

## Maquis vegetation in the eastern Cantabrian coastal fringe

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**Abstract.** The typology and distribution are discussed of hitherto poorly known Mediterranean-type maquis vegetation from the eastern stretch of the coastal fringe of the Cantabrian Mountains. 51 phytosociological relevés of maquis with *Arbutus unedo* ('madroñales') and *Quercus coccifera* (kermes oak shrubland or 'coscojares') were submitted to Correspondence Analysis and table rearrangement. The results are discussed and interpreted in the light of actual biogeographical and palaeohistorical knowledge. A sharp division between (uniform) acidophilous and (diversified) basophilous communities was revealed. On the basis of the phytosociological classification four new syntaxa are described: the associations *Ulici gallii-Arbutetum unedonis*, *Phillyreo latifoliae-Arbutetum unedonis* – with two subassociations: *arbutetosum unedonis* and *viburnetosum tini* – and the association *Genisto occidentalis-Quercetum cocciferae*.

**Keywords:** Biogeography; *Genisto occidentalis-Quercetum cocciferae*; Ordination; *Phillyreo latifoliae-Arbutetum unedonis*; Phytosociology; Relic vegetation; Syntaxonomy; *Ulici gallii-Arbutetum unedonis*.

**Nomenclature:** Tutin et al. (1964-1980); Greuter et al. (1984-1989).

### Introduction

The Mediterranean vegetation of the coastal fringe of the Cantabrian Mountains (northwestern Spain) has been studied by several geobotanists working in the Basque region and surrounding areas (Allorge 1941; Guinea 1949, 1953; Braun-Blanquet 1967; Navarro 1982; Loidi 1983; Velasco 1983; Onaindia 1986; Herrera 1989). This interest can be explained by the presence of conspicuous evergreen sclerophyllous Mediterranean vegetation in an area with a humid Atlantic climate otherwise dominated by deciduous broad-leaved forests. Most authors explain the local abundance of evergreen *Quercus ilex* forest as an ecological response to xeric conditions as found on rocky calcareous soils. This vegetation has traditionally been interpreted as a relic of the postglacial period, when the climate was more Mediterranean than at present.

Probably, an important northward migration took place from the Ebro Valley towards the coastal Cantabrian areas (Kutzbach & Guetter 1986; Peñalba 1989). This hypothesis has been discussed by Aseguinolaza et al. (1984), Aseguinolaza & Gómez (1988), Loidi (1987) and Montserrat Martí & Montserrat Martí (1987). Others consider that most of the Mediterranean vegetation of the Cantabrian coastal area is much older, dating from prior to the Würm glaciation, and having survived there in thermic refuges during colder periods (Costa Tenorio et al. 1990). Probably, the modern composition of the vegetation in this area results from a combination of several migratory waves. In addition, the Mediterranean-Iberoatlantic (Rivas-Martínez 1982) element, a small group of taxa from the western part of the Iberian Peninsula, occurs in the area. It consists of silicicolous plants, which are better represented in Galicia and Asturias.

*Quercus ilex* forest constitutes the most important and best studied Mediterranean vegetation type of the area, but it is not the only vegetation type here; we also find a sort of maquis, frequently dominated by *Arbutus unedo* – locally called madroñal or 'bortal' – and considered as a substitute of the *Q. ilex* forest after fire or cutting (Guinea 1949; Velasco 1983). Recently, quite peculiar communities of clear Mediterranean character, dominated by *Olea sylvestris* and *Laurus nobilis* were reported from the coastal areas of Asturias and Cantabria (Bueno & Fernández Prieto 1991); clearly, the Cantabrian *Quercetum ilicis* is not restricted to the above-mentioned holm-oak forests.

From the successional point of view, these communities have different positions; some of them, such as the *Olea* and *Laurus* communities, are permanent communities linked to lithosols; others such as the *Arbutus* and *Q. coccifera* types, are substitute communities of potential *Q. ilex* (*Lauro-Quercetum ilicis*) and *Q. robur* (*Hyperrico pulchri-Quercetum roboris*) forests.

Clearly, several of the Mediterranean shrub community types occurring in the area are still insufficiently known. The aim of our study was to confirm and extend the typology and biogeography of the *Arbutus* and *Q. coccifera* dominated maquis.

