ORIGINAL ARTICLE

In and out of Africa: how did the Strait of Gibraltar affect plant species migration and local diversification?

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ABSTRACT

Aim The biotic mechanisms by which land bridges influence the formation of regional floras remain poorly understood. We tested the hypothesis that some land bridges have biased the migration of species between landmasses according to their biological traits, and that this relative spatial isolation has caused some lineages to diversify more than others.

Location The Strait of Gibraltar Floristic Region, a major biodiversity hotspot of the Mediterranean Basin.

Methods We compiled the angiosperm flora of the study region to examine patterns of narrow endemism and species disjunctions between southern Iberia and northern Morocco. We focused on species that occur in the western portion of the Mediterranean Basin ($n = 566$) but not further east in this region, in order to test for the specific effect of the Strait of Gibraltar. Using phylogenetic supertrees, we tested whether species' life-history traits were related to their probability of occurring on both sides of the strait. We looked at patterns of narrow endemism in different families and computed birth–death model estimates of local diversification within the region.

Results Species with a short life cycle and propagules dispersed by wind or externally on animals were disproportionately likely to occur on both sides of the strait. Different plant lineages exhibited disparate distribution and endemism patterns across the strait. Some families have experienced disproportionately high rates of local diversification, and these families were systematically characterized by a low migration rate across the strait. We detected no difference of overall rates of local diversification between the southern Iberian and northern Moroccan parts of the study region.

Main conclusions Our results indicate that the Strait of Gibraltar has biased species migration between northern Morocco and southern Iberia and that reduced migration through the strait may have triggered local speciation in certain plant families. This pinpoints the fundamental interplay between species migration and evolutionary diversification in the construction of hotspots of biodiversity and narrow endemism.

Keywords
Biodiversity hotspot, land bridge, life-history traits, Mediterranean, migration, narrow endemism, species diversification.

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INTRODUCTION

Global patterns of species distribution and evolutionary diversification have been profoundly impacted by Earth's physical history, including climatic changes, continental drift and orogenies (Raven & Axelrod, 1974; Hedges *et al.*, 1996; Jablonski, 2003; Hughes & Eastwood, 2006). Land bridges, that is isthmuses or straits that have intermittently or permanently connected different continents (e.g. Elias *et al.*, 1996; Elias & Crocker, 2008), have long been key study regions

for biogeographers and evolutionary biologists. Indeed, such geographic settings constitute contact zones that have permitted species migration between otherwise disconnected continental plates, and have allowed the evolutionary diversification of particular clades (Savile, 1956; García-Moreno et al., 2006; Hughes & Eastwood, 2006; Moore & Donoghue, 2007). Land bridges thus offer unique geographical settings to study the processes that shape the distribution of biodiversity, and to elucidate the interplay between the range dynamics and the diversification of lineages, which is very difficult to discern otherwise. Notwithstanding, the actual biotic mechanisms by which land bridges affect species migration, lineage diversification and ultimately the evolution of regional floras remain poorly understood.

It is well known that land bridges have permitted intercontinental migration of numerous plant and animal lineages through the Cenozoic (Savile, 1956; Xiang & Soltis, 2001; Cavers et al., 2003; Milne, 2006). Yet few quantitative studies have addressed the long-standing hypothesis that land bridges have acted as ecogeographical filters, i.e. they have influenced species migration according to these species' biological traits (Simpson, 1940; Hopkins, 1959). The concept of ecological filter has been instrumental in the development of various theories of community ecology and biogeography (Simpson, 1940; MacArthur & Wilson, 1967; Keddy, 1992) because it allows us to address the processes that shape species assemblages based on their biological and ecological characteristics. The mechanisms by which species migrations would be filtered through land bridges should involve the two basic components of colonization processes: (1) the ability of long-distance propagule dispersal, and (2) the ability of establishing new populations at the site of propagule arrival. In plants, the first component is assumed to be favoured by certain dispersal vectors such as wind, vertebrates or sea currents (e.g. Vittoz et al., 2009), whereas the second should typically benefit from ruderal ecological strategies, usually characterized by a small stature and a short life cycle (e.g. Shipley et al., 2006). Very few studies have asked whether these plant traits have actually favoured species migration across land bridges, ultimately shaping the extant floras on both sides of these bridges (but see Jordan, 2001; Burns, 2005; Bernardello et al., 2006; Cody, 2006).

The frequency of migration events across land bridges is in turn likely to influence rates of local diversification. In particular, if rare migration events between extant landmasses can favour the colonization of vacant niches and lineage diversification (Moore & Donoghue, 2007; Johnson & Weckstein, 2011; Vila et al., 2011), frequent crossings of land bridges will ultimately tend to hamper genetic differentiation and allopatric speciation (Savile, 1959; Carlquist, 1974; Harris et al., 2002; Carranza et al., 2006; Arroyo et al., 2008). A paradigmatic example is the Palk Strait, which intermittently connected Sri Lanka to southern India during the Pleistocene. This resulted in a marked local diversification of poorly dispersed lineages of vertebrates and invertebrates within Sri Lanka, generating an endemic fauna derived from its conti-

nental counterpart (Bossuyt et al., 2004). This example illustrates how some land bridges, through their particular geographical and historical setting, have constituted an important stimulus for evolutionary diversification and the emergence of some biodiversity hotspots (see also Rodríguez-Sánchez et al., 2008).

