

PLANT DIVERSITY IN THE REGION OF THE STRAIT OF GIBRALTAR: A MULTILEVEL APPROACH

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Abstract

The Strait of Gibraltar is a high plant diversity area due to its particular history and ecological conditions which are very distinct from surrounding regions. This diversity is analyzed in a hierarchical manner, from the whole flora to communities and species. In a floristic context, the level of endemism and the characteristics of endemics are accounted, and the possible effect of the Strait as a biogeographical barrier for plants is explored. Woody plant communities have been studied in detail and the environmental correlates of floristic variation and several components of their diversity are comparatively quantified (North side vs South side of the Strait). In this context, a first account of differential recent historical changes on vegetation in both sides of the Strait is attempted through pollen analysis of sediments. Finally, accounting of diversity at species level has been done by selecting two gorse species (*Calicotome villosa*, *Genista linifolia*) and analyzing the structure and amount of genetic diversity (by means of isozyme loci) in their populations across the Strait. These species show clear differences which seem to be related to their particular life history characteristics, but irrespective of the presence of the Strait, which therefore does not seem to act as a barrier preventing gene flow between their populations at both sides.

Introduction

Some geographic areas have long promoted interest for naturalists, and botanists in particular, because they harbour a high plant diversity. One of these areas is the region of the Gibraltar Strait, which lies within the range of otherwise high-diversity area, the Western Mediterranean (WWF & IUCN, 1994.). Moreover, it represents a set of historical and ecological features which make it unique and permit search on the influence of this kind of factors in promoting plant diversity in a variety of ways. The Strait of Gibraltar includes the southern tip of W Europe and the northern part of W Africa. Here, the influence of historical and ecological factors is explored as complementary (but unclosed) parts of a research program on the account of plant diversity. Hence the influence of the separation of these two land masses, of the distinct soils and climate from surrounding areas, and of the different cultural landscapes (which mean different land use and resource management) in human historical times on the patterns of plant diversity found in this relatively small area are analysed. Our approach fits in part within the research agenda for biodiversity in its narrow sense, that is, in considering aspects beyond a mere taxonomic account (e.g., populations, see SOLBRIG, 1991), and when so, considering biodiversity to be further than merely species richness, as frequently occurs for simplicity, or due to lack of biological information or to uncritical routine accounting.

Geological and biogeographical background

The Strait of Gibraltar has some particularities which make it of enhanced biogeographical interest. It is located between the Eurasian and the African tectonic plates, which, due to continental drift, have suffered successive links and disruptions in their geological history. The last link occurred at late Tertiary, during the well-known Messinian period and was coincident with an extremely dry climate (DIDON & al. 1973, HSÜ & al. 1977). Thereafter, the Strait remained open until present situation. Most former links and disruptions are much older and their influence on the making up of the present flora of the region is not precise (and perhaps not important) at species level. More interestingly, the present width (14 km) and the submarine geomorphology during the Pleistocene pose additional questions. It is known that during maximum glacial periods sea level lowered between 100 to 200 m below present level. This made an interesting pattern of a much reduced width of the Strait and even including stepping islands. The obvious biogeographical implication is that the Strait, which sometimes might be acting as a barrier, may have also served as a bridge for plant migrations in some periods, which in addition were colder (Ice Ages) and promoted migrations from north to south (e.g., QUÉZEL, 1978), although migrations from south to north in warmer periods cannot be ruled out, despite the Strait being wider.

Environmental particularities

Present-day ecological conditions, in addition to historical constraints (climatic and geological changes depicted above), are very particular and also play a role in the high plant diversity found in the area.

