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Climatic and topographical correlates of plant palaeo- and neoendemism in a Mediterranean biodiversity hotspot

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• **Background and Aims** Understanding the evolutionary and ecological forces contributing to the emergence of biodiversity hotspots is of outstanding importance to elucidate how they may withstand current climate changes. Here we explored patterns of phylogenetic and non-phylogenetic plant endemism in a Mediterranean biodiversity hotspot. We hypothesized that areas with wet and equable climatic conditions would be prone to long-term persistence of endemic lineages (palaeoendemism), whilst areas of recent local speciation (neoendemism) would be more related to harsher environmental conditions and to high topographical relief promoting speciation.

• **Methods** We focused on the Baetic–Rifan biodiversity hotspot (southern Iberian Peninsula and northern Morocco) in combination with molecular phylogenetic information and relative phylogenetic endemism (RPE), a recent phylogenetic measure of endemism, allowing us to discern centres of palaeo- from those of neoendemism. Using eco-geographical regions as study units, we explored correlations between both RPE and endemic species richness with precipitation- and temperature-related variables and with elevation range.

• **Key Results** Centres of neoendemism were concentrated towards the easternmost part of the hotspot, while centres of palaeoendemism were clustered in the vicinity of the Strait of Gibraltar. The RPE index, indicating more palaeoendemism, was positively correlated with total annual precipitation, while endemic species richness showed a poor correlation. In contrast, elevation range and mean annual temperature were poor predictors of RPE, despite elevation range showing a strong correlation with endemic species richness.

• **Conclusions** The Baetic–Rifan biodiversity hotspot shows clearly differentiated centres of neo- and palaeoendemism. Topographical relief may have driven evolutionary diversification of newly evolved species, while water availability seems more critical for the long-term persistence of ancient lineages in refuge areas of smoother topography. Given climatic trends towards increasing aridification, conservation planners should pay particular attention to preserve areas retaining older phylogenetic lineages, as these areas act as ‘natural museums’ of biodiversity within the Baetic–Rifan biodiversity hotspot.

Key words: Keywords: Baetic–Rifan range, endemic richness, Mediterranean flora, relative phylogenetic endemism, elevation range, water availability.

INTRODUCTION

Biodiversity is not evenly distributed over the Earth's surface. It is concentrated in so-called ‘biodiversity hotspots’, areas harbouring very high levels of plant endemic richness that are experiencing exceptional degrees of habitat loss (Myers *et al.*, 2000; Mittermeier *et al.*, 2004). Despite the fact that the planet's remaining hotspot habitats only cover 2.3 % of the land surface, they are home to over 50 % of all vascular plants as endemics (Mittermeier *et al.*, 2004), which means that an irreplaceable wealth of plant biodiversity is concentrated in just a very small part of our planet. The irreplaceable nature of the hotspots is particularly noticeable regarding relict species, a certain proportion of which can be endemic to given biogeographical regions (i.e. palaeoendemics, *sensu* Stebbins and Major, 1965). Most narrow-ranging, relictual species are the extant representatives of the past flora that existed under previous climates (Herrera, 1992; Postigo Mijarra *et al.*, 2009) and have survived in scattered refugia such as those found across the

Mediterranean Basin (Médail and Diadema, 2009) and other Mediterranean-type regions such as the California Floristic Province (Raven and Axelrod, 1978). On the other hand, the particular conditions that generate new diversity through recent speciation in the hotspots (i.e. neoendemism) are also irreplaceable. For example, the onset of the Mediterranean climate along the Tertiary/Quaternary transition acted as a diversification trigger for many lineages, which experienced repeated local speciation generating narrow-ranging endemics (Verdú and Pausas, 2013). Thus, in the end, conservation planners face the dilemma of preserving areas harbouring either the phylogenetic legacy of ancient biomes as ‘natural museums’ of biodiversity (old lineages, palaeoendemism) or new evolved lineages as ‘cradles’ of biodiversity (recent speciation, neoendemism).

The problem of determining what ecological conditions promote the persistence of palaeoendemics and the origin of neoendemics has long interested biogeographers (Stebbins and Major, 1965; Favarger, 1972). This problem gained renewed interest recently in order to preserve areas of species persistence

and diversification, in the face of climate changes. However, most traditional studies that focused on the distribution and causes of endemism have used taxonomic species as the statistical unit (but see Favarger and Contandriopoulos, 1961) and thus lack quantitative distinction between palaeoendemism and neoendemism. Recent progress in phylogenetic methods has allowed us to explicitly tackle the phylogenetic position of endemic species and explore the evolutionary history of species assemblages (see Mishler *et al.*, 2014; Schmidt-Lebuhn *et al.*, 2015). The incorporation of phylogenetic information may shed new light on the processes that generate and maintain spatial patterns of species endemism, as these processes leave tractable imprints on present-day phylogenies (Cantalapiedra *et al.*, 2014; Molina-Venegas *et al.*, 2015a).

Mediterranean biodiversity hotspots constitute exceptional regions for studying the historical origins of endemism. All of the five Mediterranean-type zones on Earth have been listed among the 34 world biodiversity hotspots (Mittermeier *et al.*, 2004). Most notably, the Mediterranean Basin harbours approx. 8% of the world's plant species, of which about 60% are endemic to the region (Quézel, 1985; Greuter, 1991). Within the Mediterranean Basin hotspot, a considerable fraction of the plant species richness (and particularly narrow endemics) is concentrated in the western Mediterranean, particularly in the southern Iberian Peninsula (notably Andalusia) and north-west Africa (northern Morocco), which together form the Baetic–Rifan biodiversity hotspot (Médail and Quézel, 1999).

