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The Strait of Gibraltar as a melting pot for plant biodiversity

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ABSTRACT

The S Iberian Peninsula and NW Africa constitute one of the main hotspots for plant biodiversity within the Mediterranean Basin. At the core of this hotspot, across the Strait of Gibraltar, lies a smaller region whose singular Cenozoic history and ecological features have created a distinct, nested sub-hotspot. In particular, an important relict flora, a high endemism, and the dominance of vegetation types other than the paradigmatic Mediterranean-type sclerophyllous forests and shrublands, are biogeographical features of paramount relevance. These singular environments may have provided suitable mesic habitats for stable human populations in this region throughout the Quaternary. Here we explore the possible causes of the unique biodiversity of this region. First, we show that endemism is associated with poor soils and mild Mediterranean climate, whereas relictness is primarily associated with riparian and humid habitats which might have remained relatively stable since the Late Tertiary. We then review and provide new results on lineage and molecular diversity of some taxa based on their evolutionary relationships inferred from phylogenetic and phylogeographical analyses. These indicate that long-lived plants, such as trees, tend to show some discontinuity in effective gene flow, in comparison with short-lived and pioneer plants. Colonization abilities rather than dispersal vectors appear to be a crucial factor. We also analyze the role of microevolutionary processes that generate plant biodiversity in terms of reproductive features involved in lineage formation, such as breeding system, pollination biology and postdispersal regeneration. The few available studies show that this region is prone to changes in reproductive systems, associated with both abiotic and biotic conditions in the new habitats that plants face during colonization. Dispersal and regeneration ecology is especially important for relict species, as most of these species face some biotic (e.g., lack of dispersers, predation) and abiotic (edaphic and/or microclimate requirements) limitations to their recruitment. Nevertheless current limitations in the recruitment of relict plant species should not obscure the fact that they have been resilient in the face of Plio–Pleistocene climate changes in the Gibraltar region, whereas they became extinct in other Mediterranean areas. The relatively stable and mild climate of this region may have provided a suitable long-term environment for many other organisms, including humans.

1. Introduction

Biodiversity, or biological diversity, is one of the hottest topics in the environmental sciences, partly due to its diffusion in the popular literature. Although biodiversity is commonly used as shorthand for species richness and relative species abundance in taxonomical or ecological accounts (Hubbell, 2001), this concept has more complex dimensions, and its definition, measure, and analysis have become a grand new challenge in research agendas. Despite the "diversity" of definitions of biodiversity, most of them agree that it includes (1) all levels of biological organization, from genes to ecosystems, and (2) ecological relationships between organisms and species, as well as evolutionary relationships between lineages (Gaston, 1996). The geographical variability of the diversity of life has long been recognized, and recently general hypotheses for its explanation have been launched (Hubbell, 2001). In addition, because of historical contingencies it is usually considered that an explanation of biodiversity is strongly dependent on the knowledge of present and past environmental scenarios and evolutionary relationships between lineages. Geography and evolutionary history are thus deeply implicated in any biodiversity analysis.

Biogeography is a field where spatial and biological organization levels profoundly affect the observed patterns. The biogeographical literature has traditionally been devoted to descriptive accounts of similarities and differences between biotas, and to the many

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available classifications of territories at different scales (reviewed in Takhtajan, 1986 for plants). However, the analysis of underlying processes has remained relatively elusive due to the inherent limitations of past approaches. Reconstructions of organism, evolution have primarily rested on palaeobotanical data (e.g., Carrión et al., 2008), whilst inferences based on evolutionary relationships and ecological features of taxa of particular biogeographical interest have been built up only in recent decades (Arbogast and Kenagy, 2001). Because of the dynamic nature of the geographical range of species and lineages, some geographical areas constitute appropriate natural laboratories for analyzing causes of biogeographical singularities (e.g., high diversity and/or endemism, disparate species ranges, or taxonomic distinctness) due to their particular geological, historical and/or geographical features. Among these areas, islands, plate boundaries, or mountain chains are favourites among biogeographers since they limit historical movements of species, thus facilitating the interpretation of patterns. Areas intermittently connecting land masses, such as isthmuses and straits, are of outstanding relevance since they permit or hinder migration processes, especially those of sessile organisms like plants (e.g., Brubaker et al., 2005, for Beringia). In fact, land connections encouraged the formulation of one of the most remarkable confrontations of paradigms in biogeography, that is, land-bridge theory (van Steenis, 1962) versus the role of continental drift in creating biogeographical similarities at a world-wide scale (Raven and Axelrod, 1974). Once the second theory was firmly established and supported by evidence of plate tectonics, new issues arose to determine the relative role of dispersal and vicariance of lineages between continental plates (e.g., Posadas et al., 2006). In any case, land-bridge effects are still satisfactory explanations for biogeographical patterns of some biotas and taxa in areas where continental drift and sea level changes have brought land masses closer (e.g., Beringia, SW Europe and N Africa, N and S America, Wallacea –SE Asia and NW Australasia-; Lister, 2004; Milne, 2006).

The Strait of Gibraltar (SG hereafter), which has separated the African and the Iberian plates since the Pliocene, is one such area (Fig. 1). It is formed by two small peninsulas facing each other, and includes some additional environmental features which further enhance its biogeographical significance. Its somewhat mild climate throughout the Quaternary, and its geological and edaphic singularity have determined its character as an ecological and historical island (refugium). This area is nested within a well-known Mediterranean hotspot of plant biodiversity, which has been based mostly on descriptive species-counting (Arroyo, 1997; Médail and Quézel, 1997).

In this paper we review the patterns that shape the SG as a unique hotspot of plant biodiversity and explore the processes underlying these patterns. Bryophytes and pteridophytes have not been considered in this review, despite their high potential biogeographical value in this region (Vogel et al., 1999; Shaw et al., 2003), because the available information for these plant groups in the region is scarce. Throughout this paper we follow the nomenclature of taxa as included in standard floras of the region (Castroviejo et al., 1986–2003; Valdés et al., 1987, 2002).

We have taken a broad approach to the use of the term 'biodiversity', including several of the possible biodiversity levels where data are already available. We first illustrate the environmental conditions and their dynamic nature in historical times in order to set the physical context for the development of plant biodiversity. We then describe the level of present floristic and vegetation singularity, and explore the historical changes that help to explain it. Palaeobotanical evidence and reconstructions of evolutionary relationships between key taxa and populations in a geographical context serve to provide the basis for inferring historical movements of lineages. Finally, we analyze several aspects of the reproductive ecology of particular taxa, which contribute to the processes involved in the origin and maintenance of biodiversity, and explore, on purely ecological grounds, how forthcoming climate changes may affect the future of some of these critical species. Such biological and environmental richness might have a cascade effect for other organisms and has probably been a favourable factor in sustaining human populations during the Pleistocene (Finlayson et al., 2006; Carrión et al., 2008).

2. The changing history of the physical setting: geology and climate of the Strait of Gibraltar region

The geological evolution of the Mediterranean region is, to a great extent, determined by the northward movement of the

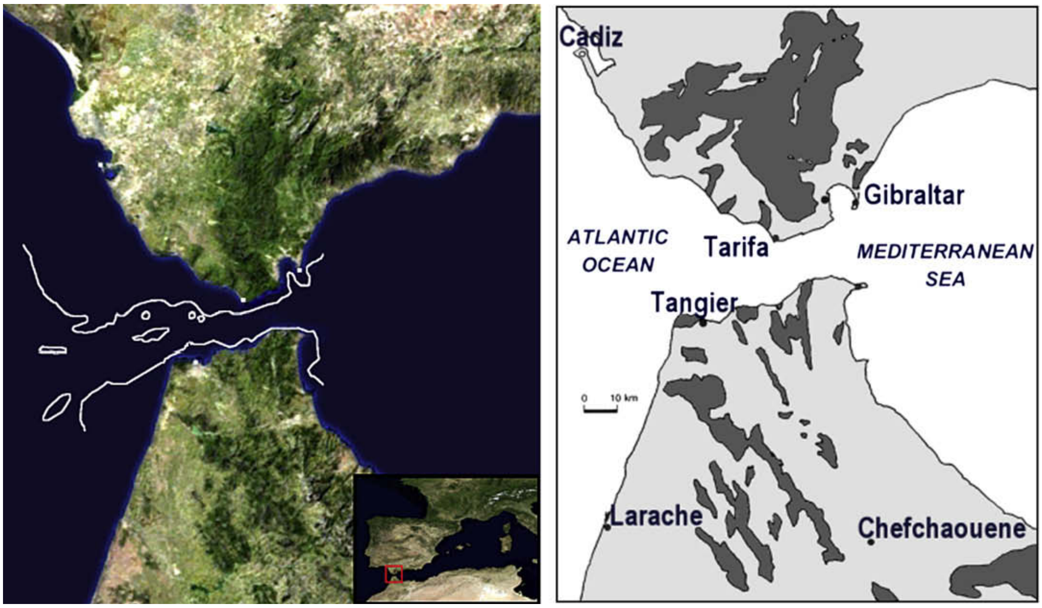

Fig. 1. Satellite image of the Strait of Gibraltar (SG) region (source: NASA's Earth Observatory); lines represent emerged land during the Last Glacial maximum (21–19 ka) as in Collina-Girard (2001). Right: map of sandstone patches (dark grey) in the SG region after Ojeda et al., 1996a.

African plate and, ultimately, its collision with the Iberian plate during the Tertiary (Rosenbaum et al., 2002). During the middle Miocene (15 Ma), the eastern end of the Mediterranean Sea (then the Tethys Sea) became separated from the Indian Ocean by the collision of the Arabian plate with the Eurasian plate (Krijgsman, 2002). In the late Miocene (ca. 6.5 Ma), the western end of the Mediterranean Sea was closed to the Atlantic Ocean by the collision of the African plate with the Iberian microplate and subsequent isostatic uplift (Duggen et al., 2003), and the Mediterranean became a closed basin. The sea level dropped markedly through evaporation, a geological phenomenon known as the Messinian Salinity Crisis (Hsü, 1972). Although the climate in the basin became increasingly arid (Hsü, 1973; but see Thompson, 2005), its western end probably remained somewhat buffered from such sharp climate change owing to the influence of the Atlantic Ocean. This episode of land-bridge connection allowed colonization and exchange of species between Iberia and N Africa (Veith et al., 2004; Agustí et al., 2006) enhancing its biogeographical significance. At the beginning of the Pliocene (5.3 Ma), the Mediterranean Sea opened again its western end to the Atlantic Ocean with the formation of the Strait of Gibraltar (Hsü et al., 1977; Krijgsman, 2002).

The climate of the Mediterranean Basin in the Early to Middle Pliocene (5–3 Ma) was warmer and more humid than the present climate (Haywood et al., 2000). Soon after this period, the SG witnessed the rise of the seasonal rainfall pattern that characterizes the Mediterranean climate (Suc, 1984).