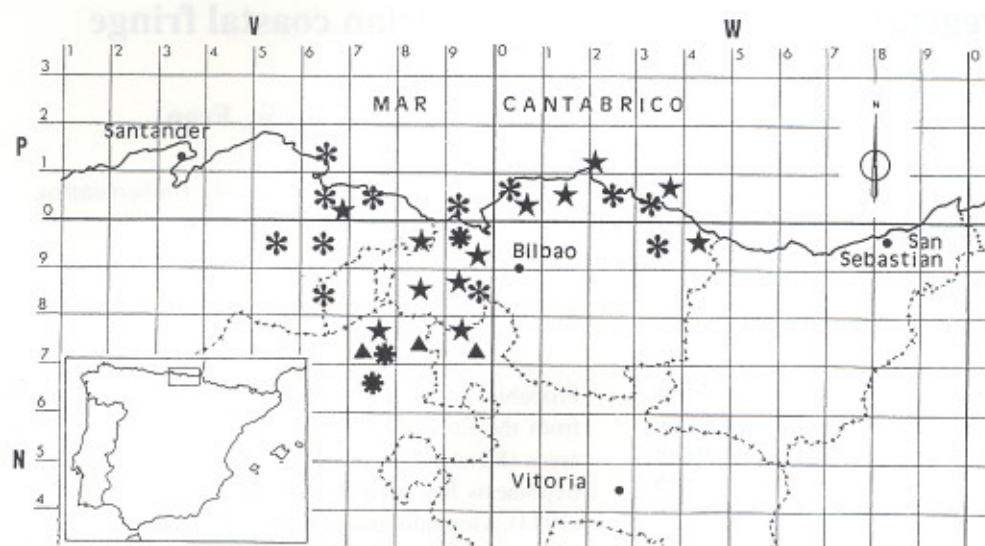


Fig. 1. Locations of the relevés of the different community types in the studied area:

- \* *Phillyreo latifoliae-Arbutetum unedonis arbutetosum unedonis*; 
 ▲ *Phillyreo latifoliae-Arbutetum unedonis viburnetosum tini*  
 ★ *Ulici gallii-Arbutetum unedonis*; 
 \* *Genisto occidentalis-Quercetum cocciferae*

## Material and Methods

The analysis was done in the eastern stretch of the Cantabrian coastal fringe (43° - 43° 30' N, 3° 30' - 4° W) between 10 and 580 m a.s.l. 51 relevés were carried out according to the Braun-Blanquet approach (Westhoff & van der Maarel 1973). Their location is shown in Fig. 1. The relevés were made by different researchers in different seasons; moreover the sample plots were rectangular, which implies that a larger number of species from the surroundings may have been included. Thus, the original data set was rather heterogeneous (Lepš & Hadincová 1992). This was remedied by taking only the more perennial phanerophyte, chamaephyte and liana species into account, and, moreover, by masking species present only once or twice. The remaining data matrix was subjected to Correspondence Analysis (CA) – with downweighting of rare species – using the CANOCO package (ter Braak 1988) and the graphical program CANODRAW (Smilauer 1993). CA was found an effective approach, which also served as a basis for the delimitation of clusters.

Finally, the clusters and relevés were arranged using the classical phytosociological procedure (Table 1). The resulting clusters were interpreted as syntaxa and given a formal name following Barkman et al. (1986). The biogeographical and bioclimatic terminology used follows Rivas-Martínez (1987).

## Results

Fig. 2 shows the species display along the first two axes of the CA ordination. *Quercus* species were made passive in the analysis for two reasons: (1) to avoid the taxonomical complexity of transitional populations between *Q. ilex* and *Q. rotundifolia* occurring in this area (Aseguinolaza et al. 1987), and (2) to eliminate the impact on the classification of maquis by the dominant species in the potential natural vegetation, i.e. vegetation series in the sense of Rivas-Martínez (1987) to which the maquis type would eventually develop. Even if these tree species are included in the community, we consider it more realistic to determine the floristic-ecological relationships between the relevés by only using the typical maquis species.

The first axis clearly separates acidophilous heathland species to the right from basophilous species to the left. Most of the heathland species are characteristic of the class *Calluno-Ulicetea*, with a Cantabro-Atlantic distribution. The basophilous species are mainly Mediterranean. Some indifferent or slightly basophilous species such as *Arbutus unedo*, *Crataegus monogyna* and *Hedera helix* are found to the right of the origin of the CA diagram, because of their higher cover on acidic soils, which can be partly attributed to the lower competitive power of other shrubs (cf. Mueller-Dombois & Ellenberg 1974; Austin 1990).