Soils.- One of the most influential characteristics of the region is the predominance of acid soils. They are derived from Oligo-Miocene sandstone, which is very typical of the region of the Strait of Gibraltar. Most of these soils show pH values between 4 and 5, are very poor in nutrients and present high levels of assimilable aluminium and other metals, toxic for most of plants (CSIC-IARA, 1989; OJEDA, 1995). These features determine an important environmental stress which has been proposed as one of the most important cues for speciation and differentiation of plants (e.g., KRUCKEBERG, 1986). On the other hand this kind of soils is rather infrequent around the Mediterranean, where basic soils are dominant. In the Western Mediterranean, sandstone formations of the Strait of Gibraltar form an environmental, edaphic island, surrounded by Eocene marl and limestone, that is, basic soils (cf., DIDON & al., 1973). Moreover, this geological formation is subdivided in two ways: first by the Strait, hence determining two parts similar in size (about 2200 km² in northern part and about 1800 km² in southern part), and second, there is a different pattern of isolation on the two sides, the northern part forming mostly one large island whereas the south part is subdivided again in 17 small islands, rather fitting an "archipelago" model (see OJEDA & al. 1996a for further details).

Climate.- The climate of the region, according to standard bioclimatic diagrams, is typically Mediterranean (RIVAS-MARTÍNEZ, 1987; ASENSI MARFIL & DÍEZ GARRETAS,

1987; OJEDA, 1995, and references therein). Nevertheless, the geographic location and the relief determine some particularities. First, the area has a strong maritime character and in fact it receives most of the western Atlantic rain fronts in autumn-winter period. Therefore the rainfall ranges from 600 to 1700 mm, although locally in highest places may reach 2200 mm. The oceanic influence also determines that temperatures do not reach extreme values. Second, more than forty percent of winds comes from the East, they are usually very strong, and more interestingly, they are much more common in summer. The consequence is that although they do not provoke rains, the presence of low clouds and very dense fogs is very common in coastal areas, hence the summer drought is strongly reduced, although these data do not appear in the usual bioclimatic diagrams (see SAUVAGE, 1961; BENABID, 1982; IBARRA, 1993; OJEDA, 1995, for additional details).

Land use.- The ecology of resource management has been studied in detail in both North (IBARRA, 1993) and South (DEIL, 1990, 1993) parts of the Strait. In a comparative context, it may be stated that current land use fits strongly different models in both parts. Rural population is twice in density in N Africa compared to S Spain (DEIL, 1990), and modes and intensity of natural resource management are also different, in Morocco being predominant a more intense slashing for fuel and overgrazing of woody vegetation (OJEDA & al., 1996a), whereas in S Spain cork oak silviculture and extensive live stock are prevailing.

The consequence of these stressing and isolating, and somewhat temperate environments, should be a rich and differentiated flora, with many endemics. We should also find many temperate taxa and vegetation types which do not correspond closely to the paradigmatic maquis and garrigue, which are widespread along the Mediterranean. On the other hand, although a strong floristic link is suggested to exist between S Spain and N Morocco (VALDÉS, 1991), this resemblance has not been comprehensively analysed in a species by species way, nor has it been followed at other levels, i.e., plant communities and populations, which are probably more sensitive to ecological factors, especially those acting in the short term (e.g., human disturbance) which may have not caused plant extinction but rather changes in community composition or population fragmentation, processes which are prior to extinction. Here, comparisons across the Strait are attempted at flora, community and species (populations) levels. Additinally, a first account on the recent historical past is aimed at.

Level of flora

Floristic diversity

The uniqueness of the flora is apparent when examining standard floras of the region. For this purpose the *Flora Vasculare de Andalucía Occidental* (VALDÉS & al., 1987) and the *Catalogue des Plantes du Maroc* (JAHANDIEZ & MAIRE, 1931-1934) were used, considering only species present in the closest areas to the Strait of Gibraltar

(Algeciras and Tanger areas as depicted in these floras), being subjected to the ecological and historical factors commented before. The spermatophyte flora of the region includes about 1700 species in an area of about 7000 km². Nevertheless, this figure may represent an underestimate, given the current lack of a comprehensive knowledge of the Moroccan flora, which is presently being studied in detail in its northern part -Rif- (B.Valdés, pers. com.). We see the richness of the Gibraltarian flora when comparing this four-figure number with that of the whole flora of W Andalusia, which is well-known and includes about 2400 species over 45000 km². Others authors have reported the high richness and singularity of this region with regard to bryophyte (ACÓN & MORLA, 1993) and pteridophyte (DÍEZ & SALVO, 1981; SALVO, 1994) floras.