Here we focus on the Strait of Gibraltar Floristic Region (Valdés, 1991), which is particularly well-suited to investigate the interplay between species migration and diversification. First, the Strait of Gibraltar (Fig. 1) has been an intermittent land bridge between Southwest Europe and Northwest Africa and hence a potential filter to plant migration. Second, the Strait of Gibraltar is a major hotspot of plant biodiversity of the Mediterranean Basin (the Baetic–Rifan hotspot, Fig. 1b; Médail & Quézel, 1997) containing many late Paleogene–Neogene relicts and recent narrow endemic species (Postigo Mijarra et al., 2009). In this work, we focused on species occurring in the western Mediterranean Basin but not further east ($n = 566$), that is, those species that are likely to have crossed the Mediterranean Sea through the Strait of Gibraltar (and not via more eastern land bridges or its eastern end). Based on comprehensive floristic data, patterns of species distribution and endemism, species' life-history traits and phylogenetic supertrees, we assessed whether the strait has affected species migration and diversification. More specifically, we tested: (1) whether species occurring on both sides of the strait tend to show particular life-history traits that can be assumed to favour colonization events, (2) whether local species diversification (i.e. the emergence of narrow endemic species) has been higher within certain plant lineages and higher on one side of the strait than the other, and (3) whether local diversification of certain lineages (i.e. emergence of local endemics) has been favoured by reduced migration through the strait.

MATERIALS AND METHODS

Study region

The study area extends over c. 7200 km^2 (Fig. 1a) and is composed of two physiographically similar regions: the Algeciras Peninsula (about 2600 km^2), located at the southeastern tip of the Baetic Range in southern Spain (Fig. 1a,b), and the Tanger Peninsula (4600 km^2), located at the northwestern tip of the Rifan Range in northern Morocco (Fig. 1a,b). The two peninsulas share peculiar topographic, climatic and ecological conditions which distinguish them from surrounding regions (Ojeda et al., 1996; Rodríguez-Sánchez et al., 2008). The current climate of the region is Mediterranean with strong oceanic influence, and has prevailed since c. 3.6 Ma (Tzedakis, 2007). The area constitutes an important centre of biodiversity and endemism nested within the Baetic–Rifan biodiversity hotspot (Fig. 1a,b; Médail & Quézel, 1997). The evolution and persistence of its diverse flora has been favoured by extraordinarily heterogeneous environmental conditions and a climate that has
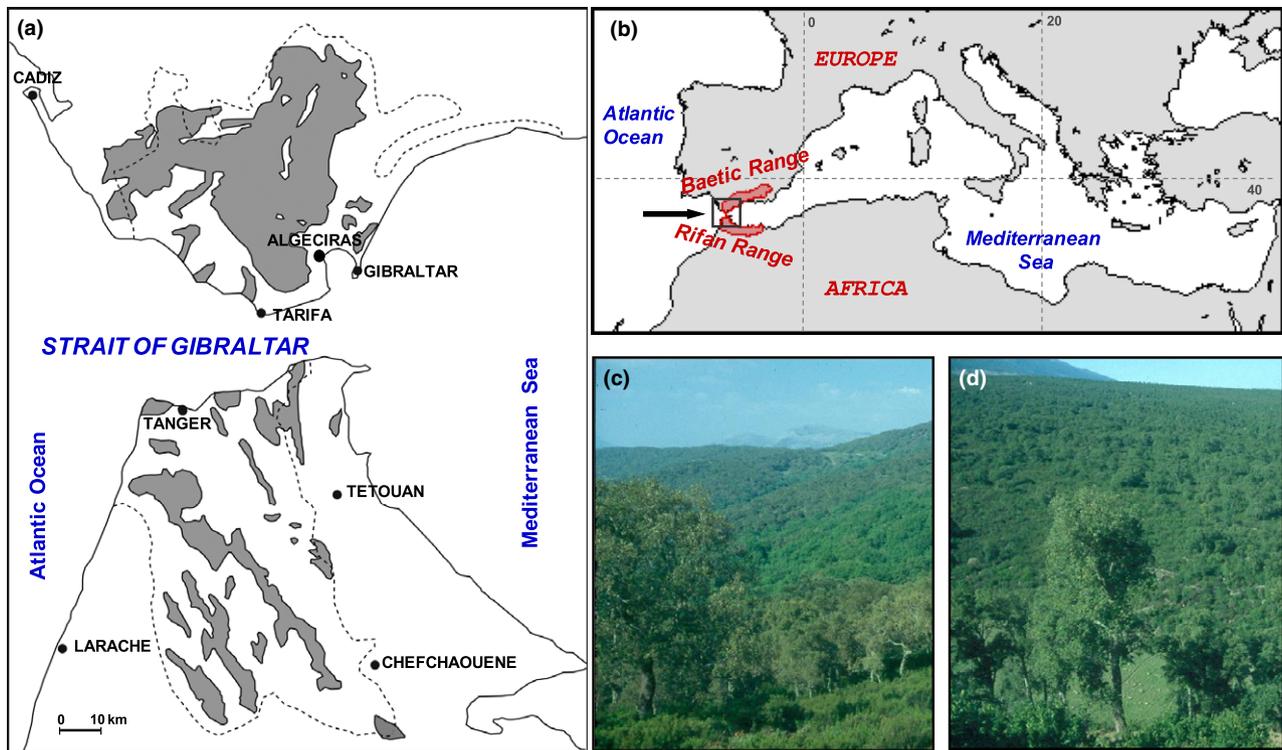
Figure 1 Description and situation of the study region. (a) Map showing the geographical setting of the Strait of Gibraltar, and the spatial extent of the Strait of Gibraltar Floristic Region (dashed line). The position of major cities of the Algeciras Peninsula (southern Iberia) and Tanger Peninsula (northern Morocco) is indicated (black dots), along with the endemic-rich sandstone formations (grey areas). (b) Map of the Mediterranean Basin showing the position of the Strait of Gibraltar Region (frame indicated by an arrow) relative to the Mediterranean Sea and to the Baetic (southern Iberia) and Rifan (northern Morocco) mountain ranges, which together form the Baetic–Rifan hotspot of Mediterranean biodiversity. (c–d) Landscapes of mixed *Quercus suber–Quercus canariensis* woodlands which are typical of Algeciras (c) and Tanger (d) peninsulas.

remained relatively stable since the late Neogene, even through the major climatic fluctuations of the Pleistocene (Rodríguez-Sánchez & Arroyo, 2008; Rodríguez-Sánchez *et al.*, 2008).