The basophilous species, which are concentrated to the left of axis 1, are widespread along axis 2, while the acidophilous species are found near the origin. Axis 2



reflects an oceanicity-continentiality gradient. In the lower left part of the diagram we find the Mediterranean xerophilous species *Dorycnium pentaphyllum* and *Teucrium chamaedrys*, and at the opposite end the oceanic *Laurus nobilis* and *Ulex europaeus*. In between them, two more groups can be distinguished, one of mesophytic forest-mantle species, such as *Cornus sanguinea* and *Ligustrum vulgare*, the other one including basophilous shrub species such as *Genista occidentalis*, *Lithodora diffusa*, *Tamus communis* and *Erica vagans*.

The position of the relevés along CA axis 1 (Fig. 3) shows the same distinction as revealed by the species position (Fig. 2), i.e. between base-poor soils to the right and base-rich soils to the left. Axis 2 separates the acidophilous relevés with heathland species on flysch at the positive side and those *Quercetea ilicis* and *Prunetalia* taxa on sandstone at the negative side.

The continentality-oceanicity gradient can be recognized (Fig. 3) by connecting the *Quercus coccifera* dominated stands, rare and very particular for the Cantabrian coastal fringe, with the coastal relevés dominated by *Laurus nobilis* and *Ulex europaeus*, which are from rocky calcareous substrates. The majority of the basophilous relevés are situated in between these two extremes and correspond to intermediate situations.

The pattern described can be further elucidated by showing the relative importance of four species groups (Fig. 4): (A) Mediterranean shrubs (*Quercetea ilicis*); (B) acidophilous heathland species (*Calluno-Ulicetea*); (C) basophilous Mediterranean shrubs (*Ononidetalia striatae*) + submediterranean basophilous shrubs (*Quercetalia pubescentis*); (D) other species (mainly *Prunetalia*). Species of group A occur most in the basophilous relevés, of group B mainly in the acidophilous ones. Group C has its optimum in the continental basophilous samples, especially in those dominated by *Quercus coccifera*.

#### Syntaxonomical discussion

Table 1 shows the arrangement of relevés, the acidophilous ones to the left and the basophilous ones to the right. The former relevés represent a less diversified community type which probably extends over a wide area in the Cantabrian region. The low representation of *Quercus ilex* in the acidophilous community type is explained by the fact that this community does not occur much in areas where this species constitutes the potential forest. Rivas-Martínez et al. (1988) proposed the name *Lauro nobilis-Arbutetum unedonis* for these acidophilous madroñales, but the name is not valid according to the Code of phytosociological nomenclature (Barkman et al. 1986). In the inner areas of Galicia with Mediterranean climatic conditions, a related association

*Erico scopariae-Arbutetum unedonis* was described (Ortiz et al. 1991), but this unit differs floristically from our silicicolous madroñales, due to both biogeographic and climatic factors; species such as *Daphne gnidium*, *Lavandula sampaiana*, *Cistus ladanifer*, *C. populifolius* and *Erica australis* ssp. *aragonensis*, are absent from the Basque community. Consequently, a new association should be distinguished for this oligotrophic *Arbutus* community, which we will call *Ulici gallii-Arbutetum unedonis* ass. nova (holotypus: relevé 10).

The basophilous maquis communities are more difficult to interpret due to their higher diversity. Those from the inner areas are characterized by the occurrence of *Viburnum tinus*, *V. lantana*, *Quercus faginea* and *Q. rotundifolia* (+ *Q. × gracilis*) as well as the high frequency of several Mediterranean shrubs such as *Dorycnium pentaphyllum*. The latter species also occurs in a few particular localities dominated by *Quercus coccifera*; relevés of these localities are included in this group as noted above. This situation is completely different from that of all other known *Quercus coccifera* maquis communities. In our opinion, a new particular xeric association can be distinguished, the *Genista occidentalis-Quercetum cocciferae* ass. nova (holotypus: relevé 49). Its distribution is very much restricted; it may well be a relic community.