Pleistocene glaciations (1.8 Ma to 10 ka) would not have significantly affected the southwestern end of the Mediterranean Basin, due to its latitude and the influence of the Atlantic Ocean and the Mediterranean Sea. In fact, SW Iberia constituted one of the main glacial refugia for the European fauna and flora (Hewitt, 2000). One of the critical consequences of the Ice Ages, beyond climate change, is that they determined the existence of periodic concomitant changes in sea level, due to the increasing extension of the ice sheets during the glacial maxima and the ice melting during Interglacials. In the Last Glacial, relative sea level dropped more than 100 m below its present level in some areas (Lambeck and Chappell, 2001). Due to the proximity of the Iberian and African plates and the rugged submarine topography, this decrease in sea level should have had important effects on the SG, since some small islands and islets emerged (Collina-Girard, 2001, but see Gracia et al., 2008, Fig. 1), enhancing the connection between both plates as stepping stones.

Most climate reconstructions for the region during the late Pleistocene and Holocene rest on palaeobotanical information, which – albeit fragmentary – also highlights important but previously neglected factors, such as anthropogenic impact of fires and herding (Arroyo et al., 2004, for Iberia and Reille, 1977, for northern Morocco). Diverse palynological and lake-level data indicate that the Mediterranean climate developed rapidly at the beginning of the Holocene (Cheddadi et al., 1998; Jalut et al., 2000). Several aridification pulses occurred throughout the Holocene, with a marked humid period around 6 ka (Reed et al., 2001).

The present climate of the SG region, although Mediterranean, shows a strong oceanic influence with mean annual temperature ranging from 14.6 °C to 19.0 °C and mean annual rainfall from 494 mm to 2169 mm (Ajbilou et al., 2006; Mejías et al., 2007). Although rainfall is scarce in summer, frequent, strong winds produce dense, low clouds and mist on coastal mountains close to the SG, which help to mitigate the effects of summer drought on the vegetation. This drought alleviation is more relevant in particular microhabitats such as gorges and deep valleys where streams usually flow year-round. In these habitats, microclimatic conditions are in marked contrast to Mediterranean areas surrounding SG and even to milder habitats occupied by oak forests (Fig. 2). These habitats could resemble the prevalent climatic conditions in wider areas during former, milder periods.

The SG region has a rough topography, mainly composed of Oligo–Miocene siliceous sandstone, which gives rise to acid, nutrient-poor, sandy soil patches on both sides of the SG (Fig. 1). These sandstone soils are also characterized by a high content of soluble aluminium, a toxic element to plants, mainly on mountain summits and ridges (Ojeda, 1995; see also Ojeda et al., 2000a). Limestone outcrops, which produce limy, basic soils, are also found, although scattered and much less abundant. In the lowlands fringing the mountains, non-acid, loamy or marly soils are dominant (Ojeda, 1995).

In summary, both geographical location and oceanic influence rendered the SG area climatically stable during geological times which, together with a high habitat diversity linked to soils and topography, promoted its role as an important refugium for humans and biodiversity throughout the Quaternary. The positive effect of habitat heterogeneity and warm and wet climates for sustainability of human populations has been effectively documented elsewhere (e.g., Collard and Foley, 2002; Ashton et al., 2006; Carrión et al., 2008, Finlayson, 2008).

3. The uniqueness of the present flora and vegetation: endemism and relictness

The SG has long been considered an outstanding place for botanical exploration and its floristic singularity has been acclaimed, particularly since botanical expeditions in the 19th century (Valdés, 1996). Traditional, descriptive biogeographical

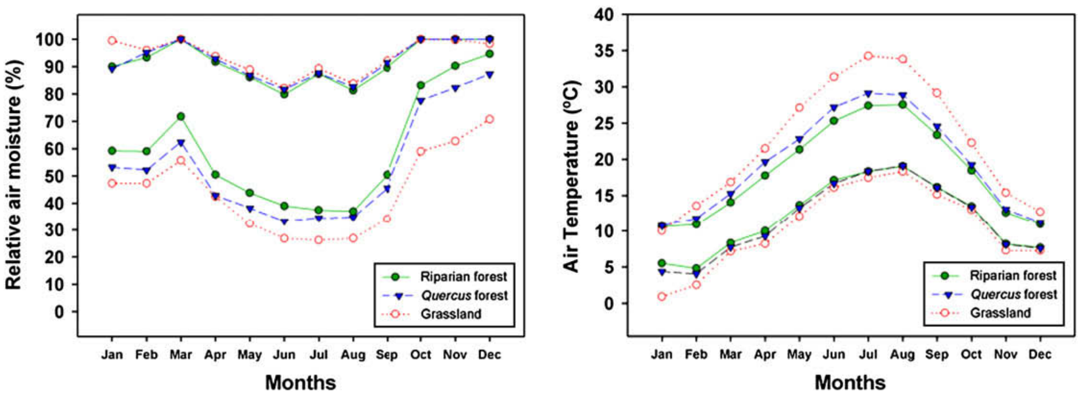

Fig. 2. Monthly variation of maximum and minimum relative humidity (left) and air temperatures (right) inside riparian forests, compared to adjacent *Quercus* forests and grasslands, typical plant communities in the Strait of Gibraltar. Data averaged from hourly records by data-loggers (Hobo H8, Onset Corp.) in ''La Jarda'', Sierra del Aljibe (Cádiz prov., Spain) during 2005.

classifications have considered both sides of the SG as separate units, mostly because these studies were carried out in separate countries and continents (e.g., Barbero et al., 1981; Benabid and Fenanne, 1994 on N Africa; Rivas-Martínez et al., 1998 on S Spain). Nevertheless, Takhtajan (1986) proposed in his global account of plant biogeography that both S Iberia and Mediterranean NW Africa belong to the SW Mediterranean Province. More recently, at a more local scale, several authors have highlighted the floristic continuity of the two shores of the SG and have thus proposed the creation of a Tingitanian-Aljibean floristic sector that includes the two SG peninsulas (e.g., Galán de Mera et al., 2003). Unfortunately, most analytical biogeographical studies of both the flora and fauna in this region overlook this continuity and focus only on the northern side of the SG (reviewed in Arroyo et al., 2004). Therefore, additional joint analyses including both sides of the SG are needed.

The complex geological and climatic history of the SG region during the Neogene, together with its physiographical and environmental heterogeneity, contribute to a great extent to the intricate biodiversity patterns of its flora and fauna (e.g., ecological diversity, existence of refugia, contact and/or transition areas, high endemism, Ojeda et al., 1996a, 2000b; García-Barros et al., 2002; Sanmartín, 2003).

3.1. *Vegetation*

The unique flora of the SG is combined in vegetation types which are also distinct from paradigmatic surrounding sclerophyllous Mediterranean forests and garrigue/maquis scrublands. Evergreen *Quercus suber* (cork oak) woodlands dominate this area, this species being the least sclerophyllous of all the evergreen oaks in the Mediterranean Basin. They are replaced by semi-deciduous *Quercus canariensis* forests on moist, shady slopes and valley bottoms on sandstone-derived deep soils. Deep sandstone gorges conceal a very interesting type of moist, warm-temperate forest known locally as *canutos*, where a diverse tree and arborescent shrub flora is found, including most presumed Tertiary (pre-Mediterranean) relict species. The sandstone ridges and hilltops are covered by open Mediterranean heathlands (locally known as *herrizas*), which harbour most of the endemic flora of the SG region (Ojeda et al., 1996a, 2000b). At altitudes higher than 700 m on sandstone soils, and in wind sheltered areas, *Quercus pyrenaica*, another semi-deciduous oak tree species, forms small, dense patches. On sandstone mountains, at altitudes higher than 1200 m, only attained on the Moroccan side of the Strait, *Q. pyrenaica* forests coexist with cedar tree (*Cedrus atlantica*) forests (Ajbilou et al., 2006). Finally, limestone outcrops, and marly and loamy lowlands, are dominated by sclerophyllous shrublands. These shrublands, which represent the paradigm of Mediterranean-type vegetation, are composed of robust, sclerophyllous shrub species such as the kermes oak *Quercus coccifera*, the mastic tree *Pistacia lentiscus*, the wild olive tree *Olea europaea*, and the true myrtle *Myrtus communis*. Also, in the driest shrublands of the Moroccan side of the SG, the araar tree *Tetraclinis articulata* can become dominant.

3.2. *A sanctuary for relict Tertiary taxa*

The effectiveness of the SG region as a buffering zone for climate change throughout the main geological events of the Mio–Pliocene and the Pleistocene (Section 2) contributes largely to explaining a main component of plant biodiversity in the region: the presence of putative Tertiary relict taxa, mainly ferns (Salvo, 1994) and lauroid tree and treelet species (e.g., *Rhododendron ponticum*, *Frangula alnus*, *Laurus nobilis*), which have suffered severe range constrictions since the Mio–Pliocene (Mai, 1989; Rodríguez-Sánchez and Arroyo, 2008). Although the number of species considered Tertiary relicts is much lower than that of endemic species, SG woody relicts present a dense cover in river valleys, thus becoming an important component of the present-day vegetation of the SG region (Mejías et al., 2002, 2007). They are also found in the scattered mist forests still present in the SG. This "warm and moist" habitat of the SG relict flora is in sharp contrast with the cool temperate (montane) habitat of most relict taxa across the Mediterranean. The latter are well-represented in the high mountains of the SE Iberian Peninsula and the Atlas mountains of N Africa, where they have become isolated since the Ice Ages (Castro et al., 2004). By contrast, "warm and moist" SG relicts are the legacy of a pre-Mediterranean, subtropical climate (Mejías et al., 2007), which disappeared at the Plio–Pleistocene boundary, coincident with the onset of glaciations. Extinction has played an important role, stressing the singularity of these relicts, a difference with the eastern Mediterranean and Black Sea regions, where Tertiary relicts are more abundant (Denk et al., 2001).

3.3. *The singularity of the endemic element*

Sandstone soil patches constitute true edaphic islands, harbouring a rich associated endemic flora (12.8% of the species). This endemism is considerably higher than that of neighbouring areas of similar elevation but with limestone dominant bedrock (5–10%, Ojeda et al., 2001). Thus endemism in the SG is considered primarily edaphic, as a result of ecological isolation (Ojeda et al., 1996a, 2000b, 2001). It is noteworthy that up to 37.9% of the SG endemic species have a woody life-form, whereas this figure goes down to 12% in neighbouring limestone areas of similar elevation (Ojeda et al., 2001). Moreover, these endemic shrubs are usually dominant in Mediterranean heathlands on sandstone soils, and their regeneration ecology is particularly well-adapted to the present ecological conditions of the SG region (see Section 5.2).

These distinct features of the endemic element – edaphic endemism and tight association with the woody life-form – make this region a singular hotspot of plant biodiversity within the Mediterranean Basin. In the rest of the biodiversity hotspots of the Mediterranean region, by contrast, endemism is mainly of orographic and/or insular nature (Favarger, 1972; Médail and Quézel, 1997) and markedly associated with herbaceous perennial life-forms (Thompson, 2005). How such singularity arose remains an open question.

Whereas the biodiversity value of the SG flora is high due to its richness in endemics, its taxonomic distinctiveness at a regional (SW Spain, NW Morocco) scale is relatively low because both measures are negatively correlated, that is, SG endemic species belong to highly diversified genera within the western end of the Mediterranean Basin (Arroyo and Marañón, 1990; Ojeda et al., 1995, 2001).