The Paleogene–Neogene geological history of the region has been marked by the progressive northward drift of the African tectonic plate and its collision with the Iberian plate, until the complete closure of the Mediterranean Sea at its western end about 6.5 Ma (Krijgsman, 2002; Duggen *et al.*, 2003), which resulted in the Messinian salinity crisis. Since its definitive re-opening about 5.3 Ma, the Strait of Gibraltar has constituted a narrow marine canal separating southern Iberia and north-western Africa. Today it is 14 km wide, although during Pleistocene glaciations this distance shrinked repeatedly to *c.* 10 km due to sea level fluctuations (see Rodríguez-Sánchez *et al.*, 2008).

Landscapes of the Strait of Gibraltar Region are dominated by sclerophyllous *Quercus suber* and semi-deciduous *Quercus canariensis* woodlands (Fig. 1c,d), dissected by deep gorges that contain a diverse woody flora with several pre-Mediterranean relict species (Hampe & Arroyo, 2002; Mejías *et al.*, 2007; Rodríguez-Sánchez & Arroyo, 2008). Other sclerophyllous Mediterranean forests (*Quercus ilex, Q. coccifera, Olea europaea*) and scrublands (*Pistacia lentiscus*) are mostly limited to lowlands and the periphery of the Strait of Gibraltar

Region. Apart from limestone outcrops and marly or loamy soils in lowlands, bedrock is mostly composed of Oligo-Miocene siliceous sandstones which give rise to acid, nutrient-poor and aluminium-toxic patches of sandy soil (Rodríguez-Sánchez *et al.*, 2008). These infertile edaphic islands harbour exceptionally large numbers of narrow endemic plant species, which mostly result from recent speciation (Ojeda *et al.*, 1996, 2000).

In summary, the ecological conditions and the flora of the Strait of Gibraltar Region are very different from those of surrounding regions. This peculiarity, together with the old age and relative stability of the strait, renders the study region a sort of 'ecological island' within the western Mediterranean Basin, characterized by a singular flora and separated in its centre by a narrow strait. This configuration provides a unique ecogeographical setting for a quantitative study of species migration and local speciation.

Species lists

The angiosperm flora of the study region has been exhaustively described in two standard floras (Valdés *et al.*, 1987, 2002). These were written by the same botanists using similar taxonomic criteria, which minimizes potential taxonomic bias between the two works. We used these sources to

'compile a list of 1546 native, non-cultivated angiosperm species occurring in the study area (Fig. 1a). We extracted information about the geographical range of each species from the two mentioned floras, complementing information with other floras of the region (Jahandiez et al., 1931–1941; Maire, 1951–1987; Negre, 1961–1962; Quézel & Santa, 1962; Tutin et al., 1964–1993; Ozenda, 1977; Greuter et al., 1984–1989; Fennane & Ibn Tattou, 1998, 2005; Charco, 2001).

Based on the obtained chorological information, we further delimited our study sample by selecting those species whose geographical distribution encompasses only the western Mediterranean Basin (except southern Italy and Tunisia). In addition, we also excluded species that were typical of coastal shoreline habitats. These criteria were introduced to minimize the probability that the species considered would have crossed the Mediterranean Sea via Italy or Greece or bypassed it at its eastern end, enabling us to focus only on those species whose geographical distribution is likely to have been influenced by their ability to cross the Strait of Gibraltar. With our selection criterion, the geographical distribution of study species may extend beyond the Mediterranean Basin but does not encompass the eastern or central Mediterranean. The procedure reduced our dataset to a total of 566 species. Of these, 298 species occur on only one side of the Strait of Gibraltar (116 species on the Algeciras Peninsula and 182 species on the Tanger Peninsula). We considered that the remaining 268 species occurring on both sides had (1) actually crossed the strait (regardless of the direction), and (2) successfully established on the other side.

We cannot completely rule out that species older than the closure of the Strait of Gibraltar could occur on both sides without having crossed the strait (Hampe & Petit, 2007). However, the proportion of species with such an ancient range should be very low (Herrera, 1992), and the probability that such species would have survived in the western Mediterranean but gone extinct everywhere further east seems even lower. We thus believe that potential biases arising due to extinction events are unlikely. Indeed, the study region is known to have experienced reduced extinction rates with respect to surrounding regions, and the last major extinction period in the area seems to have occurred before the definitive opening of the Strait of Gibraltar (Finlayson & Carrión, 2007; Postigo Mijarra et al., 2009).

Finally, we identified those species that are endemic to the Baetic–Rifan Biodiversity Hotspot (termed narrow endemic species hereafter), in order to estimate the diversification rate of each family in the local flora (termed local diversification rate hereafter, see 'Data analyses'). We assigned our 566 species to a total of 66 families following the APG II nomenclature (Angiosperm Phylogeny Group, 2003).

Life-history traits

We expected that species would be more likely to occur on both sides of the strait if: (1) they exhibited apparent morphological adaptations to 'efficient' dispersal agents (wind or birds, which are likely to carry propagules over large distances), and (2) they were associated with early successional habitats (ruderal species with small stature and short life cycle). Such a trait-based approach has certain drawbacks (discussed below), but it is the only feasible option when working with datasets of several hundred species. Based on morphological descriptions and illustrations found in Charco (2001), Maire (1951–1987) and Valdés et al. (1987, 2002), we compiled the following traits for each species:

1. Long-distance dispersal agent, with the following classes: no identifiable adaptation, anemochorous (propagules with wings, plumes or pappus being more than twice as large as the surface of the seed body, or dust seeds less than 0.5 mm long), endozoochorous (fleshy fruits) and epizoochorous (hooked, sticky or spiny propagules).

