pressure in Cabo de Gata Natural Park (ALADOS & al., 2006; NAVARRO & al., 2006).

This paper provides basic data concerning the wide diversity existing in architectural models, which should facilitate comparisons between different ecosystems and demonstrate the ecological amplitude of each architectural model. The results of this study can be applied to providing a framework for ecological assessment for the biodiversity conservation in semi-arid ecosystems and contribute to developing new approaches and methodologies.

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