3.4. *The Strait of Gibraltar as a biogeographical bridge and barrier*

The major biogeographical significance of past climatic events in the SG region, particularly the Messinian Salinity Crisis and, to a less extent, the Pleistocene glaciations, is that they would have facilitated north–south dispersal routes (see Fig. 1). This, together with the edaphic and climatic similarities, helps to explain the strong floristic similarities shared by the two shores (Valdés, 1991). The only available comparative studies refer to woody species (e.g., Ojeda et al., 1996a; Marañón et al., 1999). At the forest community level, these authors found that Iberian understorey species showed higher endemism and taxonomic singularity than that of the corresponding N African forests. At the regional level, the tree flora was also richer (in terms of number of species) on the northern than on the southern side (Ajbilou et al., 2006). Both long-term (historical) and present-day (ecological) processes have been proposed to account for such differences (see Sections 4 and 5).

Despite the geological and ecological continuity across the SG region, the distribution of many plant species appears sharply truncated by the SG. From the checklist of vascular plant species present on the north side of the SG, about 17% are not found on the south side, whereas 27% of the south side flora does not cross the SG. Some notable cases are *Rhododendron ponticum*, *Corema album*, *Prunus lusitanica*, *Cedrus atlantica*, *Erica multiflora*, *Tetraclinis articulata*, and *Hedera* species, in contrast with some extremely abundant species on both sides (e.g., *Erica australis*, *E. arborea*, *Quercus canariensis*, *Q. suber*, *Pinus pinaster*, *Calicotome villosa*, *Narcissus papyraceus*). This pattern suggests that the SG has also been acting, to some extent, as a biogeographical barrier. While determining this fact is not possible from a simple account of species ranges, past movements can be inferred from the evolutionary history of the species concerned.

4. Reconstructing the past: phylogeny and phylogeography

Phylogenetic and phylogeographical analyses are powerful tools to infer the evolutionary history at the species and population level, respectively. While phylogenetic reconstructions based on molecular markers are used to make inferences above the species level, phylogeographical approaches have been the major contribution of molecular population genetics to the analysis of historical processes underlying the present geographical distribution of species lineages (Avise, 2000). Timing of speciation has been debated for decades in a biogeographical context. For instance, analysis of chromosomal evolution in plants gave a speciation rate estimate of 1.15 Ma for continental herbs (Levin and Wilson, 1976), while molecular clocks based on DNA variation revealed a rate of $<$0.8 Ma for speciation of plants in oceanic islands (Baldwin et al., 1998). Considering that the end of the Messinian Salinity Crisis ca. 5 Ma coincided with the formation of the SG, plant groups have since then had the opportunity to evolve into different species on the Iberian and African plates. In addition to these estimates of speciation rates, it is worth mentioning that species can originate abruptly in a single generation (e.g., by polyploidy), while others persist over millions of years with virtually no morphological change ("living fossils").

In principle, population divergence is faster than, and antecedent to, speciation. Despite the vast knowledge on geographical distribution and ecological requirements of Mediterranean species, the use of phylogeographical analyses to test hypotheses of population relationships in Mediterranean plants is scattered. The question remains as to whether the SG has played any role as a barrier or as a corridor in divergence or connection of plant populations. We review the available evidence of several case studies, first at the species level (by means of biogeographical interpretation of phylogenies), then at the population level (phylogeography), in order to reconstruct historical processes of colonization and differentiation. Assuming that phylogeographical data are informative of the colonization process, its direction and relative timing and tempo, we may expect an association between genetic relatedness of populations and plant traits associated with their dispersal and colonization ability. Inferences on actual seed dispersal based on morphological traits are strongly limited and even long-distance dispersal events could be frequently caused by unexpected vectors (Higgins et al., 2003). However, these traits are the only available line of evidence for dispersal for most species. In any case, we consider only sharply distinct dispersal syndromes (e.g., fleshy fruits, winged seeds, etc) to account for migration in the flora of the SG, as have already been analyzed for Macaronesian plants (Vargas, 2007). Colonization and establishment ability may play an even more relevant role than dispersal in determining plant distribution, but they are more difficult to infer from single morphological traits. Thus we additionally considered life-form and habitat requirements of plants under scrutiny as providing only indirect clues to their colonizing ability.

4.1. Speciation across the Strait of Gibraltar

Interpretation of molecular phylogenies contributes to our understanding of the historical biogeography on both sides of the SG. Table 1 summarizes the phylogenetic patterns in plant groups coping with a putative barrier to dispersal which share a similar geographical range across the SG. As a whole, a significant association between evolutionary patterns and plant groups sharing similar dispersal syndromes is not observed. Multiple patterns of speciation are inferred, illustrating the complexity of the species-rich area of the SG, in which woody and herbaceous plants do not necessarily share a common pattern of diversification.

W Mediterranean fir trees (*Abies pinsapo* group). Isozyme variation revealed that a deep genetic gap does occur between *A. pinsapo* (S Andalusia) and *A. maroccana* (N Morocco), indicating limited contact, if any, between fir species across the SG (Scaltsoyiannes et al., 1999). The third W Mediterranean fir (*A. numidica*, Algeria) appeared to be remotely related. Strong differentiation between populations on both sides of the SG has also been found by using plastid microsatellite markers (Terrab et al., 2007).

Bay laurels (*Laurus* species). Only two species of bay trees are recognized in the genus, *L. nobilis* in the Mediterranean and *Laurus azorica* in the Macaronesian islands and two small ranges in the Atlas Mountains (Morocco). Success of laurels in colonizing multiple mesic habitats throughout the Mediterranean and related areas, together with dispersal and establishment of *L. azorica* in Macaronesia, illustrates that these two endozoochorus species

Table 1
Biogeographical patterns of speciation in the region of the Strait of Gibraltar (SG) as revealed by molecular-based phylogenies

Plant group	Molecular markers	Reference	Evolutionary pattern
Abies pinsapo group	Isozymes, cpSSR	Scaltsoyiannes et al. (1999), Terrab et al. (2007)	Long-term isolation of populations on both sides of the SG, but still more relatedness than that with the other northern African species (*A. numidica*)
Cistus	ITS, *trnL-F*, *matK*	Guzmán and Vargas (2005)	Active processes of speciation and colonization over the SG
Hedera	ITS, *trnT-L*	Vargas et al. (1999a), Valcárcel et al. (2003)	Full isolation of three European and two northern African species, as well as of the European polyploid lineage
Laurus	AFLP, *trnK-matK*, *trnD-trnT*	Arroyo-García et al. (2001), F. Rodríguez-Sánchez et al., (unpubl.)	Limited differentiation in the W Mediterranean, with close relationships between *L. nobilis* and *L. azorica*. No significant isolation by the SG
Narcissus sect. Apodanthi	*trnL-trnF*, *trnT-trnL*, *trnQ-trnR*	Pérez et al. (2004), Pérez-Barrales et al. (2006)	The SG and high mountains have been effective barriers to isolate Apodanthi species over the last million of years
Saxifraga globulifera group	ITS, *trnT-L*	Vargas et al. (1999b)	Formation of *S. reuteriana* in Iberia after vicariance of *S. globulifera* on both sides of the SG
Ulex and Stauracanthus	cpSSR	Cubas et al. (2005), Pardo et al. (2008)	Gene-flow between Iberian and African populations. Speciation by polyploidization
Antirrhinum spp	cpDNA, ITS	Vargas et al; in press	The SG played a major role in separating multiple lineages and species

underwent events of long-distance dispersal (Vargas, 2007). The analyses of plastid sequences of both *Laurus* species (F. Rodríguez-Sánchez et al., unpublished) suggest an increasing divergence of laurel populations toward the two extremes of the Mediterranean Basin, but limited divergence between Iberia and N Africa. Both *Laurus* species appear closely related (Arroyo-García et al., 2001; F. Rodríguez–Sánchez, unpublished data).

Rockroses (*Cistus* species). Speciation in *Cistus*, which is a Mediterranean genus of 20 species typically characterized by seeds in multi-valved capsules, appears to have primarily post-dated the opening of the SG (Guzmán and Vargas, 2005, and unpublished data). On both continents, no further limitation of species dispersal and establishment is revealed by plastid and nuclear sequence similarity of accessions of *Cistus albidus*, *C. crispus*, *C. monspeliensis*, and *C. pouzolzii*. Therefore, the SG has not been particularly determinant either in speciation or as a barrier for rockroses.

Ivies (*Hedera* species). A clear-cut distribution of three W European species (*Hedera helix*, *H. Hibernica*, *H. maderensis, H. iberica*) and two N African species (*H. maroccana*, *H. algeriensis*) is intriguing given the abundance of mesic habitats in both areas, coupled with a demonstrated capability for long-distance dispersal of typically bird-dispersed fruits (Vargas et al., 1999a). In fact, *Hedera* colonized Macaronesia at least three times independently and speciation occurred after founder events on the Azores (*H. azorica*), Madeira (*H. maderensis*) and Canary (*H. canariensis*) islands (Valcárcel et al., 2003). The question remains about the processes hindering successful migration but promoting differentiation of ivy species across the SG, where they are abundant.

Gorses (*Ulex* and *Stauracanthus* species). Polyploidy appears to have played an important role in *Ulex* and *Stauracanthus* speciation (Cubas et al., 2005, Pardo et al., 2008). Distribution of plastid haplotypes (cpSSR) and species indicates the existence of active gene flow by seeds across the SG associated with an increase of the ploidy level in two species (*U. borgiae*, *U. congestus*).

Summer-dormant bud saxifrages (*Saxifraga globulifera–reuteriana* complex). High levels of ITS and *trnT-trnL* sequence variation are congruent with an ancient split of S Iberian and N African populations of *S. globulifera*, followed by paraphyletic speciation of *S. reuteriana* exclusively from Iberian plants (Vargas et al., 1999b). Seeds in capsules displaying no apparent long-distance dispersal syndrome succeeded in colonizing Madeira (ca. 1000 km) from a N Iberian ancestor of a different lineage (*Saxifraga trifurcata–S. maderensis–S. portosanctana*). In contrast, similar seeds in capsules of *S. globulifera* presumably failed colonizing Iberia and blurring speciation of *S. reuteriana*.

Daffodils (*Narcissus* sect. Apodanthi). The seven *Narcissus* species within the section Apodanthi are endemic to the W Mediterranean and restricted to mountain areas of Iberia and NW Africa. Molecular phylogenetic reconstructions (Fig. 3) are congruent with one lineage of Portuguese endemics (*N. scaberulus*, *N. calcicola*) and two lineages of Iberian-northern African species (*N. rupicola–N. watieri–N. marvieri*; and *N. cuatrecasasii–N. albimarginatus*) (Pérez et al., 2004). Considering previous phylogenies and levels of sequence divergence, we can conclude that not only the SG, but also high mountains have been effective barriers in isolating these seven Apodanthi species over the last million years. Additional *trnT-trnL* sequences (R. Pérez-Barrales, P. Vargas and J. Arroyo, unpublished data) revealed that population relationships are complex within each lineage, although the above-described biogeographical pattern of evolution is consistently retrieved, particularly the split between Iberian *N. cuatrecasasii* and Moroccan *N. albimarginatus*, which are the closest relatives in the SG region.