2. Plant height (m), as the mid-point of height ranges reported in different sources.

3. Growth form, with the following classes: herbaceous annual, herbaceous perennial and woody.

Phylogenetic information

We used both family-level and species-level phylogenies to perform phylogenetically informed data analyses. We derived the phylogenetic relationships of our 66 study families from the comprehensive tree of angiosperm families published by Davies et al. (2004). While this tree is a supertree assembled from published phylogenetic studies, the authors used sequence data (plastid rbcL gene) to estimate branch lengths and calibrated its branching times with known fossil dates, based on the clock-relaxed method of nonparametric rate smoothing (Sanderson, 1997).

The species-level phylogeny was derived using the 'phylomatic' web-tool (Webb & Donoghue, 2005), which returns a supertree topology from a species list with genus and family assignation according to APG II nomenclature. As the obtained phylogenetic hypothesis is a supertree without branch lengths, we set all branch lengths equal to unity (Martins & Garland, 1991).

Data analyses

First, we examined whether the presence of species on both sides of the strait was related to their life-history traits and phylogenetic position. To do so, we modelled the probability of species occurrence on both sides of the strait as a binomial response, with individual height, growth form and dispersal agent as predictor variables. Analyses were performed using a generalized linear model fitted by maximum likelihood (GLM; Venables & Ripley, 2002) and using a phylogenetic generalized linear model fitted by generalized estimating equations (GEE; Paradis & Claude, 2002).

Second, we tested whether there was a relationship between the migration rates of different families across the strait and the number of local endemics they accumulated in the study region (taken as a proxy for local diversification

rate). Because data were not normally distributed, we used quantile regression models because these are particularly suitable to depict nonlinear or triangular relationships (Cade *et al.*, 2005; Koenker, 2005). Quantile regressions allow modelling of the probabilistic distribution of a dependent variable instead of its expected value (as in ordinary least-squares regression). More precisely, quantile regression quantifies the effect of an independent variable on the distribution of a dependent variable around a given quantile τ – in other words, on the probability of observing large or small values. In our case, one can test whether the probability of a family having a number of local endemic species above a given quantile of the data is significantly related to its migration rate across the strait. We repeated quantile regressions over the entire range of numbers of endemic species per family, i.e. from the 2.5th to the 97.5th quantile in order to determine whether the effect of family migration rate varied across the range of our data. Significance levels of quantile regressions were tested by bootstrapping (1000 independent draws). All quantile regressions described above were also repeated including family age as a covariate in the model, in addition to family migration rate.

In order to test whether observed patterns were driven by a few closely related families, we also modelled the number of local endemic species per family with a phylogenetic Poisson regression model, fitted by GEE (Paradis & Claude, 2002), with family migration rate as the predictor variable as previously done with the quantile regressions. To account for potential confounding factors, we tested whether the migration rate of families was related to family age or family size (i.e. the overall number of species present in the study region), using maximum-likelihood logistic regressions.

Third, we estimated flora-wide rates of species diversification by fitting a birth–death model. This family of models depicts the temporal growth of given clades by a random speciation–extinction process (Nee, 2006) using two distinct parameters, namely the net rate of diversification (speciation rate – extinction rate) and the relative rate of extinction (extinction rate/speciation rate). Here we used the improved likelihood-based method develop by Rabosky *et al.* (2007) to estimate diversification rates from incomplete phylogenies and species richness data. In our case, we used numbers of endemic species per family and the family-level phylogenies (see above) to perform rate estimations for all Baetic–Rifan endemic species together, as well as for Baetic (Algeciras, southern Iberia) and Rifan (Tanger, North Africa) endemic species separately. We then tested whether local diversification rate differed between Algeciras and Tanger following the method of Bokma (2003). We computed the likelihood ratio $T = 2(L_{Baetic} + L_{Rifan} - L_{Baetic–Rifan})$, where L_{Baetic}, L_{Rifan} and $L_{Baetic–Rifan}$ are the log-likelihood values of the birth–death models fitted for Baetic, Rifan and Baetic–Rifan endemics, respectively. The T statistic was then compared to a chi-square distribution with two degrees of freedom. The rationale of this test is to quantify whether a single birth–death model for the entire region fits the data better than two distinct models for each subregion, respectively (Bokma, 2003). The whole analysis was repeated assuming two extreme extinction rates (0 and 0.99) to account for possible uncertainty in the inference of relative extinction rates. We also computed likelihood profiles of the three flora-wide birth–death models (all Baetic–Rifan, Baetic only, Rifan only) in order to determine whether local maxima of maximum likelihood functions could exist due to peculiarities in our data.

All statistical analyses were performed using R 2.10 software (R Development Core Team, 2010) using the packages ape (Paradis *et al.*, 2004), geiger (Harmon *et al.*, 2007), laser (Rabosky, 2006) and quantreg (Koenker, 2005).

RESULTS

Different families varied substantially with respect to the proportion of species present on both sides of the strait (Fig. 2). The probability of species occurring on both sides was significantly related to some of the studied life-history traits. Plant height did not affect patterns of species occurrence, both in the non-phylogenetic and phylogenetic models (Table 1, Fig. 3a). In contrast, both growth form and propagule morphology were related to patterns of species occurrence across the strait, although the effect of growth form was significant only in the phylogenetic model (Table 1). Annual species were more likely to occur on both sides of the strait than both herbaceous perennial and woody species (Fig. 3b). Concerning propagule morphology, species with no apparent adaptation were less likely to occur on both sides than species with propagules favouring long-distance dispersal (Table 1, Fig. 3c). The effect of all three types of diaspores (anemochorous, epizoochorous, endozoochorous) was significantly higher than the one of diaspores with no apparent adaptation (phylogenetic logistic model, $F_{(d.f.=1)} = 20.2$, $P \ll 0.001$, non-phylogenetic logistic model $F_{(d.f.=1)} = 13.0$, $P \ll 0.001$). The positive effect of propagule morphology on species' probability of occurring on both sides of the strait was significant for anemochorous and epizoochorous propagules, but not for endozoochorous propagules (Fig. 3c). The effects of anemochory, endozoochory and epizoochory were not significantly different from each other.

