ORIGINAL ARTICLE

Investigating the evolutionary assembly of a Mediterranean biodiversity hotspot: deep phylogenetic signal in the distribution of eudicots across elevational belts

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ABSTRACT

Aim To reconstruct the historical assembly of the eudicot flora of Mediterranean sierras by examining compositional (CBD), phylogenetic (PBD) and functional (FBD) beta diversity between elevational belts among disjunct mountain ranges (sierras), and relating these measures of turnover to environmental and geographical distances.

Location Baetic ranges, Andalusia, southern Spain.

Methods We compiled eudicot species and subspecies ('entities') checklists for three elevational belts within each of eight sierras of Andalusia ('sites') and tested for non-random patterns of PBD and FBD of all entities and of endemic entities separately among sites between and within sierras. Multiple regression on distance matrices was used to determine the respective contribution of climate, lithology and geographical distance to CBD, PBD and FBD. Finally, we decomposed PBD into the turnover and nestedness components of beta diversity, and quantified the phylogenetic diversity (PD) within sites.

Results The observed PBD and FBD among elevational belts within sierras for all entities were generally higher than expected based on their respective null distributions, whereas CBD among elevational belts within sierras was similar or even lower than between sierras. In contrast, the observed PBD and FBD for endemics were non-significant in most of the comparisons. Temperature-related variables best explained patterns of CBD, PBD and FBD for all entities, whereas lithology and geographical distance were the main drivers of endemic CBD. The observed PBD among elevational belts within sierras was mainly attributable to differences in PD rather than 'true' turnover.

Main conclusions There is strong structuring of plant lineages along elevational gradients in the Baetic range, probably due to habitat filtering acting on life forms and character syndromes that show strong phylogenetic signal. The differentiation of the endemic flora that contributed to the emergence of this western Mediterranean biodiversity hotspot was probably driven by geographical isolation and/or by repeated specialization to contrasting lithologies.

Keywords

Climate, elevation, eudicots, functional beta diversity, lithology, Mediterranean flora, phylogenetic beta diversity, southern Iberian Peninsula.

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INTRODUCTION

The Mediterranean Basin harbours 8.3% of the world's total floristic richness (Médail & Quézel, 1997). Approximately 18% of this floristic richness is concentrated in the southern portion of the Iberian Peninsula (Andalusia) and northern Morocco (see Molina-Venegas *et al.*, 2013), and within the Baetic–Rifan mountain range complex in particular (Médail & Quézel, 1997). The well-studied flora, high levels of topographic and climatic heterogeneity, and the division between two continental plates makes this centre of plant diversity an excellent study system for better understanding the evolutionary and ecological processes that have shaped plant assemblages within Mediterranean biodiversity hotspots.

The Mediterranean flora is characterized by high compositional beta diversity (CBD) (Thompson, 2005), mostly because of the large number of narrow-endemic species (Médail & Quézel, 1999). In their analysis of the Baetic ranges, Molina-Venegas *et al.* (2013) found that climate was the most significant driver of CBD between the floras of ecoregions (territories characterized by the existence of homogeneous climatic, topographical and geological features) within the Baetic range, whereas CBD of the flora endemic to the range was driven by both lithology and climate. These patterns may have arisen as a result of the climatic stability – particularly in southern Europe – during the Plio-Pleistocene (Finlayson & Carrión, 2007) and the evolution of traits linked to limited colonizing potential but high population stability in particular substrates (Lavergne *et al.*, 2004). Given that species share part of their evolutionary histories and are not always functionally equivalent, however, the inclusion of phylogenetic and functional information in analyses of beta diversity (Graham & Fine, 2008) allows us to improve our understanding of the ecological and evolutionary mechanisms that shape biodiversity patterns (Swenson *et al.*, 2012; Siefert *et al.*, 2013).

The Baetic ranges comprise a set of disjunct mountain ranges (sierras) containing many peaks over 2000 m a.s.l. (Fig. 1), with the highest peak at 3482 m. The rugged topography yields steep temperature and precipitation gradients, with contrasting soil types derived from outcrops of differing lithology (Mota *et al.*, 2002). This strong environmental heterogeneity explains much of the spatial structure of plant diversity and the great richness of narrow-endemic species in this hotspot (Molina-Venegas *et al.*, 2013). We would thus expect that niche-related traits should be strongly structured along these gradients, resulting in high functional beta diversity (FBD). Similarly, if niche-related traits show strong phylogenetic signal, we would expect high phylogenetic beta diversity (PBD) along elevational gradients, because different clades should be non-randomly structured with respect to ecological conditions (Hardy & Senterre, 2007). On the other hand, PBD among sites of contrasted lithology should be high if there is phylogenetic signal in species' substrate preferences. Finally, dispersal limitation could result in plant assemblages that are close together in space being more phylogenetically similar than those that are further apart, as predicted by a distance decay null model (Condit *et al.*, 2002).