The remainder of the relevés, located in the upper right quadrant of Fig. 3, represent more or less coastal communities characterized by *Laurus nobilis* and *Ulex europaeus*. They cannot be correlated with ecological (edaphic or climatic) factors other than a high oceanicity and a calcareous substrate. This situation resembles that described for the *Laurus* forests of Asturias and Cantabria (Bueno & Fernández Prieto 1991); the latter community has a different species composition where mesophyte species occur, but *Arbutus* and *Phillyrea latifolia* are lacking. They may be interpreted as remnants of ancient lauroid formations which once occurred widely along the Cantabrian coast. However, the present distribution and ecology of these species in the area is not strictly correlated with the above-mentioned factors (Aseguinolaza et al. 1984; Aizpuru et al. 1990). Nevertheless, the present-day *Laurus* populations, although many of them are of anthropogenic origin (gardening), could be interpreted as representatives of that old palaeo-mediterranean element.

The occurrence of *Pistacia lentiscus*, a well-known thermophilous Mediterranean species, occurring occasionally along the coast, is also remarkable. The relevés with this species do not form a group and it was not considered necessary to create a special syntaxon for this group; these relevés indicate a relic frost-free situation (cf. Aseguinolaza et al. 1984; Braun-Blanquet & Bolós 1958).

## Species present in one, two or three relevés:

**Rel. 2:** *Potentilla erecta* 1, *Quercus pyrenaica* 1, *Ilex aquifolium* 1, *Hypericum pulchrum* 1, *Euphorbia dulcis* 1, *Castanea sativa* pl. +, *Quercus x andegavensis* +, *Veronica officinalis* +. **Rel. 4:** *Agrostis curtisii* 1. **Rel. 5:** *Ilex aquifolium* 2, *Agrostis capillaris* +, *Potentilla erecta* +, *Quercus pyrenaica* +, *Rubus* sp. 2, *Sorbus torminalis* 1, *Brachypodium sylvaticum* 1, *Fagus sylvatica* +. **Rel. 6:** *Agrostis curtisii* 2, *Erica lusitanica* 1, *Primula vulgaris* +, *Euphorbia amygdaloides* +, *Hypericum pulchrum* +. **Rel. 9:** *Centaurea debeauxii* +, *Cirsium palustre* +, *Holcus mollis* 2, *Pseudarrhenatherum longifolium* +. **Rel. 10:** *Hypericum androsaemum* +, *Fragaria vesca* +. **Rel. 11:** *Agrostis capillaris* 1, *Potentilla montana* 1, *Euphorbia dulcis* 1, *Crataegus* pl. +, *Quercus robur* pl. +, *Serratula tinctoria* 1, *Viola gr. sylvatica* 1, *Pseudarrhenatherum longifolium* 1. **Rel. 12:** *Thapsia villosa* +, *Thymelaea ruizii* +, *Phillyrea angustifolia* 4. **Rel. 14:** *Erica scoparia* 1, *Hypericum pulchrum* 1, *Iris foetidissima* +, *Thapsia villosa* +. **Rel. 17:** *Ilex aquifolium* +. **Rel. 19:** *Prunus avium* +. **Rel. 20:** *Thymelaea ruizii* +, *Erica lusitanica* +, *Pseudarrhenatherum longifolium* +, *Thapsia villosa* +. **Rel. 21:** *Euphorbia amygdaloides* +. **Rel. 22:** *Pulmonaria longifolia* +. **Rel. 23:** *Potentilla montana* +, *Sesleria argentea* +. **Rel. 25:** *Carduus artemone* +, *Rosa micrantha* +, *Sorbus aria* +. **Rel. 28:** *Asphodelus albus* +. **Rel. 30:** *Pistacia terebinthus* +. **Rel. 31:** *Pistacia terebinthus* 1, *Erica lusitanica* +. **Rel. 32:** *Primula columnae* +, *Euphorbia amygdaloides* +. **Rel. 33:** *Helianthemum nummularium* +. **Rel. 36:** *Pistacia terebinthus* 1, *Helianthemum nummularium* 1, *Osyris alba* 1. **Rel. 37:** *Osyris alba* 2. **Rel. 40:** *Hepatica nobilis* 1, *Euphorbia dulcis* 1, *Prunus avium* +, *Rubus* sp. 1, *Vicia cracca* +, *Buglossoides purpuracaerulea* +, *Cirsium arvense* 1, *Echium vulgare* +, *Prunella vulgaris* 1, *Rosa squarrosa* 1. **Rel. 41:** *Hepatica nobilis* +, *Hypericum androsaemum* +, *Sorbus torminalis* 1, *Vicia cracca* +, *Clematis vitalba* +, *Helleborus occidentalis* +, *Melittis melissophyllum* +, *Seseli libanotis* +, *Corylus avellana* +. **Rel. 42:** *Seseli montanum* +, *Clinopodium vulgare* +, *Daphne laureola* +, *Rosa squarrosa* +. **Rel. 43:** *Carex flacca* 1, *Bromus erectus* +, *Dactylis hispanica* 1, *Festuca rubra* 1, *Filipendula vulgaris* +, *Medicago lupulina* +, *Trifolium pratense* +, *Rosa squarrosa* +. **Rel. 44:** *Corylus avellana* 2. **Rel. 45:** *Carex flacca* +, *Allium* sp. +, *Arum italicum* +, *Asplenium trichomanes* 1, *Geranium rotundifolium* +, *Lonicera etrusca* +, *Rosa nitidula* +, *Vicia nigra* +, *Viola gr. alba* +, *Vincetoxicum intermedium* 1. **Rel. 46:** *Fraxinus ornus* +, *Blackstonia perfoliata* +, *Dactylis*