Twenty-two of the 66 families in our sample have experienced local speciation. This has resulted in a total of 80 narrow endemic species, out of which 55 occur only on one side of the strait. The families that experienced the most local speciation were Asteraceae (15 local endemic species), Fabaceae (13), Caryophyllaceae (9), Poaceae (7), Scrophulariaceae (5), Amaryllidaceae (4) and Lamiaceae (4).

When assuming a null extinction rate, the birth–death model fitted on the endemic flora of the entire study area yielded an overall estimate of relative diversification rate of 0.021 species Myr^{-1} (Table 2). Estimated net diversification rates for the two Baetic and Rifan subregions were substantially lower and did not significantly differ from each other (Table 2). This result was robust to the assumption of null extinction because rankings of diversification rates were
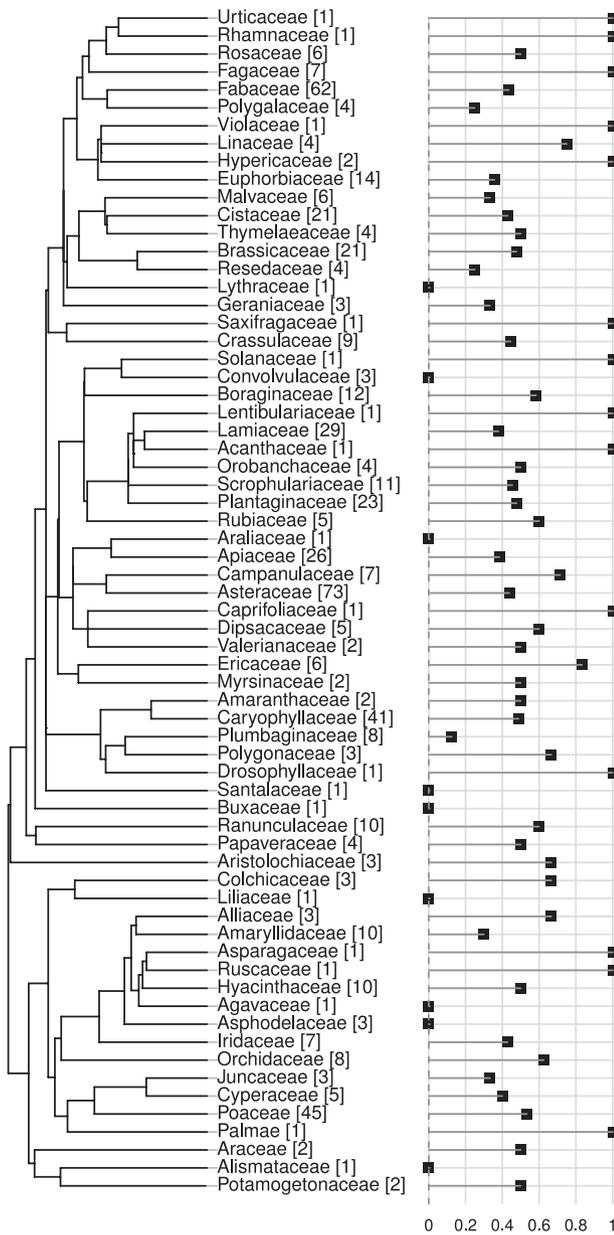
Figure 2 Phylogram representing the phylogenetic relationships of the 64 angiosperm families included in our species sample, along with the proportion of species within each family occurring on both sides of the Strait of Gibraltar (right panel). Phylogenetic relationships are derived from Davies *et al.* (2004). The total number of species in each family is indicated in brackets after each family's name.

Table 1 Results of non-phylogenetic and phylogenetic logistic models depicting the probability that a plant species occurs on both sides of the Strait of Gibraltar as a function of its life-history traits. Studied traits are height, growth form (annual, herbaceous perennial, woody) and morphological adaptation to potential long-distance dispersal vectors (no adaptation, anemochory, endozoochory, epizoochory).

		non-phylogenetic model (GLM)		phylogenetic model (GEE)	
	n	F (d.f.)	P-value	F (d.f.)	P-value
Plant height	507	1.73 (1)	0.1887	2×10^{-3} (1)	0.964
Growth form	516	0.51 (2)	0.599	5.03 (2)	<0.01
Long-distance dispersal	524	4.58 (3)	<0.01	6.04 (3)	<0.01

GLM, generalized linear model fitted by maximum likelihood (Venables & Ripley, 2002); GEE, phylogenetic generalized linear model fitted by generalized estimating equations (Paradis & Claude, 2002).
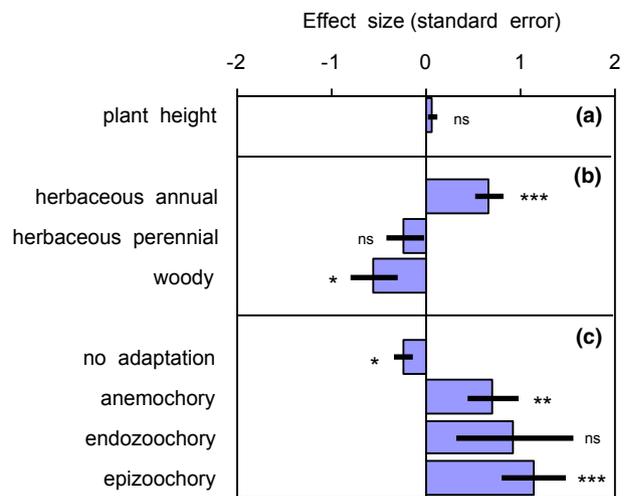
Figure 3 Histogram depicting the estimated effect and its standard error (error bar) of different life-history traits on the probability that a plant species occurs on both sides of the Strait of Gibraltar. Life-history traits were (a) plant height, (b) growth form and (c) putative long-distance dispersal vectors. Effect size of each life-history trait was computed by generalized estimating equations, taking into account phylogenetic relationships between species. See Table 1 for models' goodness of fit.

unchanged when assuming a very high extinction rate of 0.99 (Table 2). Likelihood profiles of the three birth–death models suggest that relative extinction rates should be close to zero (Fig. 4).