Recent studies exploring life-history traits in a phylogenetic context have made valuable contributions to our understanding of the mechanisms that drive community assembly and plant evolution within the Mediterranean (Paula & Pausas, 2011; Pausas & Schwilk, 2012). Herrera (1992) found that, as a consequence of adaptive processes, phylogenetic constraints, historical effects and sorting processes, the woody flora of southern Spain could be grouped
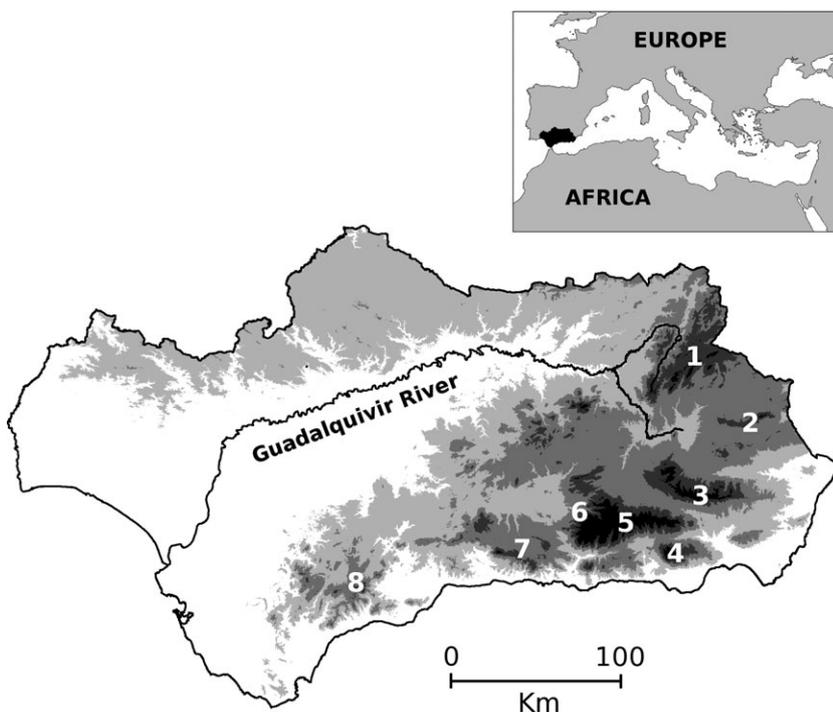
Figure 1 Map of Andalusia (southern Iberian Peninsula) showing the position of the eight disjunct mountainous areas (sierras) analysed in the study. The inset shows the location of Andalusia within the Mediterranean Basin. The numbers correspond to: (1) Sierra de Cazorla, (2) Sierra de María-Los Vélez, (3) siliceous Sierra de los Filabres, (4) Sierra de Gádor, (5) siliceous Sierra Nevada, (6) calcareous Sierra Nevada, (7) Sierras de Tejeda, Almijara y Alhama, and (8) Sierra de las Nieves.

into two contrasting character syndromes: sclerophyllous and non-sclerophyllous plants (see also Verdú & Pausas, 2013). Plants with sclerophyllous leaves and small, unisexual, uncoloured, wind-pollinated flowers with a reduced perianth, and large seeds dispersed by animals occur in lineages whose characteristics pre-date the appearance of the Mediterranean climate, whereas plants with alternative character states arose in lineages that evolved after the emergence of this climatic regime (Herrera, 1992; Verdú & Pausas, 2013). Further work triggered by the seminal paper by Herrera (1992) has focused on the relationship between the syndromes and ecological strategies (Verdú, 2000; Verdú & Pausas, 2007) and lineage diversification (Verdú & Pausas, 2013). The spatial distribution of these relevant syndromes along environmental gradients has not been previously explored, however, and it could help to understand the ecological and evolutionary factors that shape patterns of biodiversity in this Mediterranean biodiversity hotspot.