Biogeographic diversity

In addition to species diversity, the area presents a high biogeographic diversity, and it is worth stressing the high percentage of endemic taxa: 5.3% of species present only in the territory under consideration (Algeciras and Tanger) and 12.1% present in the Iberian peninsula and/or the Mediterranean part of Northwestern Africa. This makes 17.4% of endemics, which is a comparable figure to those obtained in most high mountain areas throughout the Mediterranean, where geographic isolation has been considered the strongest driving force for endemism (FAVARGER, 1972). Here, we can see that in some cases ecological isolation (mostly through acid soils, and in lesser extent through temperate climate) may be of similar importance at the level of flora, given the lack of strong elevational differences. The elevation range is 0-1650 m in the Moroccan part and 0-1092 m in the Spanish part, and the orographic isolation of these mountains is scarce.

Going further in the analysis of endemics, we were interested in their distribution among different life forms. In order to analyze it, we selected a small area within the Algeciras region (N part of the Strait) whose flora is particularly well known and the habitats include almost exclusively sandstone and temperate areas (GIL & al., 1985), hence it represents a paradigm for the factors supposed to promote differentiation of plants in the area. When comparing life-form distribution of the endemic flora with that of the whole flora of this small area, the strong association between endemism and shrubs is apparent (Table 1). There is an over-representation of shrub species and an under-representation of annual and biennial species within the endemic flora. Although there is some phylogenetic effect due to the presence of many gorse species (Genisteae) (e.g., *Genista tridentata*, *G. triacanthos*, *G. tridens*, *Cytisus baeticus*, *C. striatus*, *C. tribracteolatus*, *Stauracanthuis boivinii*), some actual pattern should underlie, since these endemic shrubs also include species in 12 families (e.g., Thymeleaceae, Cistaceae, Umbelliferae, Ericaceae, Boraginaceae, Labiatae among the most represented). This is particularly interesting since most experimental studies on differentiation and adaptation to stressing edaphic conditions have shown these processes in annual or herbaceous perennial plants (ANTONOVICS & al., 1971; BRADSHAW & MCNEILLY, 1981). However, this may rather reflect the feasibility of these non-woody plants for experimental work.

	Endemics (%)		Whole flora (%)
	Iberian	Ibero-North African	
Annual and biennial	28.3	4.1	45.2
Herbaceous perennial	44.8	48.3	43.5
Shrub	26.9	20.7	9.7
Tree	0.0	6.9	1.6

Table 1. Life-form distribution of endemics (Iberian and Ibero-North African) and of the whole flora of Algeciras mountains (northern side of the Strait of Gibraltar).

In a comparative manner, it would be desirable to have life-form spectra of endemics in other areas where differentiation is presumably driven by different factors (such as elevation).

Biogeographical barriers

It was formerly stated that in addition to ecological factors (stressing soil conditions) a two-way geographic isolation can be acting in the differentiation of the flora of the region: isolation of sandstone patches, mostly in Morocco, and isolation imposed by the Strait of Gibraltar which might split the species. Whereas at present it is not possible to check the archipelago effect of the sandstone fragmentation due to lack of suitable floristic data on the fragments, it is possible to test whether the Strait represents a biogeographical limit and to examine some biological correlates in the flora of the region by using the floristic and biological information included in the mentioned floras (JAHANDIEZ & MAIRE, 1931-1934; VALDÉS & al., 1987). Despite the fact that northern Moroccan flora is worse known than that of W Andalusia (S Spain), we believe that the available checklist may represent an unbiased large sample which can be used to make comparisons at a general (floristic) level. We compared the frequency of some biological features of species present in only one side and in both sides of the Strait. The array of features examined was both wide and limited as the information in usual floras. Another shortcoming of the method is that we considered species as independent data points, without including information on their phylogenetic relationships which may modify the patterns (i.e., phylogenetic correction). This has recently been subjected to considerable debate (e.g., RICKLEFS, 1996, and references therein), and although there are some surrogates which can be used when phylogenies of the species are not available (which is this study case), we prefer to make first a classic, non-phylogenetic account, without denying the future prospects which can be achieved given the rapid development of phylogenetic methods or the use of selected available species groups with robust phylogenies. Therefore, most relevant results concern the relationship of life-form, dispersal type and a rough account of ecological requirements of plants with the presence of species across the Strait.