Snapdragons (*Antirrhinum species*). The 25 species of *Antirrhinum* are primarily distributed in the Western Mediterranean, including a hotspot of species diversity in the Iberian Peninsula (22) and a lower number in N Africa (4). A geographical pattern of speciation is observed, in which the SG has played a major role separating the single N African and the four Iberian lineages in the Pliocene-Pleistocene (Vargas et al., 2008).

4.2. *Phylogeographical patterns*

Phylogeographical approaches have been successfully implemented to describe postglacial colonization routes of trees in Central Europe (e.g., Demesure et al., 1996; Petit et al., 2002b). Quaternary glaciations may not have dramatically affected the survival of plants in S Europe, in contrast with a nearly total extinction of angiosperms in N Europe. Three main refugia in the Iberian, Italian, and Balkan peninsulas have been proposed, from which recolonization to Central and N Europe occurred (Hewitt, 2000). Thus these refugia may record a phylogeographical signal dating back to climatic events in the Late Tertiary, evidence a longer and more complicated history than that in Europe (Hampe and Petit, 2005).

Phylogeographical analyses C. have been primarily focused on woody species in the Mediterranean and show multiple biogeographical patterns of genetic diversity. Some of the studied species are of high abundance and ecological relevance in present Mediterranean forests and scrublands and include sampling across the SG. This has given the SG region additional significance as a refuge area and allowed testing its role as a barrier to plant migration and differentiation. Despite trees playing an important role in the building of large vegetation formations, they do not necessarily share similar patterns of diversity, evolution and biogeography. Here we summarize some of the best documented phylogeographic studies displaying significant evolutionary patterns across the SG (see Table 2).

Sclerophyllous oak trees (*Quercus ilex* s.l. and *Q. suber*). Both species are characteristic of Mediterranean forest on both sides of the SG, particularly the cork oak (*Q. suber*), which forms extensive forests in the SG region. These species have been analyzed with plastid markers and a detailed population sample allows the reconstruction of their colonization history (Lumaret et al., 2002, 2005). In both cases, there exists a discontinuity of lineages across the SG, which is more pronounced in the holm oak (*Q. ilex*/*rotundifolia*). Summarizing, lineages of both species originated somewhere in the central-eastern Mediterranean and migrated through N Africa to the Iberian Peninsula during the Late Tertiary. Populations of these two oaks contracted to form two distinct glacial refugia in S Iberia and N Africa. The separation between these refugia was stronger in the holm oak, and African populations probably did not participate in N Iberian recolonization after the Ice Ages (Lumaret et al., 2002). The reconstruction of the migration history of the cork oak (*Q. suber)* has been more complex, due to some introgression with *Q. ilex* (the latter as maternal parent), and to the intense management this species has undergone (Lumaret et al., 2005). Nevertheless, it seems that there have been episodes of both isolation and migration across the SG during glacial/interglacial periods for *Q. suber*. Therefore, both S Iberian and N African ranges of the SG can be considered together as glacial refugia (Lumaret et al., 2005, see also Carrión et al., 2000 for the fossil record). This relative isolation across the SG points out difficulties either for long-distance seed dispersal or for population establishment in both species (but see López-de-Heredia et al., 2005). The stronger isolation of the holm oak through the SG is perhaps related to the scarcity of suitable environments in areas close to the SG, in comparison with those for the cork oak. However, human influence cannot be ruled out, particularly because the cork oak has been intensively managed and some forests result from old plantations.

Deciduous and semi-deciduous oak trees (*Quercus canariensis*, *Q. pyrenaica*, *Q. faginea*). These white oaks form the second most

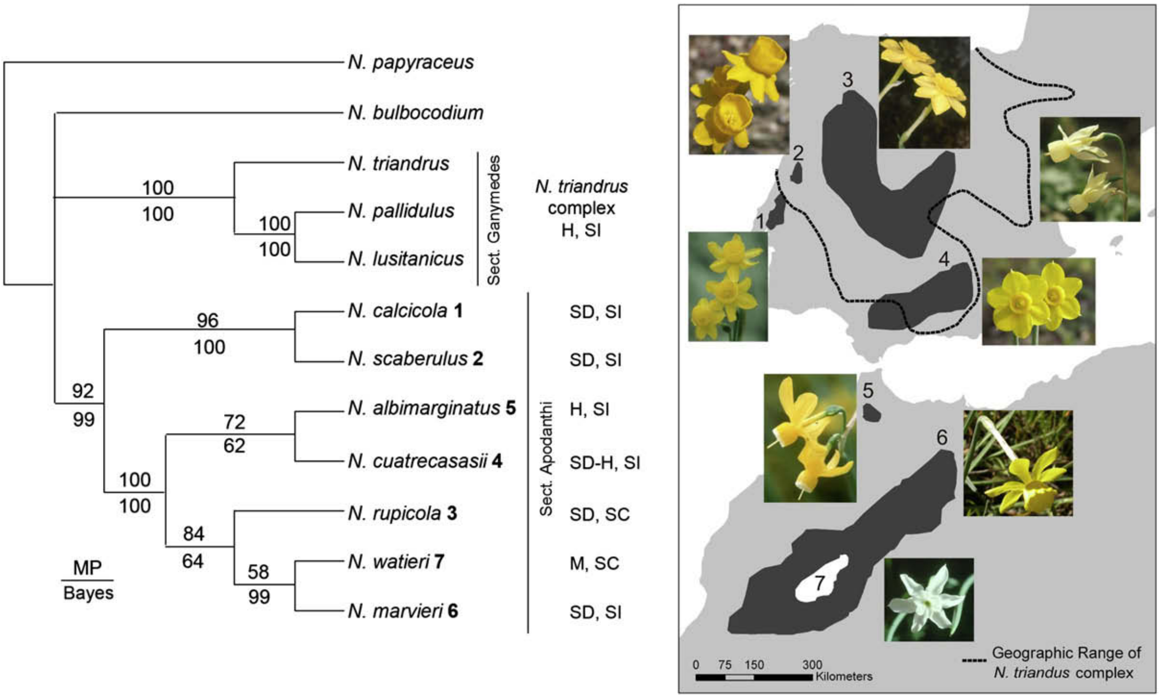

Fig. 3. Geographical range of the species of *Narcissus* sect. Apodanthi and *N. triandrus* showing complex, phylogenetic relationships between them (maximum parsimony and Bayesian support is shown above and below branches), and breeding system (SI, self-incompatible; SC, self-compatible; H, heterostylous; SD, style dimorphic; M, monomorphic; based on Pérez-Barrales, 2005 and Pérez-Barrales et al., 2006).

extensive forest type on both sides of the SG. Unfortunately, the available phylogeographical information for the SG region is very limited because of a poor sample from this region, particularly from N Africa. The current hypothesis of phylogeographical reconstruction in the Iberian Peninsula suggests explicit migration routes of haplotypes only across the northern half of Iberia (Olalde et al., 2002), despite some other lines of evidence confer a role of N Africa (Petit et al., 2002a). A somewhat wider sample showed that these oaks in the SG belong to a W Iberian (both sides of the SG) or to an E Iberian (north side only of the SG) lineage (Petit et al., 2002b), but

Table 2
Phylogeographical patterns shown by species distributed on both sides of the Strait of Gibraltar

Species	Molecular markers	Reference	Geographical pattern in the Strait of Gibraltar
Quercus ilex	cpDNA (RFLP)	Lumaret et al. (2002)	Migration from S to N of the SG, followed by limited gene flow by seed between both sides. Both areas are glacial refugia
Quercus suber	cpDNA (RFLP)	Lumaret et al. (2005)	Migration from S to N of the SG and later sporadic migrations in both directions. Genetic differentiation between both sides. Both areas are glacial refugia
(*Quercus canariensis*, *Q. pyrenaica*)	cpDNA (RFLP)	Olalde et al. (2002), Petit et al. (2002a,b)	Recolonization of Iberia from S Iberia and N Africa after Ice Ages
Olea europaea	cpDNA, ISSR, AFLP, RAPD, allozymes	Besnard et al. (2002), Vargas and Kadereit (2001), Rubio et al. (2006), Lumaret and Ouazzani (2001)	Active gene flow in both directions in the SG. The highest genetic diversity of the Mediterranean in the SG
Laurus nobilis	cpDNA	F. Rodríguez-Sánchez et al. (unpublished data)	Both sides of the SG share a common Mediterranean haplotype. An additional haplotype occurs exclusively on the northern side of the SG
Frangula alnus	cpDNA (RFLP)	Hampe et al. (2003)	The Iberian refugiA contributed little to recolonization of temperate Europe. Populations in the SG show a strong genetic differentiation
Pinus pinaster	Isozymes, mtDNA, cpDNA (RFLP), cpSSR	Salvador et al. (2000), Burban and Petit (2003), Gómez et al. (2005), Bucci et al. (2007)	Refugia in S and SE Iberia and N Africa. Limited gene flow by seeds but higher by pollen
Pistacia lentiscus	RAPD	Werner et al. (2002)	Strong genetic differentiation across the SG
Calicotome villosa	Isozymes	Arroyo et al. (2008)	Isolation by distance between populations, regardless the SG. High gene flow by seed
Narcissus papyraceus	AFLP	R. Pérez-Barrales et al. (unpublished data)	Populations at both sides of the SG form a distinctive group, in contrast to peripheral populations
Saxifraga globulifera complex	ITS, *trnT-trnL*	Vargas et al. (1999b), P. Vargas (unpublished data)	Ancient divergence between Iberian and N African lineages, but a most recent colonization from N Africa to Gibraltar
Hypochaeris salzmanniana	AFLP	Ortiz et al. (2007)	Differentiation among Moroccan populations, but high gene flow between Moroccan and S Iberian populations. Migration from S to N
Cakile maritima, *Crithmum maritimum*, *Eryngium maritimum*, *Halimione portulacoides*, *Salsola kali*	AFLP	Kadereit et al. (2005)	Long-term differentiation of populations on W and E coasts of the SG, followed by sporadic colonizations
Carex helodes	AFLP, cpDNA, ITS	Escudero et al. (2008)	Founder effect in N Africa from S Iberia. No further gene flow

these authors admit that more intense sampling from this region is needed. Concordance with fossil pollen data allows the inference of a south to north recolonization from either S Iberian or N African refugia (Petit et al., 2002a). Interestingly, E and W Iberian lineages merge in the SG region, and they are mostly represented respectively by *Q. canariensis* and *Q. faginea* subsp. *broteroi*, which have strong morphological and ecological resemblances (Amaral Franco, 1990).