The southern edge of the Iberian Peninsula has acted as a refugium for cold-sensitive taxa through the dramatic climatic oscillations that occurred from the late Miocene onwards (Postigo Mijarra et al., 2009; Rodríguez-Sánchez & Arroyo, 2011). Refugia in climatically mild lowlands allow the persistence of several old and phylogenetically distinct lineages (e.g. Coriaria, Ilex, Myrtus, Osyris and Pistacia) that represent the sclerophyllous syndrome (Herrera, 1992; Verdú & Pausas, 2013). The aridity trend of the late Miocene–Pliocene transition, which marks the onset of the Mediterranean climate in the region, has been placed between c. 10 (Brachert et al., 2006) and 3.6 Ma (Suc & Popescu, 2005), roughly coincident with the beginning of the uplift of the Baetic Cordillera approximately 8 Ma (Braga et al., 2003). Thus, we expect sclerophyllous lineages to be ecologically restricted to warmer low elevations, whereas non-sclerophyllous lineages are expected to occur across higher-elevation ranges of colder climatic conditions. Diversification in the latter is related to the appearance of the current Mediterranean climate regime (Verdú & Pausas, 2013) and the climatic oscillations imposed by ice ages of the Pleistocene (Hewitt, 2000; Willis & Niklas, 2004). Non-sclerophyllous lineages represent the vast majority of species diversity in the Mediterranean.

Although the character syndromes of Herrera (1992) are useful for developing predictions for the woody taxa of the Baetic range, they are not applicable to non-woody species. Raunkiær (1934) classified the life-forms of plants according to the locations of buds and apical shoots destined to survive the unfavourable period of the year (e.g. summer drought). These life-forms seem to be geographically and elevationally structured within the Mediterranean (Danin & Orshan, 1990; Giménez Luque et al., 2004), which may affect the assembly of the flora of Mediterranean sierras. The life-form spectrum of the endemic flora of the southern Iberian Peninsula does not comply with the general patterns previously observed in a number of local floras in the southern Iberian Peninsula and other regions of the Mediterranean Basin (Melendo et al., 2003; Giménez Luque et al., 2004), suggesting different diversification rates among life forms in the Mediterranean sierras. Thus, if there is phylogenetic signal in the distribution of life forms in the flora, we expect high PBD along elevational gradients, reflecting the deterministic ecological structuring of lineages mediated by life-history traits.

In this paper, we aim (1) to examine the spatial patterns of compositional, phylogenetic and functional (character syndromes and life-forms) beta diversity across elevational belts of sierras in a Mediterranean biodiversity hotspot, and (2) to quantify how environmental factors such as climate, lithology and spatial effects (distance decay) affect these patterns.

MATERIALS AND METHODS

Study area and plant dataset

We compiled an exhaustive dataset of native eudicot plant species and subspecies (hereafter, 'entities') recorded in eight disjunct mountain ranges (sierras) of Andalusia (Fig. 1, Table 1; see Appendix S1 in Supporting Information for further details). Using information on elevational ranges from Blanca et al. (2009), we created a second dataset by assigning each entity that we recorded in the study sierras to three elevational belts (belt 1, 700–1300 m; belt 2, 1300–1800 m; belt 3, 1800–2700 m), making a site-by-species matrix of 24 sites (elevational belts within sierras) and 1982 entities in total.

Table 1 Baetic sierras of Andalusia considered in the study. The table shows the name of the sierras, area of the elevational belts (belt 1, 700–1300 m; belt 2, 1300–1800 m; belt 3, 1800–2700 m), total area, maximum elevation, predominant lithology, species richness, endemic species richness and floristic sources of eudicots for each sierra.

| Sierra | Area (km²) | | | Total area (km²) | Maximum elevation (m) | Lithology | Species richness | Endemic richness | Source |
	Belt 1	Belt 2	Belt 3						
Nieves	119.77	38.20	0.38	158.35	1918	Limestone	895	77	Cabezudo et al. (1998)
Tejeda-Almijara	242.86	100.56	4.85	348.27	2065	Marble	755	87	Cabezudo et al. (2005)
Calcareous Nevada	292.57	203.62	15.98	512.17	2450	Limestone	758	84	Pérez Raya (1987)
Siliceous Nevada	225.51	525.48	660.72	1517.86	3482	Schist	995	111	Blanca et al. (2009)
Gádor	325.39	146.99	58.11	530.49	2240	Limestone	774	74	Giménez Luque (2000)
Siliceous Filabres	428.43	421.99	146.7	997.12	2168	Schist	624	47	Peñas de Giles (1997)
Cazorla	1666.94	1224.99	89.93	2981.86	2383	Limestone	1189	138	Blanca et al. (2009)
María	153.90	62.69	7.52	224.11	2045	Limestone	648	72	Cueto & Blanca (1997)