Life-form has a strongly uneven distribution across the Strait: there is an over-representation of annual plants in both-side class of species in comparison with one-side class. The remaining life-forms (biennial, perennial herbs, shrubs, trees, aquatic plants, climbers) are equally represented. The simplest cause we can suggest is that annual taxa have lesser requirements for their establishment given their short life cycle. Nevertheless, there could be other alternative explanations, such as some breeding systems prevailing in annual plants and precluding isolation and differentiation, or some allometric relationship between plant size and diaspore size which could determine annual plants having smaller seeds, hence crossing the Strait would be easier.

Information on dispersal type is far from accurate in standard floras since we have to make assumptions based on morphology of supposed diaspores (that is, syndromes) and this has proved to be of limited use. However, when very distinct morphofunctional types are considered some insights may be fruitful. Hence, anemochory, endozochory and mostly epizoochory are over-represented among both-side species, in the last dispersal type both-side species being twice that of one-side species. Species without any differentiated dispersal syndrome are equally represented in both classes (one-side, both-side). The implication is that dispersal types which are supposed to be efficient in long-distance dispersal are more frequently found in both sides of the Strait. Hence it does not seem to be a barrier for them and supports the idea that a number of species have reached their ranges through relative long-distance dispersal.

Information on ecological requirements of species is rarely found in standard floras in a detailed manner. Thus, information should be obtained through specific studies. However, we have carried out a very preliminary account making species rarity (a measure routinely included in floras) a surrogate of ecological specificity. Despite the bias it may involve (lack of correlation between ecological and geographical rarities), it became very clear that rare species are much more frequently found among one-side species in comparison with both-side species, which tend to be frequent and very frequent. Nevertheless, this account needs to be more specifically tested (i.e., with regards to particular ecological factors).

Level of plant community

Analysis based on floristics of the region is interesting in the account of long standing historical and evolutionary factors influencing plant diversity. When it is aimed to add also present day ecological factors it is practical to focus on plant community diversity, where these factors determine consequences even at short time scale (e.g., through disturbances), whereas the flora remains mostly unchanged (plants are increasingly threatened but only a few become extinct). Therefore we carried out a detailed study of the woody plant communities in the region (since woody species seemed to be more characteristic of this region; see above). This was carried out by selecting 31 plots in S Spain and 32 plots in N Morocco, and by determining the species composition of these plots and their environmental correlates and patterns of biodiversity (OJEDA, 1995). A direct gradient analysis (DCCA, TER BRAAK, 1991) showed that most variation among plots is explained by a multivariate axis correlated

with soil acidity and disturbance (OJEDA, 1995; OJEDA & al., 1995, 1996a). A preliminary cluster analysis classified plots in six community types: *Q. canariensis* woodlands, open heathlands on ridges, *Quercus suber* woodlands with *Erica arborea* understorey, *Q. suber* woodlands with *E. scoparia* understorey, *Q. coccifera* shrublands and barren heathlands (see details in OJEDA, 1995, and OJEDA & al., 1996a). The presence and abundance of these types are different in S Spain, where *Q. suber-E. scoparia* woodlands are dominant and *Q. canariensis* woodlands are exclusive, and N Morocco, where *Q. suber-E. arborea* are best represented and barren heathlands are exclusive. It should be noted that some apparent community types (e.g., river forest, chasmophyte communities) were not included in the study, given their more or less azonal or extrazonal character. The quantitative analysis of the relationship between community types and environmental characteristics provided a sound basis for ascertaining the patterns of biodiversity at community level.