The local diversification rate of families within the study region was not independent of their putative rate of migration across the Strait of Gibraltar. Instead, the probability of a family having a number of local endemics above the 75th quantile was negatively correlated with its proportion of spe-

cies occurring on both sides of the strait (Fig. 5a). This pattern persisted when integrating family age as a covariable into the 75th quantile regression model ($\beta_{(se)} = -4.86_{(1.6)}$, $P < 0.01$). Bootstrapping tests showed that the relationship between migration rate and number of local endemics was consistently null up to the 50th quantile (Fig. 5b). The effect of family migration rate on the number of local endemics per family was, however, significantly negative for the 50th and higher quantiles (Fig. 5b). The number of local endemics per family was also negatively related to family migration rate in the phylogenetic Poisson regression ($F_{(1)} = 6.72$, $P < 0.05$), showing that this pattern was not only due to a

Table 2 Results of birth–death models fitted to obtain flora-wide estimates of local diversification across the Strait of Gibraltar.

	$\mathcal{C} = 0$			$\mathcal{C} = 0.99$		
	Log-Lik	N	r	Log-Lik	N	r
Baetic endemics (southern Iberia)	−54.9	11	0.010	−58.3	11	0.00015
Rifan endemics (northern Morocco)	−89.6	16	0.016	−96.1	16	0.00028
Test for differential diversification rate	$T = -67.8$ ns			$T = -70.31$ ns		
All Baetic–Rifan endemics	−136.9	22	0.021	−145.6	22	0.00047

Models were fitted using the number of narrow endemics per family and a fossil-dated family-level phylogeny (see Materials and Methods for details). Three models were fitted: for species endemic to the Baetic range (southern Iberia), for species endemic to the Rifan range (northern Morocco), and for all Baetic–Rifan endemic species together. Each model was fitted both assuming that relative extinction rate ($\mathcal{C}$) was null or equal to 0.99. The outcome of birth–death models are shown, with the maximum-likelihood estimate of the net diversification rate (r), model log-likelihood (Log-Lik), and the number of families used to fit each model (N). Results of the test for differential diversification rate between the southern Iberian and northern Moroccan parts of the Gibraltar biodiversity hotspot are also reported, with the likelihood ratio statistic T, and its significance level when compared to a chi-square distribution with two degrees of freedom. Both tests (for the two assumed extinction rates) were non significant (ns).
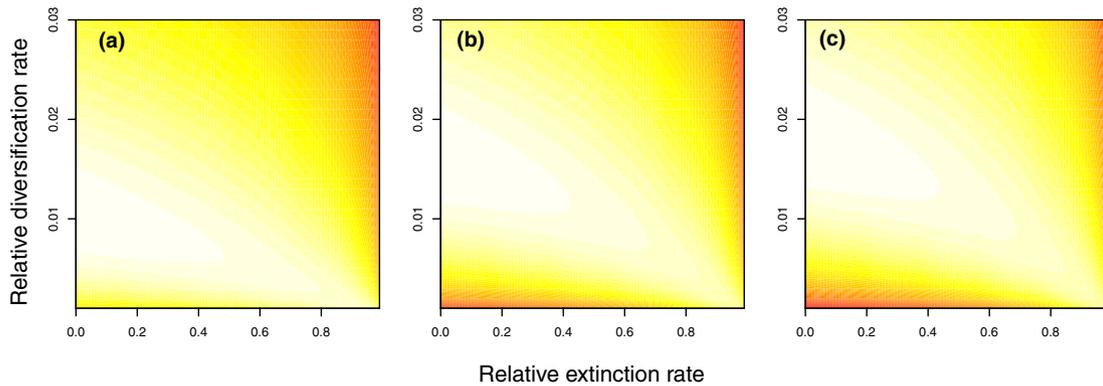
Figure 4 Results of analyses of local plant diversification for the Gibraltar biodiversity hotspot, based on family-level phylogenies and number of local endemic species per family. The plots represent model likelihoods on a colour scale (dark shading for low likelihood, light shading for high likelihood) as a function of parameters depicting relative extinction rate (*x*-axis) and relative diversification rate (*y*-axis), (a) for Baetic endemic species, (b) for Rifan endemic species and (c) for all Baetic–Rifan endemic species together.
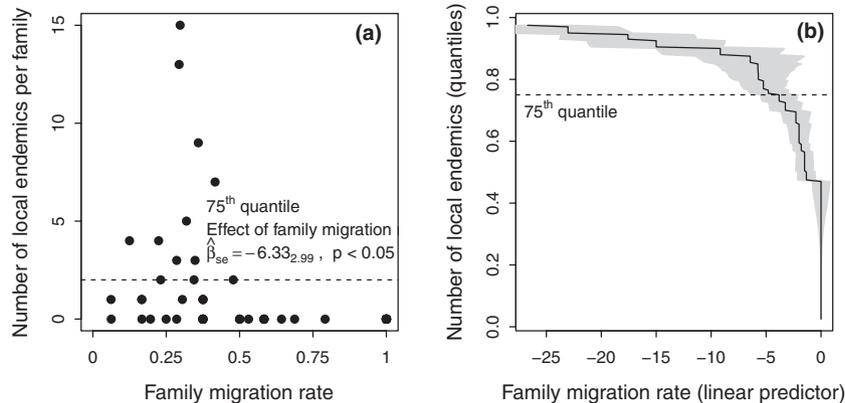
Figure 5 (a) The relationship between plant family migration rate (i.e. the proportion of species occurring on both sides of the Strait of Gibraltar) and the number of narrow endemic species per plant family (i.e. a proxy for local diversification rate). The dashed line represents the 75th quantile for the number of narrow endemic species per family. The result of the 75th quantile regression with family migration rate is also given, testing the effect of family migration rate on diversification rate to be greater than the 75th quantile (*P*-value based on 1000-draw bootstrapping). (b) Results of quantile regressions of the number of narrow endemic species per family versus family migration rate, performed from the 2.5th to the 97.5th quantile of the number of narrow endemic species per family. The solid line represents the effect of family migration rate on the probability of diversification rates to be greater than a given quantile. The grey envelope depicts the 95% confidence interval for the linear predictor of migration rate on the number of narrow endemic species. The dashed line represents the 75th quantile for family diversification rate.