*glomerata* 1, *Rosa corymbifera* +, *Vincetoxicum intermedium* +. **Rel. 47:** *Fraxinus ornus* +, *Seseli montanum* 1, *Rosa agrestis* +, *Viburnum* pl. 1, *Vicia incana* 1, *Vincetoxicum intermedium* 1. **Rel. 48:** *Argyrolobium canoni* +, *Fumana spachii* +, *Helianthemum apenninum* +, *Teucrium pyrenaicum* +, *Osyris alba* 3. **Rel. 49:** *Aphyllanthes monspeliensis* 1, *Asperula cynanchica* +, *Carlina corymbosa* 1, *Fumana ericoides* 1, *Helianthemum nummularium* +. **Rel. 50:** *Corylus avellana* +. **Rel. 51:** *Sesleria argentea* 1, *Amelanchier ovalis* 1, *Bupleurum rigidum* +, *Galium mollugo* +, *Sanguisorba minor* +.

## Localities:

1. Balmaseda, 30TVN8181(BI). 2. Hornes, 30TVN7377(BU). 3. From Urduliz to Berango, 30TWP0201(BI). 4. Muskiz, Montellano, 30TVN8993(BI). 5. Hornes, 30TVN7376(BU). 6. Sopuerta, Alén, 30TVN8490(BI). 7. From Lekeitio to Ondarroa, 30TVN4399(BI). 8. Cabo Machichaco, 30TWP2011(BI). 9. Ibarraquelua, 30TWP3003(BI). 10. From Lekeitio to Ondarroa, 30TVN4597(BI). 11. Abiega, 30TVN9275(VI). 12. Güeñes, 30TVN8290(BI). 13. Arminza, 30TWP0809(BI). 14. Arceniega, Ureta, 30TVN9175(VI). 15. Somorrostro, 30TVN9192(BI). 16. Galdames, Montellano, 30TVN8892(BI). 17 y 33. Bakio, 30TWP1709(BI). 18. Gorliz, 30TWP0607(BI). 19. Liendo, 30TWP6804(S). 20. Zaramillo, 30TVN9887(BI). 21. Mundaka, 30TWP2406(BI). 22. Axpe-Busturia, 30TWP2401(BI). 23. Voto, from Ogarrio to Matienzo, 30TVN5494(S). 24. Sopelana, 30TWP0104(BI). 25. Guriezo, Cayuso, 30TVP7203(S). 26. Kanala, near S. Pedro de Atxarre, 30TWP2605(BI). 27. From Butron to Laukiz, 30TWP0600(BI). 28 y 32. Islares, 30TVP7506(S). 29. Gorliz, 30TWP0407(BI). 30. Ibarraquelua, Laidá, 30TWP2505(BI). 31. Zaramillo, 30TVN9887(BI). 34. Izpazter, 30TWP3800(BI). 35. Gorliz, Elejalde, 30TWP0607(BI). 36. Santoña, Monte Buciero, 30TWP6409(S). 37. Somorrostro, 30TVN9198(BI). 38. Valle de Oma, 30TVN3198(BI). 39. Ayala, La Blanca, 30TVN9374(VI). 40. Rio de Mena (Merindad de Montija), 30TVN8276(BU). 41. Las Bárcenas de Bortedo, Montija, 30TVN8277(BU). 42 y 47. Retes de Tudela, 30TVN8674(VI). 43. Ungo, Valle de Mena, 30TVN7976(BU). 44 y 46. Retes de Tudela, 30TVN8673(VI). 45. La Presilla, Villasana de Mena, 30TVN7875(BU). 48 y 49. Monte Montaña, Abanto y Ciervana, 30TVN9297(BI). 50. Mercadillo (Valle de Mena), 30TVN7873(BU). 51. Peñas de Cantonad (Valle de Mena), 30TVN7069(BU).