Biodiversity is a complex issue which frequently is equated to species richness at several geographical scales, from large regions to communities (e.g., the well-known 0.1 ha species diversity: WESTMAN, 1988). Sometimes ecological diversity, which includes species abundances is also taken into account, although it is frequently correlated with species richness, as occurs with the studied communities (ARROYO & MARAÑÓN, 1990; OJEDA & al., 1996a). Only recently other components of diversity have been taken into account which consider intrinsic values of species according to their phylogenetic relationships (MAY, 1990) or their role in communities (RICKLEFS, 1987). This approach fits a restrictive concept of biodiversity and has been only rarely aimed, although it is increasingly studied at the level of flora (and fauna) and of complete taxonomic groups over large areas. In particular, we have considered three components of biodiversity applied to community level: 1) species richness, 2) chorological diversity, measured through geographically rare plants, that is, endemics, and 3) taxonomic diversity, measured through singularity. We made a rough estimate of singularity as a function of species number within each genus (see ARROYO & MARAÑÓN, 1990; OJEDA, 1995; OJEDA & al., 1995, 1996a for details on the methods). Therefore we correlated each one of the biodiversity components with DCCA multivariate axis 1, accounting for most of the floristic and environmental gradients. All the components showed significant correlations, fitting either a curvilinear unimodal (species richness) or a linear (chorological diversity, taxonomic diversity) regression model. It is worth noting that: 1, community samples in the middle of the soil favourableness and disturbance gradient showed the highest species richness, whereas samples in the most favourable conditions showed, 2, the lowest endemism and 3, the highest taxonomic singularity (just the opposite was found in the poorest, acid stressing soils, as was suggested above for endemism in the whole flora) (see OJEDA & al., 1995). When Moroccan samples were compared with those in the Spanish part it was found that for all the three components of biodiversity considered the Moroccan regression lines are below the Spanish lines, that is, Moroccan woody communities are less biodiverse than Spanish communities (OJEDA & al., 1996a). There is just one example which illustrates well this loss of biodiversity in Morocco: heath species (*Erica* and *Calluna*), which are very characteristic of the region (OJEDA & al., 1996b); although both sides of the Strait present a similar heath species list, at community level Moroccan

heathlands are overdominated by *Erica arborea*, whereas in S Spain there is a replacement of species throughout the environmental gradient: *E. arborea*, *E. scoparia*, *C. vulgaris*, *E. umbellata* and *E. australis*, from more mesic, richer sites to more stressing conditions (OJEDA, 1995).

We have suggested two possible, non-exclusive explanations for this loss of biodiversity in Morocco which are currently under testing. The first is natural and due to the fragmented spatial pattern of sandstone in N Morocco, which could lead to local extinction of some populations closely associated to acid soils (edaphic endemics). The second is the much stronger and disturbing land use by the much denser rural human population in N Morocco (see above). Some preliminary data suggest a role of this second, human disturbance factor. At present, fossil pollen is being recorded and studied in peat-like deposits of S Spain (RODRÍGUEZ & al., 1996) that can be compared with the detailed study by REILLE (1977) on the Moroccan counterpart. Despite there are obvious problems in comparing pollen data from different studies that arise mainly from different techniques and controversial identification of some pollen types, there is an important difference between the two sides of the Strait with strong ecological implications. There is an almost constant presence and dominance of *Erica arborea* pollen throughout the Moroccan samples, in sharp contrast with the shared dominance by *E. australis*, *E. arborea*, and especially, *E. scoparia* in S Spanish sample. The Spanish sample has been radiocarbon dated in the deepest pollen analysed part as 1200 ± 70 BP. REILLE (1977) observed in his Moroccan samples a decrease of oaks (natural forests) and an increase of *Olea europea* pollen (coincident with a remarkable expansion of olive cultivation as found in historical records) corresponding to a similar date. This would imply that low diversity Moroccan heathlands has been long established in historical times and probably expanded with arab invasions during that time (see also MIKESELL, 1960). Additionally, pollen of Cistaceae (many of the species being typical to disturbed places) are also more frequent throughout the Moroccan samples. Nevertheless, more samples need to be analysed in S Spain to ascertain these patterns.