Wild olive tree (*Olea europaea*). One of the best indicators of the Mediterranean region is the Mediterranean olive tree (*O. europaea* subsp. *europaea*). Its geographical distribution is to some extent the result of successful long-distance dispersal, making exchange of migrants common even to Macaronesian Islands (Hess et al., 2000). A long history of plantation, due to its importance as a source of oil and edible fruits for humans since the Palaeolithic, is also responsible for its current distribution. Multiple molecular inferences indicate that wind pollination and endozoochorous bird dispersal in *O. europaea* may account for extensive gene flow among lineages across the SG irrespective of the markers considered (Vargas and Kadereit, 2001; Besnard et al., 2002; Rubio et al., 2006). Additionally, the highest diversity is found in the western Mediterranean, and particularly on both sides of the SG (Lumaret and Ouazzani, 2001; Rubio et al., 2006), and this species may have provided a rich source of food for humans in the course of migration to SW Europe and NW Africa since early times (Rodríguez-Ariza and Moya, 2005).

Mediterranean laurel (*Laurus nobilis*). This species has been considered as belonging to the Late Tertiary relict element in the Mediterranean Basin, where it was more widespread than the present patchy, isolated small ranges along the Mediterranean coast (Rodríguez-Sánchez and Arroyo, 2008). As with other lauroid species (e.g., *Rhododendron ponticum*), it appears that the, we suggest that genetic differentiation is probably also aided by humans. Mediterranean laurel was never able to recolonize C Europe after the general cooling of climate during the first Ice Age due to its sensitivity to cold. The SG region emerges as a long-term refugium for the species, harbouring an exclusive haplotype which is however absent from Moroccan populations (Rodríguez-Sánchez et al., unpublished).

Mediterranean azalea (*Rhododendron ponticum*). This species and other close relatives had a widespread range during the Tertiary. At present, it is one of the most restricted examples of the Tertiary relict element in the Mediterranean, being somewhat abundant in the Black Sea Basin but extremely rare in the west. Indeed, it is confined to the Iberian side of the SG and to small isolated patches in S and C Portugal (Mejías et al., 2007, and references therein). Historical biogeography of this species and its clade is puzzling since the estimated divergence times within the clade are 3.2–4.9 Ma, including its closest relative, the eastern North American *Rhododendron maximum* (Milne, 2004). This implies that species divergence must have occurred after the Messinian Salinity Crisis (see above) had caused extinction and disjunct ranges in the region. Geographical divergence of species in the clade over large distances (Mediterranean versus E North America) implies a high dispersal success of the Mediterranean azalea ancestor. Despite similar habitat availability on both sides of the SG and the dispersal ability of the Mediterranean azalea, this species is completely absent in N Africa. Although there is evidence of a wider distribution of *Rhododendron* in Southern Spain until the Middle Würm (Pons and Reille, 1988), its presence has not yet been documented in N African fossil records (Reille, 1977).

Buckthorn alder (*Frangula alnus*). Although at present this species is abundant and even a pioneer woody species in most of temperate Europe, there is conclusive palaeobotanical evidence suggesting a process of range advance and retreat across Europe, at least during the Last Interglacial and glacial maximum (see Hampe et al., 2003, and references therein). However, it is likely that the buckthorn alder underwent an earlier process of extinction and isolation in the Late Tertiary in S Europe, given the high level of genetic differentiation of haplotypes between Iberia and Anatolia (Hampe et al., 2003). S Iberian and N African populations have been described as a different subspecies (*baetica*), which are also scattered in small isolated ranges. Genetic differentiation among these two ranges is stronger than among temperate populations, indicating a long process of isolation, even between close populations on both sides of the SG. Despite having fleshy, bird-dispersed fruits, limited dispersal together with strict habitat requirements for successful establishment (permanent water courses in the Mediterranean), may account for the striking differentiation among nearby populations and across the SG (Hampe and Arroyo, 2002; Hampe et al., 2003).

Maritime pine (*Pinus pinaster*). This pine species is endemic to the western Mediterranean. Extensive plantation makes difficult to recognize native populations, since it shows a high regenerative capacity in appropriate habitats. The S-SE Iberian Peninsula and the NW Africa constituted two independent glacial refugia out of which two recolonization pathways, one northwards to N Iberian Peninsula and S France and other eastwards along N Africa to Italy, might have occurred (Gucci et al., 2007). Nevertheless, although there seems to exist strong limitation to gene flow by seeds across the SG, gene flow by pollen exchange has definitely occurred (Salvador et al., 2000; Burban and Petit, 2003; Gómez et al., (2005).

Mastictree (*Pistacia lentiscus*). Despite limited sampling around the SG, this widespread Mediterranean shrub or treelet appears to have a strong differentiation between populations on both sides of the SG (Werner et al., 2002).

Thuriferous or Spanish juniper (*Juniperus thurifera*) also shows strong differentiation between populations in the Iberian peninsula and N Morocco (Terrab et al., 2008). However this pattern should be also influenced by the isolated mountain habitat of the species, which is not present in close areas to SG.

Hairy thorny broom (*Calicotome villosa*). This broom species has a circum-Mediterranean range, being extremely abundant in open shrublands subjected to strong human and cattle pressure on both sides of the SG. Isozyme variation (Arroyo et al., 2008) reveals that the populations show a degree of isolation by distance. However, the SG does not represent a barrier interrupting gene flow. Assuming low pollen exchange between populations (pollinated mostly by bees), seed movement appears to be mostly responsible for the observed genetic structure. Although the seeds and fruits have a morphology unsuited to long-distance dispersal, cattle ingestion and unintentional movement by humans may have influenced the present-day distribution of the species, in disturbed habitats.

Gum rockrose (*Cistus ladanifer*). An intercontinental colonization is inferred from the disassociation between geographical and lineage distributions of plastid haplotypes (Guzmán and Vargas, in press). Molecular-clock estimates of two plastid (*rbcL*, *matK*) and one nuclear (ITS) data set are fully consistent with a second event of long-distance dispersal of *C. ladanifer*, significantly post-dating the opening of the SG (ca. 5 Ma). N. Africa appears to be the source in both cases.

Herbaceous species. "Paper white" daffodil, *Narcissus papyraceus* is distributed throughout the Mediterranean, being well-represented in terms of population number and size in marl and clay lowlands close to the shores of the SG, becoming rarer inland. A study with AFLPs was carried out on 116 individuals from 26 populations across the SG (R. Pérez-Barrales, P. Vargas and J. Arroyo, unpublished data). A Neighbour-Joining tree based on AFLP fingerprints using the Nei & Li genetic distance coefficient produced a well-supported group of coastal populations of large size on both shores of the SG. The rest of the populations were distributed peripherally to the SG (Fig. 4). *N. papyraceus* is abundant in disturbed habitats,

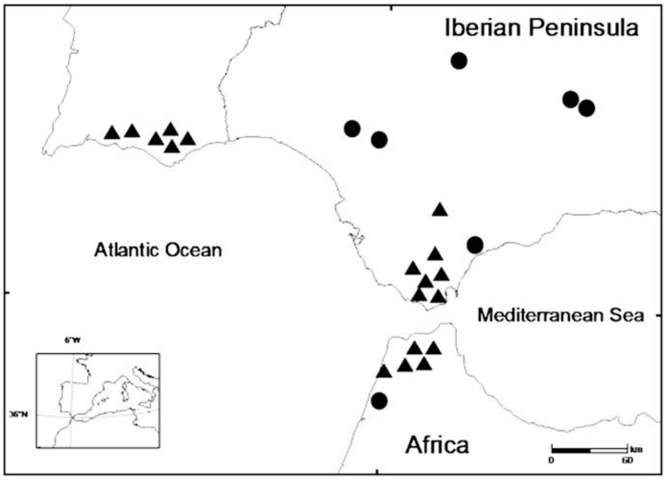

Fig. 4. Geographical distribution of AFLP fingerprints inferred by Neighbour-Joining analysis of 116 individuals from 26 populations of *Narcissus papyraceus*, based on Nei & Li genetic distance coefficient. Triangles represent a well-supported (90% bootstrapping support) lineage; circles represent unresolved lineages.

and frequently co-occurs with *Calicotome villosa*. Given the apparent poor seed dispersal of this daffodil species (seeds in capsules not consumed by animals). A saxifrage species (*Saxifraga gibraltarica*) within the summer-dormant bud saxifrages group (*S. globulifera* group) has been recognized as a taxonomic variety in the most recent accounts (Vargas et al., 1999b and references therein). Interestingly, nuclear and plastid markers (ITS and *trnT-trnL* sequences) clearly revealed that, even though an ancient divergence of *S. globulifera* occurred, splitting S Iberian and N African populations (see Section 4.1 above), a recent colonization of the Iberian Peninsula is responsible for the presence of this saxifrage variety on the cliffs of Gibraltar (Vargas, unpublished data). *Hypochaeris salzmanniana* is an annual species distributed in sandy soils of the W Mediterranean and displays a robust phylogeographical structure in which a basal population divergence occured on both sides of the Loukos River (Morocco), whereas a recent colonization took place on the northern tip of the Tangier Peninsula (N Morocco) and then on the Iberian side (Ortiz et al., 2007). Interestingly, the ancestral habitat reported for this species is cork oak woodlands, which share the same refugium in N Africa (see above). Five coastal plants (*Cakile maritima*, *Crithmum maritimum*, *Eryngium maritimum*, *Halimione portulacoides*, *Salsola kali*) appeared to have been deeply affected by the long isolation period of the Mediterranean as a consequence of the closing of the SG in the Messinian (Kadereit et al., 2005). Despite extensive habitat availability along Eurasian coasts and dispersal potential, seems to have rare migrant exchange between the Mediterranean Sea and the Atlantic Ocean appears to have been rare for any of the five species.

The first step in any process of range expansion is propagule dispersal (mostly seeds), but it must be followed by successful establishment for effective gene flow to occur. So, genetic differentiation between populations across the SG could be due to either limited dispersal or failure of migrating seeds to get established. Seed plants have multiple dispersal mechanisms to ensure colonization of new territories. Among them, dispersal by animals (zoochory) and wind (anemochory) have apparently been efficient mechanisms for long-distance dispersal (Ridley, 1930). In particular, zoochory accounts for over 60% of the founders in colonization of oceanic islands (Vargas, 2007). Wind dispersal has not precluded differentiation of lineages in winged seeded *Abies* and *Pinus* and pappus fruited *Hypochaeris*, even over shorter distances. Efficient epizoochory by birds is difficult to ascertain from morphological traits of propagules, or these (mucilages, hooks, hairs) are absent in the reported examples, whereas endozoochory is usually associated with fleshy fruits. Since the Pleistocene, the SG region is one of the most important places for passage of migrant birds between Europe and Africa (e.g., 371,000 non-soaring birds of 50 species were observed in a single season and location, Barros and Ríos Esteban, 2002). Only a limited number of them (approx 1%) are consistently frugivorous and can be considered as regular endozoochorous dispersers, although their role in seed dispersal across the SG depends on feeding behaviour and habitat preferences, and there are no data on the presence of seeds in passing birds. Nonetheless, these birds probably represent a much higher potential for seed dispersal between separate areas than non-migratory bird species. However, most of the plant species examined to date displaying endozoochory (fleshy-fruited and *Quercus* species) present some kind of genetic discontinuity across the SG (except for *Olea*). Probably recruitment limitation has operated differently in the two groups of species. Woody, fleshy-fruited species would suffer a combination of impaired fecundity and microhabitat limitation on successful recruitment. This could lead to genetic differentiation across the SG despite effective dispersal of seeds. In contrast, many of the species lacking differentiation on both sides of SG are ruderal (*Calicotome villosa*, *Narcissus papyraceus*) or short-lived herbs (*Hypochaeris salzmanniana*), which are probably more successful in establishing themselves.