number of closely related families having similar migration rates and numbers of local endemics. Logistic regressions showed that the migration rate of families was not related to their evolutionary age ($F_{(1)} = 2.22$, $P = 0.115$) or to the total number of their species occurring in the study region ($F_{(1)} = 0.83$, $P = 0.365$).

DISCUSSION

We used the unique ecogeographical setting of the Strait of Gibraltar to study the interplay between species migration and lineage diversification. Our results indicate that the strait has acted as a filter to plant migration in accordance with certain life-history and dispersal traits of species. This filtering has caused different plant lineages to exhibit disparate distribution patterns across the strait, with closely related families having very different proportions of species occurring on both sides of the strait. We also found that narrow endemic species have repeatedly emerged through non-random diversification of lineages and that families with low migration rates across the strait have experienced greater local speciation. These patterns were found to be robust to potential biases or confounding factors such as the age and prevalence of different plant families. Although we can only speculate about the specific mechanisms underlying these patterns, our work underpins that the Strait of Gibraltar has (1) biased plant species migration between southern Iberia and Northwest Africa, and (2) promoted local speciation in certain plant lineages by exacerbating their isolation.

Our results imply that the life-history traits we examined influence at least to some extent the two fundamental stages of plant migration, propagule dispersal and population establishment. This appears particularly noteworthy because the trait-based approach that we used in our study implies some unavoidable drawbacks. Perhaps most importantly, it has repeatedly been argued that propagule morphology is a poor predictor for the potential of long-distance seed dispersal (Nathan, 2002; Higgins et al., 2003). While we fully acknowledge this drawback, our approach can be considered conservative, because we only considered broad classes of morphological adaptations for seed dispersal by wind or vertebrates (e.g. Janson, 1983; Augspurger & Franson, 1987; Greene & Johnson, 1993). It is known that these two vectors can carry propagules over several kilometres (well beyond the 14 km of the strait), and their influence on plant population structures has also been confirmed in a recent meta-analysis of genetic data (Duminil et al., 2007). In addition, the Strait of Gibraltar should be particularly favourable for wind and vertebrate dispersal, as it regularly experiences very strong winds and is crossed every year by millions of migrating birds, many of them frugivores (Rodríguez-Sánchez et al., 2008). With respect to the potential of plant species to establish new populations, the two traits we used (growth form and plant height) are widely known to be related to the colonization potential of species (Grime, 1977; Weiher et al., 1999; Shipley et al., 2006). Clearly, our approach cannot compete with in-depth assessments of species dispersal across the Strait of Gibraltar through molecular markers (reviewed by Rodríguez-Sánchez et al., 2008). However, our goal was to obtain a flora-wide perspective of species migration and to elucidate otherwise undetectable wide-ranging ecological relationships between species range dynamics and lineage diversification.

Patterns of species migration

In general, our finding that the Strait of Gibraltar has filtered species migration according to their life-history traits provides support for the old hypothesis of Simpson (1940) that land bridges may have acted as selective migration filters, and thus generated biased species assemblages between continents. A primary result of our study was that species with a short life cycle and propagules dispersed by wind or externally on animals have apparently been most likely to cross the Strait of Gibraltar. Species with the mentioned characters are widespread in early successional habitats, which have greatly increased in historical times due to ever-increasing human activities. Notwithstanding, as reviewed by Rodríguez-Sánchez et al. (2008), the few phylogeographical studies available for early successional species indicate that their presence on both sides of the strait is considerably more ancient (Ortiz et al., 2008; Quintela-Sabarís et al., 2011), thereby discarding a direct role of man in the colonization process. Our results thus point to a biological syndrome that has apparently favoured species migration through the Strait of Gibraltar. It should be noted here that we did not consider seed dispersal by sea currents although this mechanism has proved to be critical for the colonization of oceanic islands (Cody, 2006). Indeed, the lack of readily recognizable morphological adaptations to marine dispersal and the lack of empirical information on this type of dispersal rendered any classification of species unfeasible for this study.

Contrary to our expectations, we did not find any significant effect of plant height or endozoochorous dispersal on the probability of species migration across the strait. The first result may be explained by the fact that the study area contains an exceptionally high number of low-stature woody taxa, typical of extensive heathlands in the region (Ojeda et al., 1996); hence, plant height may be less closely linked with the growth form and successional position of species than in many other floras. Additionally, fleshy-fruited species have apparently not crossed the Strait of Gibraltar more often than expected by chance. This finding contrasts with previous studies of species dispersal between oceanic islands (e.g. Burns, 2005). It also contrasts with the classic observation that fleshy fruits are a common character among the oldest, so-called 'pre-Mediterranean' taxa of the region (Herrera, 1992) that should have had most opportunities to cross the strait. We believe that two factors could help explain this unexpected result. First, fleshy fruits do not necessarily imply a high ability of long-distance seed dispersal (Hampe, 2003; Hampe et al., 2003; Worth et al., 2010), especially if seed

dispersers have to cross the sea. Hence, the width of the strait could have been enough to render it an effective barrier for endozoochorous seed dispersal (at least in comparison with wind and external seed dispersal). Second, most fleshy-fruited taxa of the region are late successional, woody species that are likely to encounter more problems than herbaceous plants during the second stage of the colonization process, that is, the establishment of viable populations from rare seed dispersal events.