As a result, all the basophylous relevés (except those with *Quercus coccifera*) should be assigned to one association: *Phillyreo latifoliae-Arbutetum unedonis* ass. nova (= *Lauro-Quercetum ilicis arbutetosum unedi* Velasco 1983). Two subassociations can be distinguished: (1) *typicum* = *arbutetosum unedonis*, common in the coastal madroñales, with local variants with (a) *Pistacia lentiscus* and (b) *Laurus nobilis*; (2) *viburnetosum tini* subass. nova (*holotypus*: relevé 46) in the inland xeric-continental madroñales.

Bueno & Fernández Prieto (1991) proposed a syntaxonomical position of these units together with similar maquis types from Asturias and western Cantabria in the *Lauro-Quercetum ilicis* forest. In our opinion this solution obscures their successional and structural nature as they are not real forests but shrublands substituting for the forest after destruction; there are also differences in the relative species composition and abundance. Rivas-Martínez (1975) included most of the shrub maquis vegetation of the *Quercetea ilicis* in his order *Pistacio-Rhamnetalia alaterni*; both floristically and structurally our communities can be easily included in this unit. In the preliminary survey of the *Quercetea ilicis* by Rivas-Martínez et al. (1988), *Arbutus unedo*, *Erica arborea*, *Laurus nobilis* and *Rosa sempervirens* are considered as characteristic taxa of the silicicolous

alliance *Ericion arboreae*. Our silicicolous association can also be included. However, it is more difficult to fit in the basophilous types. Their inclusion in the Iberic alliance *Rhamno-Quercion cocciferae* may be the best solution as it would reflect the ecological and floristical relationships between the basophilous Cantabrian madroñales and those of the inner part of the Iberian Peninsula (Ebro Valley). The syntaxonomical scheme we propose is:

*Quercetea ilicis* Br.-Bl. 1947

*Pistacio lentisci-Rhamnetalia alaterni* Rivas-M. 1975

*Ericion arboreae* (Rivas-Martínez ex Rivas-M., Izco & Costa 1982) Rivas-M. 1987

*Ulici gallii-Arbutetum unedonis* ass. nova

Nomenclatural type: rel. 10 (*holotypus*)

*Rhamno lycioidis-Quercion cocciferae* Rivas Goday ex Rivas-M. 1975

*Phillyreo latifoliae-Arbutetum unedonis*

(Velasco 1983) ass. nova

Nomenclatural type: Velasco (1983, Table 2, rel. 5 (*holotypus*))

*arbutetosum unedonis*

*viburnetosum tini* subass. nova

Nomenclatural type: rel. 46 (*holotypus*)

*Genisto occidentalis-Quercetum cocciferae*

ass. nova. Nomenclatural type: rel. 49 (*holotypus*).

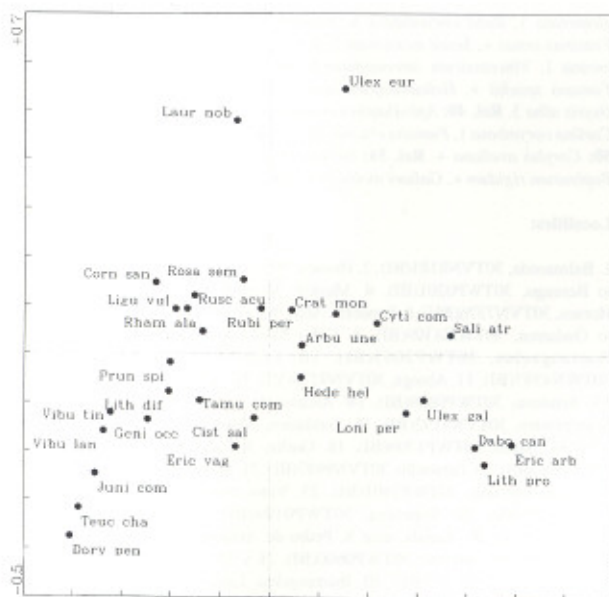


Fig. 2. Position of important species along the first two axes of the CA ordination. See Table 1 for full species names.