The historical drivers that shaped Mediterranean hotspots are complex, and may include many interacting effects of climate, geomorphology, tectonic activity and other historical factors (Thompson, 2005; Rodríguez-Sánchez *et al.*, 2008; Molina-Venegas *et al.*, 2015a). The geological history of the Baetic–Rifan biodiversity hotspot has been marked by the progressive northward drift of the African tectonic plate during the Palaeogene–Neogene and its collision with the Iberian plate (Rosenbaum *et al.*, 2002), until the complete closure of the Mediterranean Sea at its western end (Strait of Gibraltar; see Fig. 1) about 6.5 Mya and posterior reopening approx. 4.5 Mya (Krijgsman *et al.*, 2002; Duggen *et al.*, 2003). This intermittent connection is known to have encouraged spatial divergence and local speciation in several lineages (Lavergne *et al.*, 2013), thus probably generating many neoendemic species. Also, the recent uplift of the main mountain ranges in the region (i.e. the Baetic–Rifan complex, Braga *et al.*, 2003) in combination with repeated specialization to contrasting and often stressful soils may have been an important stimulus for the rapid diversification of neoendemism (Molina-Venegas *et al.*, 2015b). On the other hand, the long-term persistence of palaeoendemism and rare species in general has also been favoured by topographical heterogeneity (Lavergne *et al.*, 2005; Médail and Diadema, 2009) and a climate that has remained relatively stable in restricted areas since the late Tertiary, even through the major climatic fluctuations of the Miocene (e.g. the Messinian salinity crisis, Duggen *et al.*, 2003) and the Pleistocene (i.e. the Quaternary glacial and interglacial periods, Finlayson and Carrión, 2007; Rodríguez-Sánchez *et al.*, 2008). Therefore, whether climate and topographical relief differently shape areas prone to long-term persistence of palaeoendemism or to recent, supposedly rapid, speciation of neoendemism remains unclear. In particular, we hypothesize that centres of palaeoendemism

would be associated with wet and equable climatic conditions similar to those of ancient pre-Mediterranean climates (Raven and Axelrod, 1978; Herrera, 1992; Anacker and Harrison, 2012), whilst centres of neoendemism would be more related to harsher environmental conditions (Verdú and Pausas, 2013; Cacho and Strauss, 2014) and to high topographical relief encouraging spatial divergence (Crisp *et al.*, 2001; Vetaas and Grytnes, 2002; Molina-Venegas *et al.*, 2015b).

In this study, we explored spatial patterns of phylogenetic and non-phylogenetic endemism across Andalusia (south Iberian Peninsula) and northern Morocco (north-west Africa), which together form a major biodiversity hotspot in the western Mediterranean (Fig. 1). Specifically, we made use of the whole endemic flora of the region in combination with molecular phylogenetic information and eco-geographical regions as study units to (1) estimate both endemic species richness and relative phylogenetic endemism (RPE), a recent phylogenetic measure of palaeo- and neoendemism, and (2) explore correlations between both measures of endemism with precipitation- and temperature-related variables and elevation range. Our overarching goal was to assess whether climate and topographical relief may have shaped differently areas prone to long-term persistence of endemic lineages (palaeoendemism) or to recent local speciation (neoendemism). RPE is a recently proposed metric that allows us to distinguish between centres of palaeo- and neoendemism (Mishler *et al.*, 2014). RPE is defined as phylogenetic endemism (PE, the spatial restriction of phylogenetic diversity, Rosauer *et al.*, 2009) measured on the actual tree divided by PE measured on a comparison tree that retains the actual tree topology but makes all branches of equal length. Thus, this ratio quantifies the balance between rare long- and rare short-terminal branches, i.e. whether local phylogenetic structure of species assemblages tends to indicate the presence of palaeo- or neoendemism.

MATERIALS AND METHODS

Study area

Andalusia (south Iberian Peninsula) and northern Morocco (north-west Africa) are two environmentally heterogeneous areas in the western Mediterranean Basin (Fig. 1A). These two landmasses, divided between the Iberian and African tectonic plates, are separated by the Mediterranean Sea, which is around 14 km at its narrowest point (Strait of Gibraltar, Fig. 1B), and harbour similar overall climate, geomorphology, lithology, flora and vegetation (Molina-Venegas *et al.*, 2013, and references therein). This region is characterized by high mountain ranges (i.e. the Baetic–Rifan complex) surrounded by extensive lowlands that have been shaped by the rivers Guadalquivir (Andalusia) and Sebou (north Morocco). The geological materials that shape most of the Baetic and Rifan ranges accreted at the south-east and north-west tips of the Iberian Peninsula and Africa, respectively, around 10 Mya (Rosenbaum *et al.*, 2002), followed by the rapid uplift of the Baetic and Rifan mountains that began in the Tortonian at around 8 Mya (Braga *et al.*, 2003). The climate of the region is typically Mediterranean, but is clearly affected by the proximity of the Atlantic Ocean (Ajbilou *et al.*, 2006; Mejías *et al.*, 2007), which shapes a general decreasing precipitation gradient eastward. The current