Available genetic studies on disparate groups of animals illustrate that the degree of isolation imposed by the SG is quite species-specific, but also that a human-mediated dispersal is most likely for some species. For instance, the SG does not present a barrier for sea gulls (Guillaumet et al., 2006), whereas it does for heavier and nearly sedentary great bustards *Otis tarda* (Broderick et al., 2003). There is a strong evidence for recent (<60 ka) crossing of the SG, probably coupled to human migrations in most cases, among diverse animals lacking long-distance dispersal mechanisms, such as shrews (*Crocidura*, Cosson et al., 2005), salamanders (*Pleurodeles*, Veith et al., 2004), and snakes (*Macroprotodon*, Ca-rran-za et al., 2004). The importance of habitat preference and species behaviour in the Mediterranean is manifested by habitat-specific speciation in warblers of the genus *Sylvia* (Blondel et al., 1996). There is also a clear species-specific relationship between behaviour and success in spreading migrants in other flying vertebrates such as one bat species (Juste et al., 2004; Juste, pers. com.). Divergence time estimates for lacertid lizards revealed that colonization of *Psamodromus algirus* took place around 2 Ma, which again illustrates success in colonizing Mediterranean habitats despite absence of long-distance dispersal mechanisms (Carranza et al., 2006). In contrast, different habitat preferences coupled with poor dispersal mechanisms may have accounted for a vicariance pattern of speciation related to the reopening of the SG in frogs: the spadefoot toads *Pelobates cultripes* (Iberian Peninsula) and *P. varaldii* (northern Africa) (García-Paris et al., 2003) and the painted frogs (*Discoglossus* spp.) (Fromhage et al., 2004). The same is true for continental fishes (*Barbus* spp.), in which the single northern African species separated from the lineage of seven Iberian species after the flooding of the Strait of Gibraltar (Zardoya and Doadrio, 1999). Similarly to coastal plants, currents have favoured migration of marine animals between the Atlantic ocean and the Mediterranean sea (Patarnello et al, 2007). As shown for plants, the phylogeographical signal is not only determined by natural dispersal ability (high in birds, limited in continental fishes), but also by habitat specificity and opportunities for human-mediated colonization. However, *Homo sapiens* presents a distinct phylogeographical pattern; human populations show limited historical gene flow across the SG during the last 30 ka, as revealed by high resolution Y-chromosome polymorphisms (Bosch et al., 2001).

Disparate results obtained to date suggest that the SG *per se* is not an important barrier moulding the range structure of the species. It appears to differ little from other areas with abrupt changes, such as the Guadalquivir or Loukos valleys, which deserve a proper analysis. It is difficult to identify a general relationship between morphological traits of a given species and dispersal ability (syndrome), perhaps due to the low number of species being studied (Tables 1 and 2) and to the low functional significance of many syndromes (Nathan, 2006). However, there seems to be a stronger relationship with the ability of a species to establish itself in new territory, for both plants and animals, which depends on the habitat specificity and abundance of a species, and its life-history and demographic constraints. These factors have a stochastic component which should not be neglected in interpreting present-day distributions and speciation processes in the SG. The differentiation (at the population and species level) of tree species in the SG suggests that establishment, rather than dispersal itself, may be acting as a key factor. Many tree species need stable habitats to complete their life cycle, as those included in the long lasting refugium of the SG during the Plio–Pleistocene, which confers a frame needed for differentiation. The Biodiversity (at the phylogenetic and phylogeographical levels) shown by these long-lived forest species is thus associated with areas of paramount importance for human settlements in the SG because these forests provided "nurturing sites" in terms of food resources, as *Quercus* and *Olea* still do in many human communities (Rodríguez-Ariza and Moya, 2005). In turn, it is worth noting that long standing human presence in the SG (Finlayson, 2008) may have played an important role in the dispersal of species, either intentionally (*Quercus*, *Olea*, *Pinus*, *Laurus*) or accidentally (*Calicotome*, *Cistus, Saxifraga*), as has been increasingly suggested (Nathan, 2006).

5. Single-species traits

Geographical ranges of taxa vary through time and space in terms of extension, abundance or variation in morphological traits in response to changing environments. The resulting geographic patterns should also be considered as biodiversity components. The geographical analysis of trait variation may shed light on the causes underlying biogeographical patterns if this variation responds to environmental changes (Endler, 1977). Traits directly involved in reproduction, such as those related to floral biology or life-history are particularly meaningful since they often show adaptive adjustments to environmental changes. The SG has forced plants to face changing environmental conditions in their migration, thus offering an excellent opportunity to analyze the way plants respond.

5.1. *Reproductive biology*

The geographical analysis of floral trait variation across the SG may help to elucidate the role of environmental variability in determining biogeographical and biodiversity patterns, given its direct relation with breeding system shifts and adaptive evolutionary change. This kind of study is conceptually similar to those that analyze evolutionary changes of colonizing species, especially common in oceanic islands (Valido et al., 2004; Vargas, 2007), but little explored in continental floras. The following examples illustrate the importance of floral traits and their breeding consequences in the distribution and evolution of plants that have undergone migration and differentiation in the SG region, where the environment contrasts markedly with surrounding areas.

The annual mercury (*Mercurialis annua*) is a ruderal annual plant common in W Europe and throughout the Mediterranean. It shows an interesting geographical pattern of its reproductive biology and ploidy levels (reviewed in Pannell et al., 2004). In most of its range the species is diploid and dioecious (separate genders), whereas polyploid populations occupy dry regions of the W Mediterranean. The latter are mostly monoecious (male and female flowers in the same individuals) with some additional shifts to androdioecious (male and monoecious plants) and subdioecious (male, female and monoecious plants) populations in regions close to the SG (Fig. 5). Pannell (1997a,b) hypothesized that the shift from dioecy to monoecy may have been a response to selection for reproductive assurance during the repeated bouts of local population extinction and colonization characteristic of the species. Both genetic (Obbard et al., 2006b) and demographic data (Eppley and Pannell, 2007) are consistent with the prediction that monoecious populations should occur in areas with more rapid population turnover than populations in which males, or males and females, occur. Hexaploid populations of *M. annua*, where most of the sexual-system variation occurs, appear to be allopolyploid hybrids between tetraploid *M. annua* and another Mediterranean endemic, *M. huetii* (Obbard et al., 2006a). Genetic data further suggest that the hexaploid populations had an SG refugium, probably on both sides of the Strait, the tetraploids a north African refugium, and the diploids an eastern Mediterranean refugium (Obbard et al., 2006b) from which they migrated into Spain from the north (Buggs and Pannell, 2006).

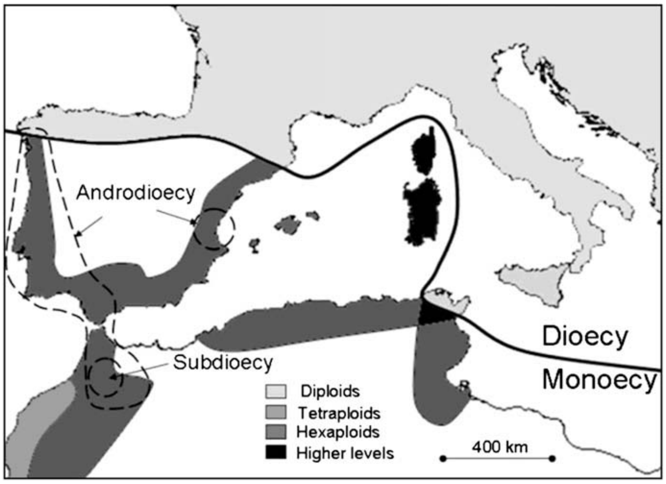

Fig. 5. Distribution of sexual systems and cytotypes of *Mercurialis annua* through the Mediterranean and Europe. Slightly modified, with permission, from Pannell, 1997b and Pannell et al., 2004.

Interestingly, another Mediterranean ruderal species, the squirting cucumber (*Ecballium elaterium*), shows a different pattern. This species has dioecious and monoecious subspecies which are geographically and ecologically separated. Monoecious populations are found in milder regions and habitats, whereas dioecious populations inhabit drier areas (Costich and Meagher, 1992). These authors suggested that more stressful environments are more easily invaded by comparatively more heterozygous, and thus genetically more diverse, dioecious populations. Dioecious lineages would have originated in the process of migration from E to W Mediterranean via N Africa, and would have then colonized the S Iberian range, as has also been proposed for some *Quercus* species (see Section 4.2).

Morphological variation of flowers in fully hermaphroditic plants has been frequently used to infer variations in their flowering biology and breeding systems. It is worth noting the recent study by Ortiz et al. (2006) on the breeding systems of the four species of *Hypochaeris* sect. Hypochaeris (Compositae), cat's ear plant, which shows the highest diversity on both sides of the SG. These authors found that there was a strong variation across species, populations and individuals on both sides of the SG in self-compatibility and associated flower-head traits (such as size or anthesis time). They suggested that these variations are explained by different demographic dynamics on both sides of the SG in very variable environments, particularly for the endemic *H. salzmanniana*, where migration from N Africa to S Iberia is associated with the loss of self-incompatibility (Ortiz et al., 2007).

Daffodils (*Narcissus* species) constitute one of the most relevant study systems on floral biology and differentiation across the SG region. This genus shows high species diversity in S Iberia and NW Africa and a strong inter- and intra-species variability in breeding systems and flower morphology of high significance for pollination ecology and reproductive biology (Arroyo, 2002). *Narcissus* has been critical for testing hypotheses on the evolution of heterostyly, a particular genetically based polymorphic breeding system of plants which has long intrigued evolutionary biologists. Thus, the existence of two or three discrete floral morphs of style length within a single population has been explained either as a result of the role of pollinators promoting pollen transfer with little interference between stamens and stigmas (Lloyd and Webb, 1992) or as a mechanism to avoid inbreeding (Charlesworth and Charlesworth, 1979). Detailed ecological and phylogenetic work on *Narcissus* sect. Apodanthi has provided new insights in support of Lloyd and Webb's hypothesis (Pérez et al., 2004; Pérez-Barrales et al., 2006). None of the seven species in the group has a geographical range extending on both sides of the SG and some of them are endemic to isolated mountains of Morocco (three species) or Iberia (four species). However, some of them show similar floral patterns which pinpoint parallel evolutionary histories on both sides of the SG (Fig. 3). Thus, both narrow endemic Moroccan *N. albimarginatus*, and the Iberian *N. triandrus* complex, in different taxonomical sections and clades, present heterostyly. Indeed, these species are the only known heterostylous ones in the genus and they have indeed similar floral traits and pollinator faunas, i.e., large solitary bees and bumblebees. These species, in addition to nearly heterostylous and somewhat similarly flowered *N. cuatrecasasii* (the sister species of *N. albimarginatus*) occur in similar habitats where these insects visit the flowers. It has been proposed that these insects are the most efficient pollinators promoting pollen transfer between morphs and thus are critical to build up heterostyly. Therefore these two independent origins of heterostyly represent a case of convergent evolution mediated by pollinators (Pérez et al., 2004). A second lineage includes species of high mountains (*N. rupicola* in C Iberia and *N. marvieri*–*N. watieri* in Atlas Mountains of Morocco). Although they have very similar flower morphologies and roughly similar pollinators, the two species living at high elevations (>2000 m), *N. rupicola* and *N. watieri*, show a loss of self-incompatibility, as a likely result of harsh environmental conditions for insect pollination (Baker, 1955).