### Biogeographical comments

The arrangement of our maquis types revealed that their Mediterranean elements are more frequently found on calcareous than on siliceous soils. Maquis on base-poor soils has a larger share of Atlantic heathland species. This does not necessarily mean that there is a difference in humidity conditions between the types: in the Cantabrian-Atlantic province, heathland species are adapted to a slight and short drought during the summer drought, the driest season (Fillat 1983). This climatic feature increases westwards along the Cantabrian coastal fringe (Rivas-Martínez et al. 1984; Rivas-Martínez 1987) and becomes quite noteworthy in Galicia where the substrate is predominantly siliceous; however this moderate summer-drought is evident in the Basque stretch as well (Loidi & Herrera 1990).

In the basophilous community group an important fact was observed: the xerophilous Mediterranean species, which probably migrated from inland areas following the recent route through the upper Ebro Valley (Montserrat Martí & Montserrat Martí 1987), are more widely represented in the inland areas, but they do reach the coast. Among the Mediterranean species linked to calcareous substrata, two subgroups can be distinguished: a continental one represented by *Quercus rotundifolia*, and a thermophilous one with *Olea sylvestris*, *Pistacia lentiscus* and *Quercus coccifera* – Cantabrian populations of this species have lost contact with those of the Ebro Valley. The distributional pattern of *Q. ilex*, *Q. rotundifolia* and their frequent hybrids (*Q. x gracilis*)

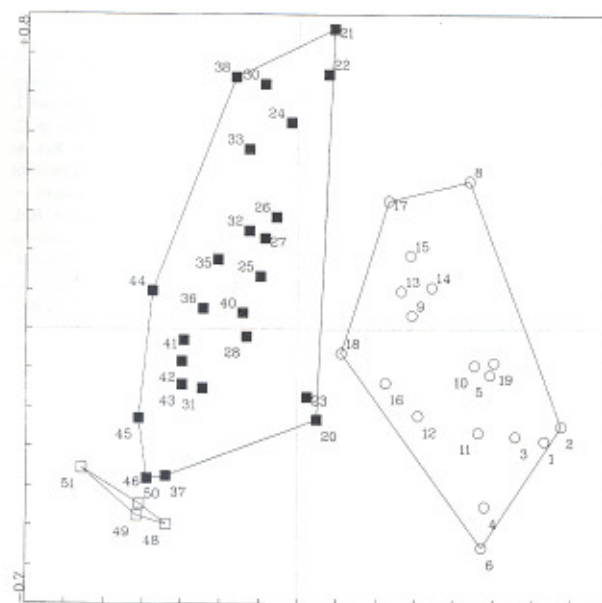


Fig. 3. Position of the relevés in the CA ordination. ○ *Ulici gallii-Arbutetum unedonis*; ■ *Phillyreo latifoliae-Arbutetum unedonis*; □ *Genisto occidentalis-Quercetum cocciferae*.

reflects this division as well. On the other hand, there is a small group of late-Mediterranean species (Mediterranean in a broad sense), adapted to a more oceanic climate, particularly *Laurus nobilis*. This species could have a much older origin, and may be related to the initial stages of the Mediterranean vegetation (palaeo-Mediterranean), which originate from the tertiary subtropical forests dominating the Madreo-Tethyan area when summer drought began to increase (Takhtajan 1981). Other taxa of scattered distribution requiring high humidity, e.g. *Prunus lusitanica* (Catalán 1987) and some ferns may also be related to this category.

### Conclusions

The study of apparently relic communities requires an approach different from the analysis of other vegetation types; both ecological and historical factors must be taken into account.

1. Maquis dominated by *Arbutus unedo* or *Quercus coccifera*, is an important Mediterranean vegetation type in the Cantabrian fringe. It is composed of at least three associations, one of them with two subassociations.
2. These maquis communities are substitution stages after fire or cutting of *Q. ilex* or *Q. robur* forests. Most of the basophilous maquis is related to *Q. ilex* forests (*Lauro-Quercetum ilicis*) and the acidophilous ones to *Q. robur* forests (*Hyperico pulchri-Quercetum roboris*).