The Gibraltar Strait area has been included in numerous phylogeographical studies of non-coastal plant species (Rodríguez-Sánchez *et al.*, 2008; Jaramillo-Correa *et al.*, 2010), which allows our results based on floristic data to be contrasted with those based on genetic data on particular clades – although keeping in mind that molecular surveys have always investigated taxa occurring on both sides of the strait. Unfortunately, most phylogeographical studies to date have been conducted on late successional, woody species. However, the few studies available for herbaceous or early successional woody species appear to be in line with our findings, as genetic breaks across the strait tend to be less pronounced than among tree species (reviewed by Rodríguez-Sánchez *et al.*, 2008). Although there are notable exceptions to this tendency (for examples in *Bellis*, *Carex* and *Erophaca* see Fiz *et al.*, 2002; Escudero *et al.*, 2008; Casimiro-Soriguer *et al.*, 2010), it indicates that species with short life cycles and ruderal strategy have probably experienced more frequent migration across the Strait of Gibraltar. Finally, some phylogeographical surveys indicate in which direction species have crossed the strait. For instance, *Abies pinsapo* agg., *Pinus nigra* and *P. pinaster* (Jaramillo-Correa *et al.*, 2010), as well as *Carex helodes* (Escudero *et al.*, 2008), probably expanded from Iberia into the Maghreb, whereas expansions in the opposite sense have been hypothesized for *Quercus ilex* (Lumaret *et al.*, 2002), *Stauracanthus* (Pardo *et al.*, 2008) or *Hypochaeris radicata* (Ortiz *et al.*, 2008). *Cistus ladanifer* is to date the only species for which probable dispersal events in both directions have been detected (Quintela-Sabarís *et al.*, 2011).

Patterns of local diversification

Different plant families, even closely related ones, exhibited disparate distribution patterns across the Strait of Gibraltar (Fig. 2). We found clear evidence suggesting that limited penetration through the strait has favoured local speciation, i.e. the differentiation of local endemic species, within certain plant lineages. This pattern was robust to bootstrapping procedures, and was not related to the age or prevalence of families. The inverse relationship between migration and local speciation may have emerged through two non-exclusive scenarios. First, complete isolation by the strait could have permitted speciation through gradual genetic divergence of taxa (allopatric speciation). Second, limited migration across the strait could have caused rare founder events that favoured speciation (peripatric speciation). One could alternatively

consider that the same biological traits influencing plant migration across the strait independently affect evolutionary rates of lineages. However, as rates of molecular evolution or speciation tend to be higher in short-lived plant groups (Smith & Donoghue, 2008; Vamosi & Vamosi, 2011), this should have acted against the pattern we observe in this study.

The wide-ranging evolutionary consequences of the migration bias imposed by the Strait of Gibraltar have probably been favoured by two particularities of the area. First, the two peninsulas present nutrient-poor and acid 'edaphic islands' surrounded by more fertile soils (Fig. 1a). These conditions appear to have stimulated the emergence of narrow endemic species through the drastic selective pressures imposed by harsh and infertile habitats (Ojeda *et al.*, 1996). These have long been regarded as a key factor for narrow endemic species differentiation in most mediterranean regions (Raven, 1964; Hopper, 1979; Kruckeberg, 1986; Cowling & Holmes, 1992; Lavergne *et al.*, 2003, 2004). Second, the remarkable climatic stability of the area has allowed *in situ* persistence and diversification of different plant clades through multiple climatic cycles of the Pleistocene (Rodríguez-Sánchez *et al.*, 2008). Given that diversification rates did not differ between the two subregions of Algeciras and Tanger Peninsulas, it seems that these two mechanisms have triggered local speciation on both sides of the Strait of Gibraltar.

Finally, our results indicate that differential diversification of plant families has been operating in the Baetic–Rifan biodiversity hotspot. Twenty-two of the 66 families present in our study area experienced local speciation, with flora-wide estimates being substantial given the small geographical scale of our study, and the relatively short time-scale during which this local speciation has likely occurred. Endemic-rich lineages belong to widely distributed plant families that either have a cosmopolitan distribution (Asteraceae, Fabaceae, Lamiaceae, Poaceae and Scrophulariaceae) or have holarctic (Caryophyllaceae) or tropical (Amaryllidaceae) origins. Two conclusions can be drawn from comparing our results with earlier studies that documented patterns of narrow endemism in other mediterranean-climate regions of the world (Cowling *et al.*, 1994; Domínguez Lozano & Schwartz, 2005). First, it appears that families with high numbers of narrow endemic species differ substantially between mediterranean-climate regions, probably due to differences in past and present climates and contrasted geological histories, but also due a certain degree of evolutionary contingency. Second, a recurrent feature of mediterranean plant assemblages is that much of their extant diversity (in particular concerning narrow endemism species) is the outcome of local diversification of widely distributed lineages of various biogeographical origins (Linder, 2005).

CONCLUSIONS

Our study provides an original quantitative test and a novel viewpoint on Simpson's hypothesis (1940) that land bridges have biased species movements between different continents. We further suggest that this filter function could have

triggered the evolutionary diversification of particular lineages. Our findings are much in line with the view of Ricklefs (2008) that unravelling historical effects on species distribution can reveal much about the processes that generate patterns of biodiversity. From a methodological standpoint, we believe that our approach could be extended to other regions of the world and species assemblages (considering either plants or animals) where clear-cut migration routes can be explicitly studied, and the diversification of particular lineages can be quantified and related to their migration history. Phylogenetically informed studies of species-rich floras, based on several clades and dated supertrees, can thus provide valuable insights into patterns of clade diversification and the biogeographical and evolutionary mechanisms that have driven the emergence of biodiversity hotspots (Cowling & Pressey, 2001; Pennington *et al.*, 2006; Forest *et al.*, 2007).

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