Level of species

In a hierarchical manner, the following step in examining biodiversity should be undertaken at species level (see SOLBRIG, 1991). This can be done in a variety of ways and sublevels but it is better accomplished by examining populations and selecting characters with a sound ecological (e.g., soil preferences) or evolutionary and historical (e.g., genetic markers) implications. Therefore the analysis of diversities of this kind in key species allow inferences about the processes involved in the whole flora. These kind of data is necessarily restricted to a few species since they are much resource- and time-consuming. Whereas assessing niche diversity of particular species requires exhaustive identification and experiments of ecological preferences of many populations and frequently differences are very small, there is a number of tools for rapid assessment of the amount and structure of genetic diversity within species, which is one of the targets of research agendas on biodiversity (e.g., SOLBRIG, 1991). Although

the use of molecular markers is particularly powerful and increasingly widespread, the use of isozyme loci is still appropriate, due to their relative low cost and rapid screening for many loci (BROWN, 1990).

We have started to study genetic diversity in a couple of gorse species (*Calicotome villosa*: Hidalgo & al., unpublished data; *Genista linifolia*: Hidalgo & Arroyo, unpublished data) which are very characteristic of the woody communities in the region of the Strait of Gibraltar (OJEDA, 1995). Five and ten polymorphic loci were screened in *C. villosa* (nine Moroccan and 15 Spanish populations) and *G. linifolia* (seven Moroccan and 12 Spanish populations) respectively, and common statistics for genetic diversity and population genetic structure (e.g., BARRETT & SHORE, 1989) were estimated. In short, parameters for estimating the genetic diversity show some differences between both species and both locations (North and South of the Strait). *Calicotome villosa* shows a higher total genetic diversity (H_t), which is similar in Spain (0.290) and Morocco (0.308), than *G. linifolia*, which presents an even more reduced diversity in Spain (0.167) in comparison with Morocco (0.220). Since genetic diversity within populations (H_s) is similar in Spanish (0.164) and Moroccan (0.141) populations of *G. linifolia*, most of its higher diversity in Morocco is due to the high proportion of total genetic diversity due to population differentiation (G_{st}) in Morocco (0.176 vs. 0.098 in Spain). *Genista linifolia* is quite uncommon at present in N Morocco, where it shows rather small and isolated populations, in comparison with its widespread occurrence in S Spain. Despite such fragmentation, the genetic diversity within *G. linifolia* populations remains high in Morocco when compared with large Spanish populations. This may be related with its proximity to the Canarian centre of diversity of the genus (GIBBS & DINGWALL, 1971). In contrast, *C. villosa* shows an extremely similar pattern at both sides of the Strait, which may be due to its origin in the study area being unaffected by the splitting of the Strait (cf. distribution map in GIBBS, 1968) and also to frequent migration (mostly by its very numerous seeds) as suggested by its widespread occurrence in disturbed places, even on roadsides.

When Nei's genetic distance between all pairs of populations of each species was estimated and UPGMA clustered, some spatial arrangement of populations occurred, but irrespective of their location in N or S side of the Strait. Therefore the Strait of Gibraltar does not seem to act as an effective barrier preventing gene flow for these two species. Nevertheless, other key species with contrasting life histories (e.g., annuals, trees, long-distance dispersed vs undifferentiated diaspore species) need to be studied to ascertain to what extent this pattern is found. In fact, the possible effect of life history on the role of the Strait as a barrier was pointed out above when considering the whole flora of the region.

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