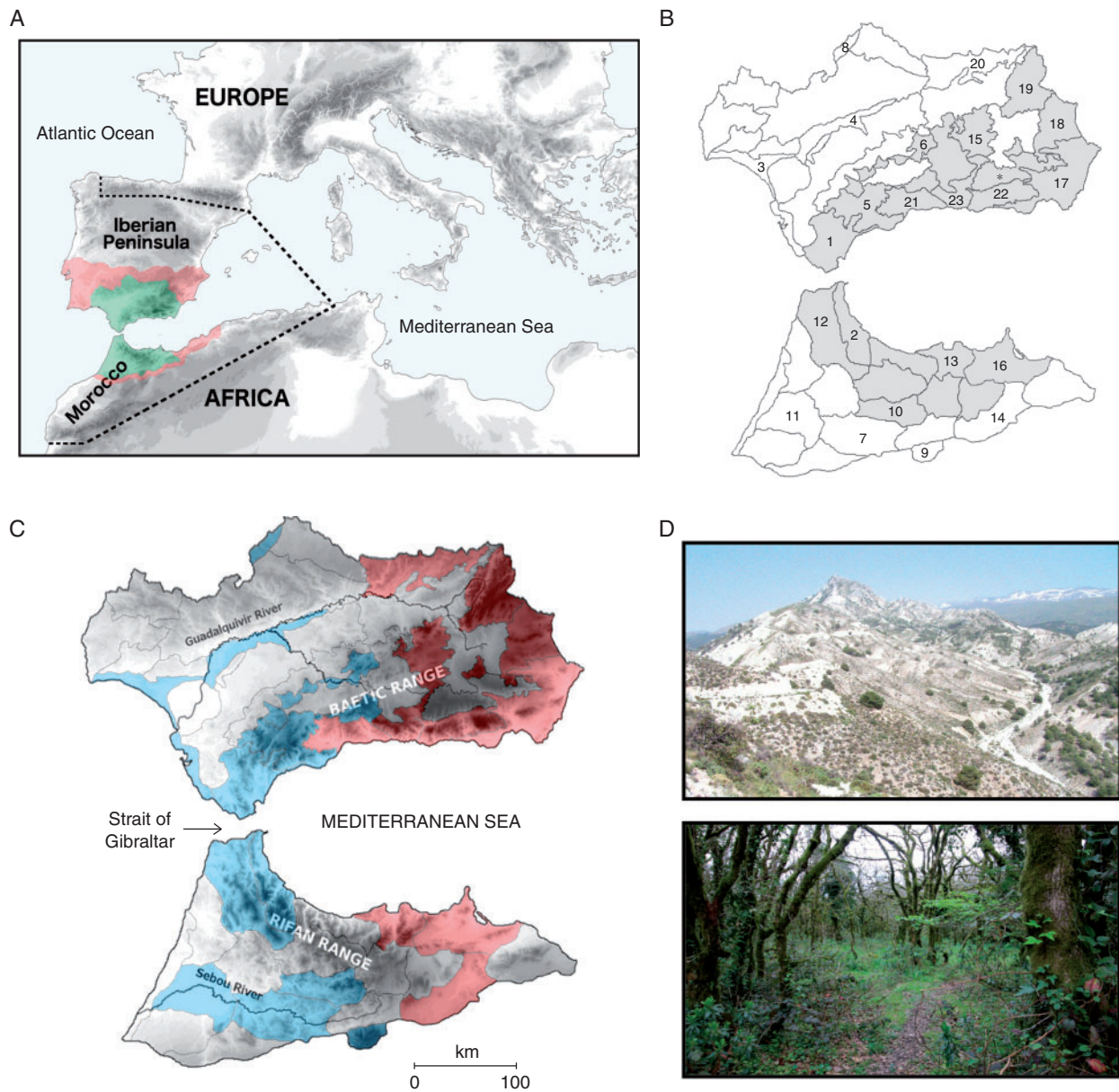


FIG. 1. (A) Location of the study area (coloured in green) in the southern Iberian Peninsula and north-western Africa (the sum of the areas coloured in green and red), the westernmost part of the Mediterranean Basin biodiversity hotspot as defined in Myers *et al.* (2000). The dashed line delimits the boundaries considered in the study for defining ‘isolated lineages’ (see text). (B) Ecoregions defined for Andalusia and northern Morocco after Valdés *et al.* (1987, 2002) and Blanca *et al.* (2009). Only ecoregions with SES_{RPE} values above or below the 75 and 25 percentiles, respectively, were labelled, in decreasing order of SES_{RPE} (see Table 1 for ecoregion names). The asterisk ‘*’ shows the location of the ‘Sierra Nevada – Filabres’ ecoregion, the highest mountain range in the Iberian Peninsula. The shaded ecoregions correspond to those that match the mountain ranges forming the Baetic–Rifan complex. (C) Map of Andalusia and northern Morocco showing the position of the Baetic and Rifan Ranges, the Strait of Gibraltar, and the Guadalquivir and Sebou Rivers. The shading represents elevation (maximum value in black). Ecoregions with SES_{RPE} values above or below the 75 and 25 percentiles of the distribution were coloured in blue (palaeoendemism) and red (neoendemism), respectively. (D) Mountainous landscape within the ‘Trevenque–Almijara’ ecoregion (top) and a relict subtropical forest within the ‘Aljibe’ ecoregion (bottom), the main centres of neo- and palaeoendemism across the Baetic–Rifan biodiversity hotspot, respectively.

seasonal precipitation rhythm of the region has prevailed at least since 3–6 Mya (Tzedakis, 2007).

Endemic species list

We compiled an exhaustive distribution dataset of all the native vascular plants endemic to the southern Iberian Peninsula

and north-western Africa (Fig. 1A). This delimitation corresponds to the westernmost part of the Mediterranean Basin biodiversity hotspot as defined by Myers *et al.* (2000), and also encapsulates one of the main centres of biodiversity in the western Mediterranean (i.e. the Baetic–Rifan complex, as defined by Médail and Quézel, 1999). To do so, we used the dataset from Molina-Venegas *et al.* (2013), which includes all native vascular plants occurring across the ecoregions defined for

Andalusia (southern Iberian Peninsula) and northern Morocco (north-western Africa) (see Molina-Venegas *et al.*, 2013, for full details on the floristic dataset compilation and Fig. 1B for ecoregion boundaries). An ecoregion can be defined generally as a territory characterized by the existence of homogeneous ecological systems involving interrelationships among organisms and their environment (Omernik, 1995). We then extracted the subset of species that are endemic to the southern Iberian Peninsula and north-western Africa (see Fig. 1B) based on standard floras and floristic checklists of the region (Valdés *et al.*, 1987, 2002; Fennane and Ibn Tattou, 2005; Blanca *et al.*, 2009; Ibn Tattou and Fennane, 2009; Castroviejo, 1986–2012).