Unfortunately, it was not possible to base the site species lists on observations. Nevertheless, our approach is justified because the latitudinal variation among the sierras (the main source of variation in species' elevational ranges) is very small (see Fig. 1) and the sample grain size (elevational belts) considered in the study is broad enough to assimilate most of the possible elevational variability of each species among the different sierras. Lastly, approximately 30% of the species are restricted to single sierras. Blanca *et al.* (2009) defined these elevational belts for the flora of eastern Andalusia according to the bioclimatic classification in Rivas-Martínez (1983), which is related to the length of the growing season. We also generated a subset from the site-by-species matrix that included only those entities that are endemic to the Baetic ranges (*n* = 333), following the criteria in Molina-Venegas *et al.* (2013) for assessing species' ranges. We did not consider entities that occurred entirely above 2700 m (only in siliceous Sierra Nevada) for the overall analyses because of the lack of replicates, but we conducted an additional analysis restricted to siliceous Sierra Nevada (four elevational belts, up to 3482 m), to further explore patterns of elevational variation in one of the widest elevational gradients in the Mediterranean.

Functional traits

We obtained life-form information from Blanca *et al.* (2009), who used Raunkiær (1934) categories as defined in Font Quer (1953). They considered five possible states: therophyte, hemicryptophyte, geophyte, chamaephyte and phanerophyte. In cases where life-form was ambiguous, we selected the most common state in the study area according to the taxon descriptions in Blanca *et al.* (2009) and Castroviejo (1986–2012). We excluded from all analyses entities that could not be assigned a life-form (*n* = 17, 0.8%), leaving 672 therophytes, 604 hemicryptophytes, 69 geophytes, 371 chamaephytes (mostly small shrubs) and 176 phanerophytes (mostly tall shrubs and trees).

In order to characterize character syndromes (Herrera, 1992), we compiled nine binary traits for all woody entities (chamaephytes and phanerophytes) in the dataset (*n* = 547) using local floras and field observations. These traits include spinescence, leaf type, flower size, flower sexuality, flower colour, perianth reduction, pollinator type, seed size and dispersal syndrome (see Appendix S2). We then summarized this multidimensional trait information in the first ordination axis of a multiple correspondence analysis, and treated entities' scores on this axis as a quantitative trait representing where they sit in the continuum between the sclerophyllous and non-sclerophyllous syndromes (Verdú & Pausas, 2013).

Phylogenetic tree

We used the genus-level time-calibrated phylogeny described in Molina-Venegas & Roquet (2014). The phylogeny includes 98% of the genera in the dataset (*n* = 565, including those genera removed from the analyses). Species and subspecies were inserted as polytomies at the midpoint of the corresponding genus and species terminal branches, respectively.

Phylogenetic signal

To test whether entities that are more closely related are more likely to share the same life-form, we calculated the mean phylogenetic distance (MPD) among entities within each life-form. MPD measures the mean of the phylogenetic distances between all possible pairs in the sample. We calculated the standardized effect size values of MPD (SES_{mpd}) as:

$$SES = X_{obs} - mean(X_{null})/SD(X_{null}), \qquad (1)$$

where X_{obs} is the observed MPD between all pairs of entities in the dataset within a given life form, and $mean(X_{null})$ and $SD(X_{null})$ are the mean and standard deviation of a null distribution of MPD scores within the site generated by 999 random draws of the same number of species from the entire species pool of the study (Kembel, 2009). The SESmpd is expressed in units of standard deviation, such that values below -1.96 indicate a significantly lower MPD than expected, and thus a strong phylogenetic signal, whereas values greater than -1.96 indicate weak or lack of phylogenetic signal.

We estimated the phylogenetic signal in the ordination axis representing character syndromes using the *K* statistic (Blomberg *et al.*, 2003). Phylogenetic trees containing many terminal polytomies can dramatically inflate estimates of phylogenetic signal using Blomberg's *K*, so we conducted a rarefaction procedure to more accurately estimate the phylogenetic signal of the character syndromes on the phylogeny of woody entities (Davies *et al.*, 2012). This involved randomly removing all but one taxon per terminal polytomy in the complete phylogeny of woody entities and estimating *K* on the smaller 'thinned' tree, this procedure being repeated 999 times (Davies *et al.*, 2012). The 'true' estimate of phylogenetic signal is represented by the mean of the generated distribution of *K* values. *K* values of 1 correspond to a Brownian motion process, which implies some degree of phylogenetic signal. *K* values closer to zero correspond to a random pattern of evolution, whereas *K* values greater than 1 indicate strong phylogenetic signal. The statistical significance of Blomberg's *K* was evaluated against a null model where taxa labels were shuffled randomly across the tips of the phylogeny 999 times (Blomberg *et al.*, 2003).