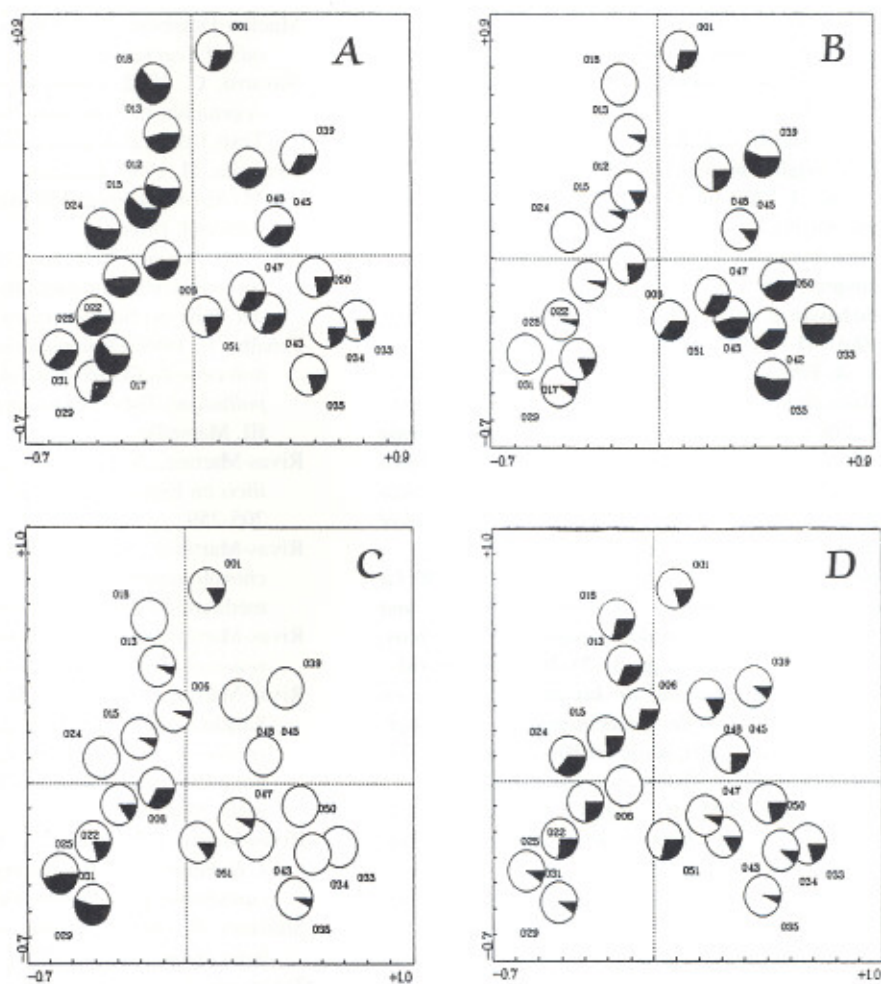


Fig. 4. Position of the relevés along the first two axes of the CA ordination, showing the participation (in numbers of species) of the groups A. *Quercetalia ilicis*; B. *Calluno-Ulicetalia*; C. *Ononidetalia striatae* + *Quercetalia pubescentis*; D. Others (mainly *Prunetalia*).

3. Mediterranean species diversity is much higher in calcareous communities than in siliceous ones. Most of the Mediterranean species seem to have arrived via the upper Ebro Basin, predominantly calcareous land which has acted as a source of basophilous taxa. Taxa generally considered indifferent (*Viburnum tinus*, *Phillyrea latifolia*) behave like strictly basophilous ones.

4. As a consequence, Mediterranean-Iberolevantine species are more frequent than Mediterranean-Iberoatlantic and Palaeomediterranean ones, especially on calcareous soils. Mediterranean silicolous (Iberoatlantic) taxa would have a West-East migration direction, originating from the western part of the Iberian Peninsula, not reaching the Basque region; the silicolous scrub (heath) flora is represented by the Atlantic element.

5. Phenomena of isolation, as in the case of the *Quercus coccifera* maquis, lead to characteristic communities of very limited range, but with a very peculiar species composition.

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