The study of spatial patterns of species endemism necessarily passes through deciding whether a set of populations occurring in the study area that are assigned to a particular taxonomic rank higher than species (e.g. genus) are sufficiently differentiated from their close relatives to be considered as different taxa (e.g. different species or subspecies). Thus, taxonomic decisions may introduce significant bias when defining the endemic flora of a particular region. As population isolation is the necessary first stage of any incipient speciation process, it is reasonable to consider endemic lineages (i.e. the sum of both endemic taxa plus species that show highly-isolated distant populations from the main species' range in the study area, thus constituting 'isolated lineages') rather than endemic taxa in the study of distribution patterns of endemism. However, disjunct-like patterns could emerge due to both contraction of a once much more widespread distribution (i.e. ancient isolation, prone to lineage divergence) and long-distance dispersal events, which hardly promote differentiation. Thus, to minimize false positives due to long-distance dispersal we only considered as 'isolated lineages' those taxa that show isolated populations in the study area and that also occur in one of the following distant disjunct ranges: (1) Cantabrian–Pyrenees axis and northwards, (2) Tyrrhenian islands and eastwards, (3) north-central Africa and eastwards, (4) High Atlas range in Morocco and southwards, and (5) Macaronesian islands and beyond (see Fig. 1A). Some phylogenetic and phylogeographical studies have proved the validity of such assumption in different lineages (Hampe *et al.*, 2003; Rodríguez-Sánchez *et al.*, 2009; Liu and Schneider, 2013; Rumsey *et al.*, 2014). This procedure resulted in a site-by-species matrix of 48 ecoregions (Fig. 1B) with 728 species and subspecies (698 were endemic to the study region and 30 were defined as 'isolated lineages' following the above definition, see species list in Appendix 1).

Phylogenetic tree

To account for the phylogenetic relationships between the lineages occurring in the study area, we used the genus-level time-calibrated phylogeny described by Molina-Venegas and Roquet (2014). This phylogeny was inferred using a maximum-likelihood inference based on a mixed supertree-supermatrix approach, following the pipeline of Roquet *et al.* (2013). Sequences used in this study correspond to various chloroplastic and nuclear DNA sequences (rbcL, matK, ndhF, trnL-F, ITS1 and ITS2). Node support was estimated using bootstrap values (70% of nodes showed a bootstrap support greater than 70), and nodes with values less than 50% were collapsed into

soft polytomies (see Molina-Venegas and Roquet, 2014, for further details on the phylogenetic procedure).

Relative phylogenetic endemism estimation

We estimated the RPE of each ecoregion in the study area based on presence/absence data. RPE is a standardized version of PE, the latter representing the spatial restriction of phylogenetic diversity (PD, *sensu* Faith, 1992) in a particular area unit (e.g. ecoregion) in relation to that occurring in the study region (Rosauer *et al.*, 2009). Specifically, RPE is PE measured on the actual tree divided by PE measured on a comparison tree that retains the actual tree topology but makes all branches of equal length (Mishler *et al.*, 2014). Thus, ecoregions with high values of RPE represent centres of palaeoendemism (phylogenetic endemism is to a great extent due to rare long-terminal branches), while ecoregions with low values of RPE represent centres of neoendemism (phylogenetic endemism is to a great extent due to rare short-terminal branches). Note that estimations of RPE in area units harbouring a high fraction of both long and short rare branches (i.e. both the numerator and the denominator showing high values in the RPE ratio) may result in values of RPE similar to those expected in area units with low concentrations of both long and short rare branches (i.e. both the numerator and the denominator showing low values in the RPE ratio). Thus, although RPE by itself will fail to distinguish such 'centres of mixed endemism' (see Mishler *et al.*, 2014, for a methodological framework designed to identify such cases) it is still appropriate to the purpose of our study. Specifically, we aim to rank ecoregions in the continuum between centres of endemism that are due to long-terminal branches (palaeoendemism) and short-terminal branches (neoendemism).

As with any other phylogenetic diversity metric, RPE may be affected by phylogenetic uncertainty (Rangel *et al.*, 2015). Thus, to account for the possible influence of intra-genus phylogenetic uncertainty on RPE estimations, we randomly resolved genus-level polytomies by applying a Yule branching process with constant birth rates, and used the resulting species-level trees ($n = 1000$) to estimate RPE values (see below). The algorithm assigns to each node the same probability of splitting in two lineages, resulting in a balanced topology (Nee, 2006). Subspecies were constrained to split within their respective species.

Null hypothesis and randomization test

Raw values of RPE are not highly informative because the magnitude of PE is clearly affected by the number of terminal taxa present. Therefore, we calculated standardized effect size scores of RPE (SES_{RPE}) as:

$$SES_{RPE} = \frac{RPE_{obs} - mean(RPE_{null})}{sd(RPE_{null})} \quad (1)$$

where RPE_{obs} represents the observed value for a particular ecoregion, and RPE_{null} is a null distribution of RPE values generated by randomizing the actual site-by-species matrix 999 times (Kembel, 2009), following an 'independent swap'

TABLE 1. Ecoregion names, location, endemic species richness, elevation range, predominant type of endemism and total annual precipitation of the ecoregions that show SES_{RPE} values above or below the 75 and 25 percentiles, respectively; ecoregions are sorted in decreasing order of SES_{RPE}