Phylogenetic beta diversity

We test for non-random patterns of phylogenetic beta diversity (PBD) between elevational belts within sierras (set 1), and between sierras within the same elevational belt (set 2) using the PhyloSor index (Bryant *et al.*, 2008). The PhyloSor index is analogous to the Sørensen index (Sørensen, 1948), computing the fraction of shared phylogenetic branch length between two samples, rather than the fraction of shared species. We

also estimated compositional beta diversity (CBD) between the same sites as for PBD using the Sørensen index. Both indices were used as distance measures (i.e. CBD = 1 − Sørensen index; and PBD = 1 − PhyloSor index).

Previous empirical studies have emphasized that CBD and PBD can be highly correlated (Bryant *et al.*, 2008; Qian *et al.*, 2013). For our dataset, the correlation between PhyloSor and Sørensen indexes was very high (Pearson's correlation coefficient, $r = 0.93$). Thus, in order to determine whether the PBD among sites was higher or lower than expected given the observed CBD, we calculated the standardized effect size values of PBD (SES_{pbd}) among sites as in equation 1, where X_{obs} is the observed PBD between two sites, and mean(X_{null}) and SD(X_{null}) are the mean and standard deviation of a null distribution of PBD values between the two sites generated by shuffling taxa labels of the community matrix 999 times. Values greater than 1.96 indicate a higher PBD than expected for the given CBD, and values below −1.96 indicate a lower PBD than expected.

In order to test for the possible timescale-dependence of the processes that generate non-random patterns, we repeated the PBD analysis including only those lineages younger than 1/2 (62.5 Ma), 1/4 (31.25 Ma) and 1/8 (15.6 Ma) of the total time from the root to the tips of the phylogeny (125 Ma) (Hardy & Senterre, 2007).

To explore to what extent PBD is driven by the nestedness versus turnover components of beta diversity, we decomposed PBD into differences arising from differences in phylogenetic diversity (nestedness component, 'PD' in the sense of Faith, 1992) from those that are due to 'true' turnover (Leprieur *et al.*, 2012). We determined whether the turnover and nestedness components of the PBD among sites were higher or lower than expected given the observed CBD by calculating the standardized effect size scores of both components among sites (SES_{turn} and SES_{nes} respectively) in the same way as for the SES_{pbd} (see above). Finally, we tested for non-random patterns of PD at each site by estimating the standardized effect size values of PD (SES_{pd}) as in Eqn 1, where X_{obs} is the observed PD within a site, and mean(X_{null}) and SD(X_{null}) are the mean and standard deviation of a null distribution of PD scores within the site generated by 999 random draws of the same number of species from the entire species pool of the study.

Functional beta diversity

We quantified the observed functional dissimilarity in life forms (FBD_{LF}) among the same sites as for PBD based on the counts of entities within each life form at each site, using the Bray–Curtis dissimilarity index. Functional dissimilarity in life forms was also highly correlated with CBD (Pearson's correlation coefficient, $r = 0.72$). Thus, in order to test for non-random patterns in FBD_{LF} given the observed CBD, we calculated the standardized effect size values of FBD_{LF} (SES_{fbdLF}) among sites as in Eqn 1, where X_{obs} is the observed FBD_{LF} between two sites, and mean(X_{null}) and SD

(X_{null}) are the mean and standard deviation of a null distribution of FBD_{LF} values between the two sites generated by randomizing the life form states among taxa 999 times.

Finally, we quantified the observed functional dissimilarity in character syndromes (FBD_{CS}) among the same sites as for FBD_{LF} using the Euclidean distance between the averaged ordination scores. We tested for non-random patterns in FBD_{CS} in the same way as for FBD_{LF} (see above), because FBD_{CS} was also highly correlated with CBD (Pearson's correlation coefficient, $r = 0.62$).

Climatic, lithological and geographical variables

To characterize the climatic variation among elevational belts, we used GIS raster layers for the period 1970–2000 acquired from the Environmental Information Network of Andalusia (REDIAM, 2013) at 1 km^2 resolution. We took monthly minimum, maximum and mean temperatures and monthly mean precipitation for each 1-km^2 cell in the study area and extracted the means for each elevational belt. We also derived the mean precipitation of the driest and wettest annual quarters from the monthly mean precipitation scores. Precipitation-related variables were log-transformed and all variables were standardized using Gower's standardization of quantitative variables (i.e. division by the range). Given that the climatic variables were highly collinear, we conducted separate principal components analyses (PCA) for the temperature and precipitation variables to reduce their dimensionality, and then used only the first principal component of each analysis. The Euclidean distance between PCA1 scores was used to represent the temperature and precipitation distances among sites.