Flower biology also presents some intra-specific variation in *Narcissus* species whose geographical range crosses the SG. *N. papyraceus* has style dimorphic (a polymorphism similar to heterostyly) and isoplethic (1:1 ratio of long-styled to short-styled morphs) populations in areas close to the SG, on both sides (Arroyo et al., 2002). Inland populations show a sharp decrease in short-styled plants until complete disappearance. A shift in the pollinator array across this geographical gradient (coast-inland) maintains style dimorphic and monomorphic populations, being this change parallel on both sides of the SG. This can be explained because the pollinator environment in coastal regions on both sides of the SG is more similar than their respective hinterlands. Short-tongued pollinators (hoverflies) are almost the only pollinators of inland populations and they cannot reach the hidden short stigmas, which remain unpollinated (Pérez-Barrales et al., 2007). There is a close correspondence between these two groups of populations and those depicted in the phylogeographical reconstruction of AFLP lineages (Fig. 4, see Section 4.2). However, the relationship between flower morphology and genetic distance of populations was weak (Pérez-Barrales et al. 2008).

Analyses of variation in floral biology of long-lived plants, such as trees, are not available. Although all examples reviewed here refer to herbaceous plants which are expected to respond faster to evolutionary forces, they illustrate how differences and similarities of selective forces may drive differentiation processes through the SG. In particular, the fine mosaic of biotic and abiotic environmental conditions in the SG region may be responsible for the building up of its biodiversity.

5.2. *Regeneration ecology*

We have already shown that the two most characteristic groups of species in the SG region are geographically rare taxa (*sensu* Rabinowitz, 1981), either endemics or Late Tertiary relicts. The first category includes a high number of taxa mostly confined to Mediterranean heathlands on acid sandstone, poor nutrient soils. A mild Mediterranean climate and the recurrent presence of fire also govern the presence of these Mediterranean heathlands (Ojeda et al., 2001). The second species group, Late Tertiary relicts, is smaller in terms of number of representative taxa, and occurs in year-round moist habitats, mainly riparian forests, deep sandstone gorges, and moist forests. We present evidence below that contributes to understanding ecological factors responsible for the narrow geographical range and/or the presumable range decline of these two groups of species.

5.2.1. *Sandstone heathland endemics*

Oligo–Miocene sandstone soils appear as patches on summits and ridges of mountains and hills on both sides of the SG (Ojeda et al., 1996a; Fig. 1). Apart from the sandy texture and low pH, they are characterized by an extremely low fertility and a high content of soluble aluminium, a toxic element for plants (Ojeda et al., 1995, 1996a). It is on these soils where the Mediterranean heathland, locally known as *herriza*, occurs. Unlike other European heathlands, the Mediterranean heathland presents a high plant biodiversity (Ojeda et al., 2001) and, despite being a Mediterranean vegetation type, it is floristically distinct from the Mediterranean garrigue and maquis (Ojeda et al., 1996a, 2000b). These Mediterranean heathlands are characterized by a dominance of woody species highly tolerant of the extreme edaphic conditions, most of them being narrow endemics (i.e. restricted to both sides of the SG; Ojeda et al., 1996a, 2000b, 2001). They are actually the major contributors to the high biodiversity of the SG (Ojeda et al., 2001).

The Mediterranean heathland is also singular from an ecological point of view, particularly regarding its tight association with recurrent fires. The ability to endure wildfires is a feature of Mediterranean shrublands in general (e.g., Keeley, 1986; Pausas et al., 2004). Most Mediterranean-type shrublands are dominated by either *seeder* species, whose adult individuals are killed by fire and whose populations are re-established by an effective post-fire recruitment, or *resprouter* species, which are fire-resilient and whose seed germination is not associated with fire (see Keeley, 1986). Verdú (2000) pointed out that seeder and resprouter species from Mediterranean shrublands basically correspond to the two morphological–functional syndromes described by Herrera (1992). Seeders are mainly non-sclerophyllous, anemochorous, dry-fruited, small-seeded species with a long-lived seed-bank, which diversified in the Quaternary (post-Pliocene), whereas resprouters are mainly sclerophyllous, vertebrate-dispersed, fleshy-fruited, large-seeded species with no seed-bank, which evolved in the Neogene (pre-Pliocene). Resprouter species, whose recruitment is not attached to fire, actually dominate the sclerophyllous garrigue and maquis shrublands present in the SG region, and most of the species have fleshy fruits with endozoochorus dispersal (e.g., see "other Mediterranean taxa" in Table 3). By contrast, seeder and resprouter species co-occur in Mediterranean heathlands (Ojeda,

Table 3
Performance of sexual regeneration and presence of traits enhancing persistence in several biogeographical types of species in plant communities of the Strait of Gibraltar (+ good performance/trait present; − poor performance/trait absent; ?, unknown; p, post-fire; f, fleshy fruit)

Floristic element	Species	Sexual regeneration						Persistence					References
		Flowering	Fruit/seed production	Seed dispersal	Survival to postdispersal predation	Seedling emergence	Seedling establishment	Longevity	Sprouting ability	Seed bank	Seedling bank	Vegetative spread	
Late Tertiary relicts (Riparian forests)	*Frangula alnus*	+	− (f)	+	−	+	−	+	−	−	+	−	Hampe and Arroyo (2002), Hampe (2004, 2005)
	Ilex aquifolium	+	+ (f)	+	?	?	?	+	+	−	+	+	F. Ojeda pers. obs.
	Laurus nobilis	−	+ (f)	−	+	+	+	+	+	−	+	+	Hampe, 2003, F. Rodríguez-Sánchez unpub. data
	Prunus lusitanica	+	+ (f)	+	+	+	−	+	+	−	+	+	Calleja (2006), Pulido et al. (2008)
	Rhododendron ponticum	+	+	+	+	−	−	+	+	−	+	+	Erfmeier and Bruelheide (2004), Mejias et al., 2002; Stout et al. (2006)
Other Mediterranean taxa	*Myrtus communis*	+	+ (f)	+	+	−	+	+	+	−	+	+	J.P. González-Varo unpub. data
	Olea europaea	+	+ (f)	+	?	+	+	+	+	+	+	+	F. Rodríguez-Sánchez unpub. data
	Phillyrea latifolia	+	+ (f)	+	?	+	+	+	+	?	+	+	F. Rodríguez-Sánchez unpub. data
	Quercus canariensis	+	+	+	−	+	+	+	+	−	+	−	Pérez-Ramos et al., 2008, Urbieta et al. (2008) F. Rodríguez-Sánchez unpub. data
	Quercus pyrenaica	−	−	?	−	+	+	+	+	−	+	+	Marañón et al. (2004), Urbieta et al. (2008), F. Rodríguez-Sánchez pers. obs.
	Quercus suber	+	+	+	−	+	+	+	+	−	+	−	Pérez-Ramos et al. (2008), Urbieta et al. (2008)
	Viburnum tinus	+	+ (f)	+	?	+	−	+	+	?	+	+	F. Rodríguez-Sánchez unpub. data
Endemics (Mediterranean heathlands)	*Cistus populifolius*	+	+	+	+	+ (p)	+	−	−	+	−	−	Ojeda et al. (1996b), pers. obs.
	Drosophyllum lusitanicum	+	+	+	?	+ (p)	+	−	?	+	?	−	Garrido et al. (2003), F. Ojeda pers. obs
	Erica australis	+	+	+	+	+ (p)	+	+	+	+	−	−	Ojeda et al., (1996b), pers. obs.
	Genista triacanthos	+	+	+	+	+ (p)	+	−	−	+	−	−	Ojeda et al. (1996b), pers. obs.
	Genista tridens	+	+	+	+	+ (p)	+	−	+	+	−	−	Ojeda et al. (1996b), pers. obs.
	Quercus lusitanica	−	−	−	?	?	?	+	+	−	?	+	Ojeda et al. (1996b), pers. obs.
	Satureja salzmannii	+	+	+	+	+ (p)	+	−	−	+	−	−	Ojeda et al. (1996b), pers. obs.
	Stauracanthus boivinii	+	+	+	+	+ (p)	+	−	+	+	−	−	Ojeda et al. (1996b), pers. obs.
	Thymelaea villosa	+	+	+	+	+ (p)	+	−	+	+	−	−	Ojeda (2001), pers. obs.

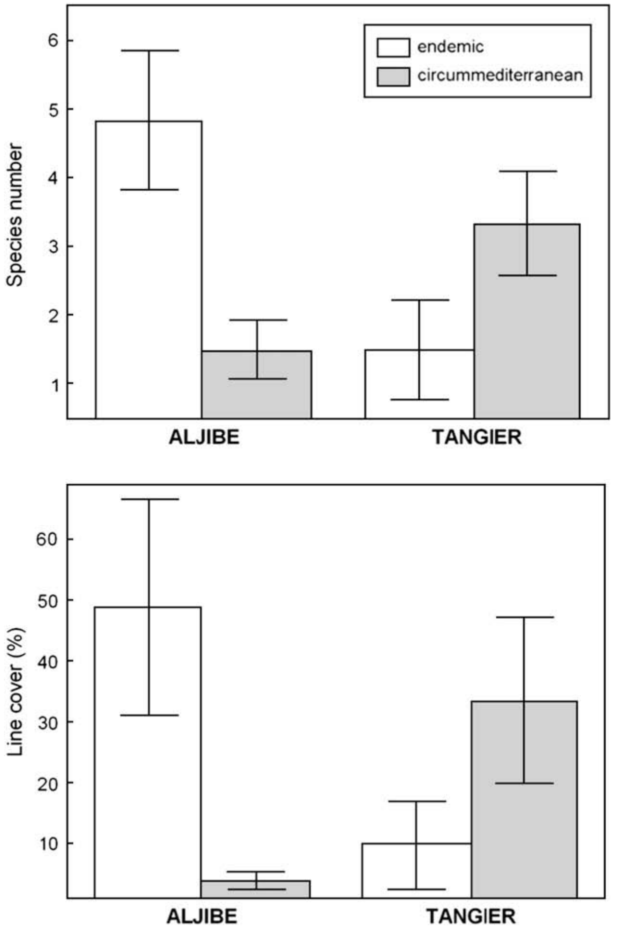

Fig. 6. Averaged values (mean ± SE) of number and relative abundance (% of line cover) of woody species restricted to the SW Iberian Peninsula and NW Morocco (endemic), and woody species with a distribution range throughout the Mediterranean Basin (circum-Mediterranean) in Mediterranean heath-community samples of the northern (Aljibe; n = 8) and southern (Tangier; n = 4) sides of the Strait of Gibraltar. Data obtained from Ojeda (1995).