ID	Ecoregion name	Location	Endemic species richness	Elevation range (m)	Predominant type of endemism	Annual precipitation (mm)
1	Aljibe	Iberia	107	1158	P	807.7
2	West Rif	Morocco	88	2053	P	832.8
3	Litoral	Iberia	78	207	P	568.0
4	Vega	Iberia	12	228	P	620.7
5	Ronda	Iberia	187	1769	P	741.7
6	Subbética	Iberia	65	1195	P	682.1
7	Central Pre-Rif	Morocco	6	751	P	609.0
8	Zújar	Iberia	6	330	P	624.3
9	Tazekka	Morocco	10	1352	P	494.9
10	High Ouerrha	Morocco	5	1521	P	650.2
11	Gharb	Morocco	8	619	P	571.4
12	Tangier	Morocco	55	1648	P	899.3
13	Imzorene	Morocco	17	1873	N	398.2
14	Guercif	Morocco	9	986	N	279.2
15	Mágina	Iberia	101	1670	N	598.2
16	Gareb	Morocco	25	1098	N	322.1
17	Almería	Iberia	107	1314	N	318.7
18	Vélez-Baza	Iberia	118	1641	N	515.8
19	Cazorla	Iberia	160	1839	N	568.2
20	Sierra Morena	Iberia	23	965	N	512.4
21	Axarquía	Iberia	58	992	N	570.8
22	Alpujarras	Iberia	125	2196	N	469.3
23	Trevenque-Almijara	Iberia	174	2023	N	573.2

P, palaeoendemism; N, neoendemism.

scheme with 10 000 iterations (Gotelli, 2000). This null model retains both species occurrence frequency and sample species richness as those of the actual site-by-species matrix, which has been demonstrated to minimize the risk of type II errors (Gotelli and Ulrich, 2012; Ulrich and Gotelli, 2013). We repeated this procedure for each species-level tree topology ($n=1000$), and used the arithmetic mean of the resultant SES_{RPE} values as an approximation to the ‘true’ values.

Environmental variables and regression analyses

We explored the relationship between SES_{RPE} and endemic species richness with precipitation- and temperature-related variables and elevation range of ecoregions by fitting linear and quadratic regression models. To do so, we used maximum resolution rasters from the WorldClim database (Hijmans *et al.*, 2005). We took monthly values of precipitation, temperature and elevation for each 1-km² cell in the study area and then extracted the monthly means for each ecoregion. Subsequently, we derived total annual precipitation, mean annual temperature and elevation range. These climatic variables have been demonstrated to be associated with variation in phylogenetic structure of plant assemblages across the study area (Molina-Venegas *et al.*, 2015a), and thus may have an impact in the spatial distribution of phylogenetic endemism. We sought spatial autocorrelation in SES_{RPE} and endemic species richness by visually exploring Moran’s I spatial correlograms of the residuals of the models and conducting global Moran’s I autocorrelation tests.

All analyses were conducted in R version 3.0.1 (R Development Core Team, 2013) using scripts published in the

GitHub repository (Rosauer, 2015) and the R packages APE (Paradis *et al.*, 2004) and NCF (Bjornstad, 2015).

RESULTS

The endemic species richness per ecoregion was rather high, 46.65 ± 49.57 (mean \pm s.d.), with maximum and minimum values in ‘Ronda’ (ID = 5; $n = 187$) and ‘High Ouerrha’ (ID = 10; $n = 5$) ecoregions, respectively (Table 1 and Fig. 1B). The area occupied by each ecoregion did not explain endemic species richness ($R^2 = -0.02$, $P = 0.77$), the latter being overall higher in Andalusia than in northern Morocco (one-way ANOVA; $F = 14.76$, $P < 0.001$). Centres of neoendemism were concentrated towards the eastern margins of the study region (ecoregions with low SES_{RPE} scores). In contrast, centres of palaeoendemism were clustered in the ecoregions around the Strait of Gibraltar (Fig. 1C). Removing ‘isolated lineages’ from the analyses did not qualitatively affect the results, although the ecoregions clustered around the Strait of Gibraltar experienced a considerable decrease in SES_{RPE} (see Supplementary Data Fig. S1 and Discussion).

Relative phylogenetic endemism (i.e. SES_{RPE}) was positively correlated with total annual precipitation ($R^2 = 0.16$, $P < 0.01$) (Table 2, Fig. 2A), although it showed a weak correlation with mean annual temperature, and particularly with elevation range (Table 2, Fig. 2B). In contrast, endemic species richness showed both a strong positive quadratic relationship with elevation range ($R^2 = 0.36$, $P < 0.001$, Fig. 2D) and a negative correlation with mean annual temperature ($R^2 = 0.41$, $P < 0.001$), although it was weakly correlated with total annual precipitation (Table 2, Fig. 2C). The ecoregion ‘Aljibe’ (ID 1) was a clear outlier towards the positive side of the distribution of

TABLE 2. Coefficient of determination values (R^2) and P -values from regressing SES_{RPE} and endemic species richness (ESR) onto climatic variables and elevation range

Biodiversity metric	Environmental variable	R^2	P -value
SES_{RPE}	Total annual precipitation	0.16	<0.01
SES_{RPE}	Mean annual temperature	0.01	0.21
SES_{RPE}	Elevation range	-0.009	0.46
ESR	Total annual precipitation	0.009	0.24
ESR	Mean annual temperature	0.41	<0.001
ESR	Elevation range	0.36	<0.001

In bold type are R^2 values with associated P -values <0.01 .

SES_{RPE} scores. Nevertheless, deleting this observation in the data did not affect the results (see Fig. 2). SES_{RPE} values showed no spatial autocorrelation in relation to total annual precipitation (Moran's $I < 0.001$, $P = 0.24$ and see Supplementary Data Fig. S2). In contrast, endemic species richness showed strong spatial autocorrelation in relation to both mean annual temperature and elevation range (Moran's $I = 0.08$, $P < 0.001$; Moran's $I = 0.18$, $P < 0.001$, respectively, and see Fig. S2).

DISCUSSION

Mediterranean biodiversity hotspots show a complex climatic and geological history, constituting a refuge area for both boreal and tropical Tertiary lineages (Axelrod, 1975; Médail and Diadema, 2009) and promoting active plant speciation at least since the Pliocene (Verdú and Pausas, 2013). The joint effect of both factors has resulted in extraordinary high levels of endemic species richness (Médail and Quézel, 1999). In this study, we have explored the climatic and topographical correlates of endemic species richness and RPE across a main regional biodiversity hotspot in the western Mediterranean, to shed new light on the processes that generate and maintain spatial patterns of palaeo- and neoendemism.

Our results highlight the importance of the region around the Strait of Gibraltar as a major centre of palaeoendemism in the south-western and north-western tips of Europe and Africa, respectively. This region stands out by its singular Cenozoic history and ecological features, which have created a distinct, nested sub-hotspot across two different tectonic plates (Rodríguez-Sánchez et al., 2008; Molina-Venegas et al., 2013). In particular, it seems that the Strait of Gibraltar region harbours an important isolated relict flora, which may comprise extant representatives of the past flora that existed under Tertiary climatic conditions (Herrera, 1992; Postigo Mijarra et al., 2009). This is demonstrated by the high levels of SES_{RPE} reported in ecoregions surrounding the Strait of Gibraltar (Fig. 1C). Furthermore, these ecoregions experienced a considerable decrease in SES_{RPE} when only strictly endemic taxa (i.e. after removing 'isolated lineages' from the dataset) were considered in the analyses (see Fig. S1), highlighting the role of the Strait of Gibraltar as a refuge for tropical-like isolated relict lineages that show strong disjunct distributions (e.g. *Psilotum nudum*, *Diplazium caudatum*, *Pteris incompleta*). Many of these relict lineages are associated with riparian and humid

habitats, and hence we observed a positive relationship between SES_{RPE} and total annual precipitation. The long-term persistence of these lineages may be explained by the particular climatic conditions of this region. The climate of the Strait of Gibraltar, although Mediterranean, shows a strong oceanic influence, and frequent wet winds produce low clouds and mist on the mountains close to the Strait of Gibraltar, which help to mitigate the effects of summer drought on the vegetation (Ojeda et al., 2000; Rodríguez-Sánchez et al., 2008). Furthermore, the relatively high water-retention capacity of sandstones (Matsushi and Matsukura, 2007), which is indeed the dominant bedrock in the Strait of Gibraltar region (Ojeda et al., 2000), might also contribute to retain moisture and maintain perennial streams, thus favouring the persistence of palaeoendemic lineages.

These humid habitats in the Strait of Gibraltar area have remained relatively stable since the Late Tertiary (Rodríguez-Sánchez and Arroyo, 2008) and particularly resilient to the drastic climatic fluctuations of the Miocene (e.g. the Messinian salinity crisis, Duggen et al., 2003) and cold periods of the Pleistocene (Finlayson and Carrión, 2007). This supports the idea that low climate-change velocity areas are potential climatic refugia for endemic species (Sandel et al., 2011; Abellán and Svenning, 2014). Furthermore, the incorporation of phylogenetic information revealed that these areas of wet and equable climatic conditions are more likely to allow the long-term persistence of palaeoendemic lineages, rather than the formation of recent endemic ones. Although our results are based on contemporary variables rather than historical conditions, there is strong evidence that despite strong variation in absolute values of precipitation and temperature over geological periods, the climatic gradient in the study region has been quite similar to that found nowadays at least since the Pliocene (Rodríguez-Sánchez and Arroyo, 2008). Nevertheless, future studies could usefully investigate the extent to which the persistence of palaeoendemic lineages and/or the formation of neoendemic species can be explained in terms of climatic stability through geological time. Finally, the ecoregions that match the valleys of the Guadalquivir and Sebou rivers in Andalusia and northern Morocco, respectively, also show high scores of SES_{RPE} (Fig. 1C). These ecoregions are shaped by extensive lowlands dominated by deep, well-drained and extraordinarily fertile soils, constituting potential habitats for many Tertiary lineages (Herrera, 1992). Nevertheless, the importance of these valleys as centres of palaeoendemism should be interpreted with caution, because despite the presence of a few palaeoendemic lineages (e.g. *Arum hygrophilum*) they show relatively low endemic species richness. It is relevant that these valleys have long been devoted to intensive agriculture (Aparicio, 2007) and have suffered most deeply the effect of human disturbances since the Neolithic (Ruíz-Mata, 2002).

Centres of neoendemism were concentrated towards the eastern part of the study area, roughly coincident with those ecoregions that match most of the Baetic-Rifan mountain range (Fig. 1). We previously showed that plant assemblages in these ecoregions were phylogenetically clustered (Molina-Venegas et al., 2015a), and hypothesized that this pattern may have arisen either by environmental filtering and/or *in situ* diversification of xeric- and cold-adapted lineages in Mediterranean mountains (e.g. *Helianthemum*, *Thymus*, *Sideritis*, *Teucrium*,