2004), and most heathland resprouter species are also dry-fruited and post-fire recruiters (Ojeda et al., 1996b; see "endemics" in Table 3, all of them heathland endemics), i.e., they do not fit into any of the two basic functional syndromes for Mediterranean shrublands (see Verdú, 2000).

Hence, woody species from Mediterranean heathlands of the SG, most of them endemics, are not only attached to acid, sandstone soils, but also to the presence of recurrent disturbance (e.g., fire). They are not only resilient to wildfires, but seem to be sensitive to the lack of fire (Ojeda, 2001, 2004). The endemic insectivorous sundew *Drosophyllum lusitanicum* constitutes a paradigmatic example of Mediterranean heathland species whose recruitment seems to be limited by the lack of disturbance (Garrido et al., 2003).

At the community level, the number of endemics is comparatively lower in Mediterranean heathlands of the southern side of the SG region (Ojeda et al., 1996a; Fig. 6). This decrease might be explained by the more fragmented and isolated pattern of sandstone patches on the southern side of the Strait (Ojeda et al., 1996a; see Fig. 1). This could lead to greater isolation of plant populations tightly attached to sandstone soils, most of them endemic, making them more vulnerable to processes of local extinction. These depauperate heath-communities are then dominated by edaphic-tolerant species, with a wider edaphic amplitude, and a subsequent wider geographical distribution throughout the Mediterranean Basin (i.e. circum-Mediterranean species; see Fig. 6), such as *E. arborea* (Ojeda et al., 2000a).

5.2.2. Tertiary relicts

We have shown that most Tertiary relicts are tightly associated with "warm and moist" habitats, and this gives a clue to why they were so severely affected by the Messinian Salinity Crisis and Pleistocene glaciations throughout the Mediterranean. What circumstances enabled the persistence of these relicts for such a long period in the SG? Apart from the peculiar geographical and environmental conditions of the area, and the particular microclimate of the habitats in which they occur (Fig. 2), there are also several intrinsic biological features of these species which may have promoted their persistence (see Table 3). Recent work on the regeneration ecology of lauroid and other woody species provides a better understanding of their mechanisms of persistence and regeneration strategies. Sexual regeneration appears seriously limited in most cases, either by abiotic or biotic factors. For instance, summer drought and winter currents cause the death of almost all seedlings of *Rhododendron ponticum* and *Frangula alnus* every year (Hampe and Arroyo, 2002; Mejías et al., 2002, 2007), creating a recurrent bottleneck for regeneration, while eventual late-spring heat waves pose a threat for fecundity in *F. alnus* (Hampe, 2005). On the other hand, biotic factors such as the inefficient mutualistic relationship between *Laurus nobilis* and its seed dispersers (Hampe, 2003), or the high predation of acorns of *Quercus* species (Pérez-Ramos et al., 2008) greatly reduce the probability of successful sexual recruitment. It should be noted that the densest *Quercus* overstoreys provide a suitable habitat for most of these relict species, whereas human activities have affected their population sizes and viability in recent millenia (Jurado, 2002).

When sexual regeneration is compromised, many plants have some demographic and life-history features – such as long lifespan, sprouting ability, the formation of seed or seedling banks, and/or vegetative spread – that enhance their probability of persistence under unfavourable conditions (Bond and Midgley, 2001; García and Zamora, 2003). These attributes are shared by most of the relict species present in the SG region (Table 3), as well as in other relict populations in different areas. For instance, the small-leaved lime (*Tilia cordata*) seems to have survived in Northern Britain exclusively by sprouting for the last five thousand years, since climate cooled and prevented reproduction (Pigott, 1992). Moreover, clonal spread has been determinant in the expansion and regeneration of local *Rhododendron ponticum* populations, as revealed by recent genetic fingerprinting studies (J. Arroyo et al., unpublished data). By having a high longevity (typically several hundred years in Mediterranean azaleas: Mejías et al., 2007), unsuccessful seedling recruitment loses demographic relevance, as populations can persist by episodic recruitment during favourable periods (e.g., Hampe and Arroyo, 2002). This regeneration strategy, combined with a long history of isolation of these populations, is responsible for the high genetic diversity of these species at a regional level (Petit et al., 2005), which confers on them a high biodiversity value and evolutionary potential, with implications for conservation (Hampe and Petit, 2005). However, removal of the seedling banks or increased adult mortality, caused either by inadequate forest management techniques (e.g., slashing and clearing, Jordano et al., 2001), increased herbivory pressure, or changes in climatic conditions (see Section 5.3), could have a strong effect on the future viability of these populations.

5.3. Recent changes and future prospects

Terrestrial ecosystems of the Mediterranean Basin have faced a long and intense history of human-derived disturbance at least since the Neolithic (Thirgood, 1981), (mean ± SE) which might account for the characteristic resilience of the Mediterranean vegetation to severe disturbance (e.g., see Lavorel, 1999). Humans have certainly interfered in the SG region, although management intensity in this region may have been comparatively less severe, owing to the topography and low fertility of the acid soils, which might explain the relatively high conservation levels.

Nevertheless, the outstanding plant biodiversity of the SG is facing an inexorable decline as a consequence of human activity. The European side is somewhat protected under the auspices of the Natural Park *Los Alcornocales*. However, Mediterranean heathlands have been traditionally disregarded or considered as mere "treeless" or degraded "pre-forest" stages, and have been systematically "restored" by afforestation with pine trees (Andrés and Ojeda, 2002). On the other hand, the Moroccan side is subject to more intensive human pressure (Mikesell, 1960; Moore et al., 1998; Ajbilou et al., 2006) in addition to an intrinsically higher vulnerability as a consequence of the more fragmented and isolated sandstone patches (Ojeda et al., 1996a).

As in many other parts of the world, this region is undergoing a process of climate change. During recent decades, temperatures have increased continuously, while annual total rainfall decreased (Castro et al., 2005), primarily because of a reduction of spring and early summer rainfall. This actually means an extension of the seasonal, summer drought characteristic of the Mediterranean climate, and this progressive aridification is predicted to continue (IPCC, 2001; Raisanen et al., 2004).

The fact that the SG region is close to the southern limits of the Mediterranean climate entails that its biota especially sensitive to present and future scenarios of climate change. Although higher CO_2 concentrations and warmer temperatures could at first translate into longer periods of vegetative activity and improved productivity for some species (Hughes, 2000), it is more likely that water availability becomes limiting in this area (Fernández-González et al., 2005). The earlier onset of the hot and dry period may have strong impacts on fecundity (Hampe, 2005), growth rate (F. Rodríguez-Sánchez et al., unpublished data), and seedling survival and regeneration of Late Tertiary relict species (Hampe and Arroyo, 2002; Mejías et al., 2002, 2007). In a situation of higher water deficit caused by warmer temperatures and less rainfall, lauroid and moderate sclerophyllous species (such as *Lurus nobilis*, *Rhododendron ponticum*, *Prunus lusitanica*, *Arbutus unedo* or *Viburnum tinus*) would be the most affected (Valladares et al., 2004), followed by other deciduous and sclerophyllous woody species such as *Q. canariensis* and *Q. suber* (Fernández-González et al., 2005). For instance, intense droughts are responsible for a high mortality of adults of *R. ponticum* in the Aljibe Mountains (Mejías et al., 2002). Reduced relative humidity could also raise the frequency and extension of wildfires (e.g., Piñol et al., 1998). In spite of that, several demographic characteristics of the species mentioned (long life-span, sprouting ability, etc, see above) and the environmental conditions of the SG region – topographic ruggedness and oceanic influence – which enhanced its role as a refugium during past climatic cycles, support the possibility that these species will persist as remnant populations through future climatic conditions (García and Zamora, 2003; Hampe and Petit, 2005). In fact, these species have already survived warmer conditions in the Subatlantic and Subboreal periods (Allen et al., 1999).

6. Concluding remarks

In this review we have addressed a two-fold approach, chronological and conceptual. We have focused on present-day patterns of biodiversity, and then we have reviewed the available evidence from phylogenetic and phylogeographical studies which may help to hypothesize underlying processes determining the pattern of distribution across the SG and its possible role as a biogeographical barrier and/or bridge. Multiple patterns of speciation in the species-rich area of the SG indicate that a higher number of examples are needed to draw general conclusions and that no morphological trait related to dispersal appears to determine a common pattern of diversification. phylogeographical studies of species typical of the SG region have shown that, in general, the process of isolation and later differentiation is not necessarily associated with the presence of an apparently efficient seed dispersal system. In fact, the observed lack of effective gene flow in most trees (even those dispersed by birds), and the scarce isolation of short-lived herbs and pioneer shrubs without a specialized long-distance dispersal mechanism, point to colonizing ability and habitat specificity – rather than dispersal itself – as the limiting factor of range expansion across the SG. Multiple lines of evidence suggest that humans may have played an important role as a long-distance dispersal vector both for animal and plant species.

Nonetheless, in the long run, most tree species end up crossing the SG, either from the N African side (*Quercus*), from the Iberian Peninsula (*Pinus*, *Frangula*), or in both directions (*Olea*). Most of these tree species show a high genetic diversity and distinctiveness in the SG region, supporting its role as a refugium in the harsh climates that have prevailed since the Late Tertiary and particularly in the Pleistocene Ice Ages. Thus, the present mild Mediterranean climate of the SG may have persisted to some extent during most of the Pleistocene without much vertical (altitudinal) movement, otherwise typical of smaller and more isolated refugia in the Iberian mountains (Carrión, 2001). These stable environmental conditions may have also accounted for the late survival of isolated Neanderthal populations in the northern coastal regions of the SG (Carrión et al., 2008, Finlayson, 2008). This small region constituted the last refugium for Neanderthals until their complete extinction at 28 ka, well after the establishment of modern human populations elsewhere in Europe (Finlayson et al., 2006).

Other lines of evidence support the SG region as a hotspot for evolutionary processes at the population level. Some abundant plant species show contrasting shifts in their breeding systems across the SG, which indicates that the crossing of the SG, together with some particular differences in key environmental conditions, promote such shifts. Stressful or unpredictable environments may have favoured the evolution of separate sexes in *Ecballium elaterium*, whereas in *Mercurialis annua*, monoecy has evolved from dioecy in response to selection for reproductive assurance, perhaps in the context of shifts in polyploidy. The presence of a similar pollinator array may have determined the convergent evolution of heterostyly (*Narcissus*) on both sides of the SG.

Endemic species of the SG are tightly associated with nutrient-poor, acid soils, but they have not yet been the subject of phylogenetic/phylogeographical research (*Ulex* and *Stauracanthus* being an exception). Therefore, it remains unanswered whether the process of edaphic differentiation is derived or ancestral in the taxonomic groups to which endemic species belong.

Tertiary relicts are probably the most relevant species of the SG region, when considering the information they provide about the past vegetation of the SG. The study of their history and ecology is throwing light on their role as key witnesses of the past SG biota. In particular, despite their contrasting evolutionary origins and different taxonomic status, all of them show recruitment failures at different stages and by different causes. Among them, harshening of climatic conditions seems to be of paramount importance, and thus makes them extremely sensitive to the present scenario of global climate change.

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