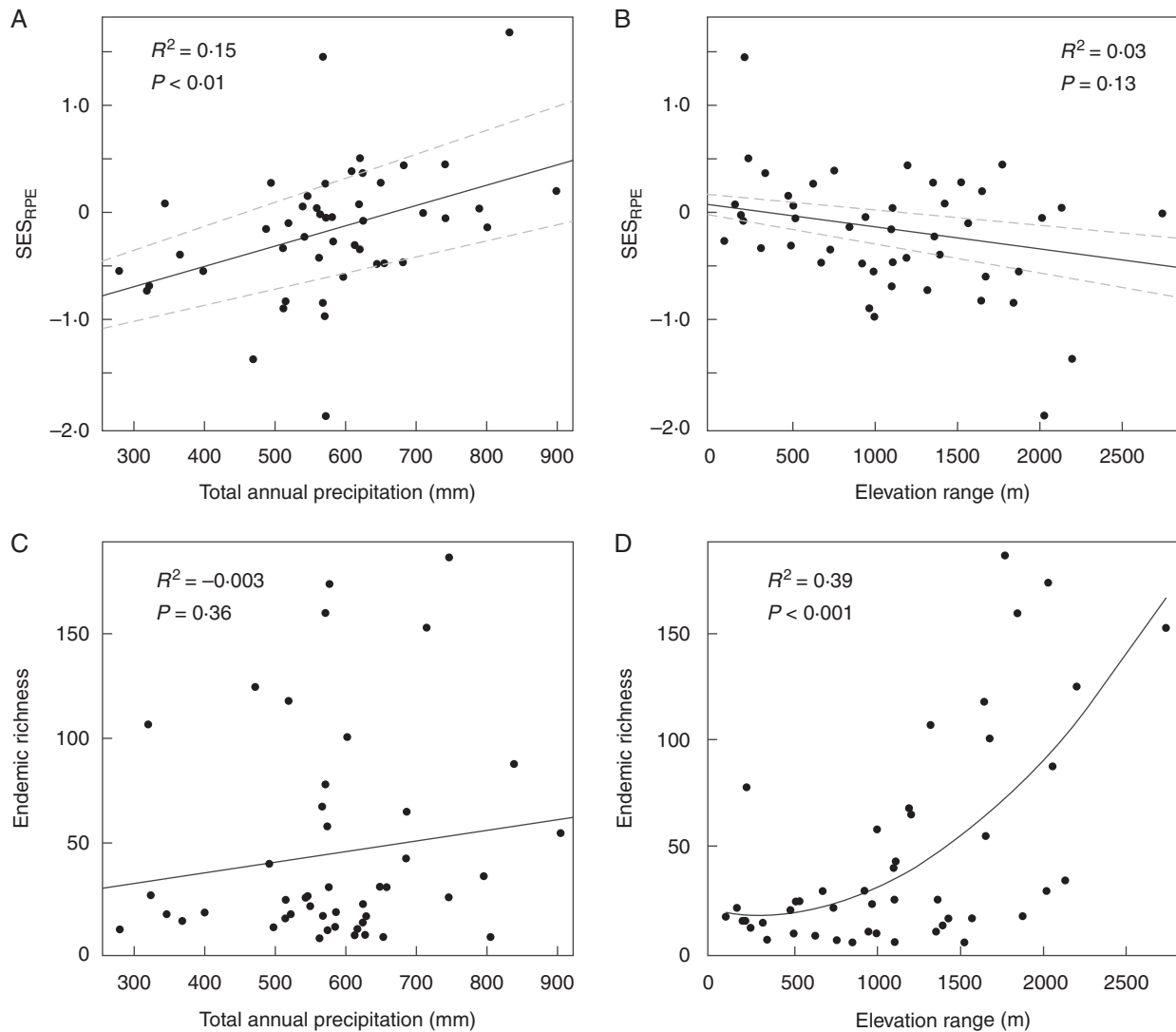


FIG. 2. Scatterplots of the relationship between SES_{RPE} and endemic species richness with total annual precipitation and elevation range, respectively. The solid lines represent the regression lines, while the dashed lines in the top panels represent the 95 % confidence intervals of the regressions while accounting for intrageneric phylogenetic uncertainty. To improve visual appreciation of data variability, all the regressions were refitted after removing the observation corresponding to the ‘Aljibe’ ecoregion, which was a clear outlier towards the positive side of the distribution of SES_{RPE} scores.

Arenaria, *Armeria*) following the onset of the Mediterranean climate (Verdú and Pausas, 2013). Our results strongly support the *in situ* diversification hypothesis, given the high concentration of neoendemism in the eastern margin of the Baetic–Rifan complex. The rapid uplift of this mountain range began around 8 Mya (Braga et al., 2003), roughly coincident with the oldest records of Mediterranean climate in the region (Brachert et al., 2006). These new combinations and diversity of climatic and geological conditions have probably generated unoccupied environmental conditions providing an ecological opportunity for the diversification of certain lineages. Furthermore, centres of neoendemism on both sides of the Baetic–Rifan complex are constituted to a great extent by phylogenetically related species assemblages (Molina-Venegas et al., 2015a), which supports the hypothesis that the last opening of the Strait of Gibraltar favoured the parallel diversification of closely related lineages on

both sides of the hotspot (Lavergne et al., 2013; Molina-Venegas et al., 2015a).

The ‘Sierra Nevada–Filabres’ ecoregion (Fig. 1B,C), a core region of the Baetic–Rifan complex, is a clear exception to the observed tendency of increased neoendemism towards eastern Baetic mountains. Indeed, this high-elevation ecoregion (up to 3482 m a.s.l.) showed an intermediate value of SES_{RPE} , whereas it is surrounded by centres of neoendemism (i.e. ecoregions with low SES_{RPE}). Furthermore, when the analyses were rerun using only taxonomic species and excluding ‘isolated lineages’, the ‘Sierra Nevada–Filabres’ ecoregion emerged as an isolated centre of palaeoendemism ringed by ecoregions of high neoendemism (see Fig. S1). The Sierra Nevada is one of the highest ranges in the Mediterranean Basin, and harbours a large number of narrow-ranging species that are mostly confined to the alpine belt (Blanca et al., 1998; Mota et al., 2002).

Thus, unlike other surrounding mountains of the Baetic–Rifan range, the Sierra Nevada acted as a climatic-refuge island for several palaeoendemics with boreal and temperate affinities (e.g. *Cotoneaster granatensis*, *Prunus ramburii*, *Rothmaleria granatensis*, *Narcissus nevadensis*). This mountain range also harbours more recently evolved artico-alpine species (e.g. *Sibbaldia procumbens*, *Silene rupestris*, *Veronica aragonensis*, *Papaver lapeyrousianum*, *Ranunculus glacialis*, *Thalictrum alpinum*), which tend to reduce the estimated SES_{RPE} of the ecoregion. This underlines the role of the Sierra Nevada range as a cold climatic refuge through the successive climate changes that have occurred since the late Tertiary and the Quaternary glaciations (Fernández *et al.*, 2007).

Interestingly, SES_{RPE} and endemic richness were decoupled in relation to climate and topography. Although SES_{RPE} was positively correlated with total annual precipitation, the correlation between endemic species richness and precipitation remained non-significant. Also, both elevation range and mean annual temperature were good predictors of endemic species richness (although both explanatory variables were strongly correlated, $r = -0.72$), but showed a poor correlation with SES_{RPE} . Furthermore, our results suggest that endemic species richness is distributed on a spatially structured environmental gradient across the hotspot (i.e. topographical relief), as it showed a strong spatial autocorrelation in relation to elevation range. This is in concordance with traditional claims that topographical relief enhances endemic species richness (Crisp *et al.*, 2001; Vetaas and Grytnes, 2002), although it failed to explain local phylogenetic structure of endemic species assemblages (i.e. SES_{RPE}). Thus, the concentration of neoendemism in highest and coldest zones of the Baetic–Rifan complex suggests that topographical relief and relative harsher climates may have driven evolutionary diversification of endemic species, probably by favouring a relative spatial isolation, as in a continental island setting (Steinbauer *et al.*, 2012). Conversely, water availability seems to favour long-term persistence of palaeoendemics, particularly in areas of mild climate and smoother topography (Rodríguez-Sánchez and Arroyo, 2008). Nevertheless, the highest ranges of the Baetic–Rifan complex may have indirectly promoted the persistence of some palaeoendemic lineages by buffering some micro-habitats from climatic variations (drought effects in particular). This would explain the poor correlation between elevation range and SES_{RPE} , despite the former being strongly correlated with endemic species richness. For example, *Abies pinsapo* is an emblematic species belonging to the group of circum-Mediterranean relict firs, which are disjunctly distributed across coastal Mediterranean mountain areas (Terrab *et al.*, 2007). This species forms dense forests that are locally confined to north-facing slopes above 1000 m. a.s.l. of the ‘Ronda’ (ID 5) and ‘West Rifan’ (ID 2) calcareous mountains, notably increasing palaeoendemism in these mountainous ecoregions close to the Strait of Gibraltar.

Our results show that the Baetic–Rifan biodiversity hotspot harbours clearly differentiated centres of palaeo- and neoendemism. However, endemic species contributing to palaeoendemism are less represented in the current floras than recently evolved taxa, as the former are mostly survivors of past floras that existed under previous geological climates. These ancient lineages are mainly found in low-elevation woodland habitats of mild climate across the Baetic–Rifan hotspot, probably due

to the combined role of phylogenetic niche conservatism and habitat filtering in shaping the regeneration niches of species (Valiente-Banuet and Verdú, 2013; Molina-Venegas *et al.*, 2015b). Unlike recently evolved taxa, palaeoendemics seem to be decoupled in relation to Quaternary climatic conditions (Valiente-Banuet *et al.*, 2006), and are thus more prone to extinction due to future climate scenarios (García-Ruiz *et al.*, 2011). In this sense, the progressive shrinking of low-temperature, high-elevation habitats in Mediterranean mountains (Gottfried *et al.*, 2012) constitutes a palpable threat to the persistence of palaeoendemic species inhabiting cold climatic refuges in the highest zones of the Baetic–Rifan complex. Given that climatic change has been denoted as the most pervasive threat to the biodiversity hotspots (Malcolm *et al.*, 2006; Bellard *et al.*, 2014) and particularly in the Mediterranean (Giorgi and Lionello, 2008; García-Ruiz *et al.*, 2011), conservation planners should pay particular attention to preserve areas retaining relatively older phylogenetic lineages, as these areas act as ‘natural museums’ of biodiversity within the Baetic–Rifan hotspot.

Note that we have included geographically isolated populations from the main species’ range in the study area as ‘isolated endemic lineages’, which are usually not considered when quantifying phylogenetic endemism using a purely geographical and taxonomical criterium. Indeed, our approach is based on a more process-orientated account of phylogenetic endemism, as there is evidence that differential extinction is behind many palaeoendemics and disjunct relict taxa (e.g. Mejías *et al.*, 2002; Rodríguez-Sánchez and Arroyo, 2008). Furthermore, some phylogeographical studies have demonstrated that disjunct range-edge relict populations in Mediterranean refugia show high levels of genetic divergence (Hampe *et al.*, 2003; Rodríguez-Sánchez *et al.*, 2009) and might be recognized as distinct taxa (e.g. Rumsey *et al.*, 2014). The presence of disjunct range-edge relict populations in Mediterranean refugia is key to understand late Tertiary, glacial and inter-glacial refugial dynamics, and should be treated as scientific evidence rather than biogeographical curiosities.

SUPPLEMENTARY DATA

Supplementary data are available online at www.aob.oxfordjournals.org and consist of the following. Appendix 1: list of the species and subspecies considered in the analyses. Figure S1: results of the RPE analysis after removing ‘isolated lineages’ from the data. Figure S2: Moran’s I spatial correlograms of the residuals of the regression models.

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