A lithological distance matrix was constructed using the Bray–Curtis dissimilarity index based on the counts at each site of the relative surface area of 86 different lithological substrates, derived from a lithological map (scale 1 : 100,000) of Andalusia (Jordán, 2000). Finally, we calculated the geographical distances among sierras as the Euclidean distance between the centroids of each sierra (note that the geographical distances between elevational belts within each sierra is zero, because they are geographically nested).

Exploring environmental correlates of beta diversity

We applied multiple regression on distance matrices (MRM; Lichstein, 2007) by relating each of CBD, SES_{pbd} and SES_{fbdLF} matrices for all entities, CBD, SES_{pbd} and SES_{fbdLF} matrices for endemics only and SES_{fbdCS} for woody entities, to climatic, lithological and geographical distance matrices. We partitioned the variance of the beta diversity matrices into the single contributions from each explanatory variable, the covariation between them and the unexplained variance (Legendre & Legendre, 1998). We also tested the significance of each univariate relationship between each beta diversity matrix and each explanatory variable using permutation tests ($n = 1000$).

All analyses were performed in R 2.15.1 (R Development Core Team, 2012), using the packages PICANTE (Kembel *et al.*, 2010), SPACODIR (Eastman *et al.*, 2012), VEGAN (Oksanen *et al.*, 2012), ADE4 (Chessel *et al.*, 2004) and ECODIST (Goslee & Urban, 2007), and the functions *thin_terminal_polytomies* (Davies *et al.*, 2012) and *betadecompo* (Leprieur *et al.*, 2012).

RESULTS

Phylogenetic signal

We found strong phylogenetic signal in all life-forms except phanerophytes, for which the mean phylogenetic distance among entities was not significantly different from expected ($SES_{mpd} = 0.15$; $P = 0.543$). The phylogenetic signal was particularly strong for hemicryptophytes ($SES_{mpd} = -16.13$; $P < 0.001$). The first axis of the ordination analysis of syndromes explained 42.40% of the variance, with negative scores representing entities with small, unisexual, reduced, uncoloured, wind-pollinated flowers and sclerophyllous leaves, whereas positive scores represent entities with large, hermaphroditic, unreduced, colourful, insect-pollinated flowers and non-sclerophyllous leaves (see Appendix S2 for details). The ordination scores showed a strong phylogenetic signal [$K = 1.33 \pm 0.0005$ (mean $\pm$ SE); $P < 0.001$ for all K estimations].

Patterns of beta diversity

The correlation between the standardized effect size of phylogenetic beta diversity (SES_{pbd}) and compositional beta diversity (CBD) was very weak (Pearson's correlation coefficient, $r = -0.03$), implying that our null-model approach broke down the inherent correlation between phylogenetic beta diversity (PBD) and CBD. Thus, despite similar or lower CBD within sierras than between, the observed PBD among elevational belts within sierras (set 1) for all entities was generally higher than expected for the given CBD (Fig. 2a,b). In contrast, the observed PBD between sierras within the same elevational belt (set 2) did not deviate significantly from the null expectation (Fig. 2b). This pattern was quite robust among different time partitions of the phylogeny, particularly with regard to the observed PBD between the lowest and the highest-elevation sites, where the significance levels were only slightly reduced when only lineages younger than 15.6 Ma were considered (Fig. 2c). The observed functional beta diversity in life forms (FBD_{LF}) and PBD for endemic entities were not significantly different from the null expectations in most comparisons. The nestedness component of PBD (differences in phylogenetic diversity, PD) was higher than expected for the given CBD in 20 of the 24 pairwise comparisons between elevational belts within sierras, whereas the turnover component of PBD was non-significant (data not shown). PD decreased from low to high elevations in all

cases, regardless of the age of the lineages considered (Fig. 3).

The observed FBD_{LF} among elevational belts within sierras for all entities was higher than expected in all cases (Fig. 2d), whereas the observed FBD_{LF} between sierras within the same elevational belt was also higher than expected in some cases. The observed functional beta diversity in character syndromes (FBD_{CS}) among elevational belts within sierras was generally significantly higher than expected in almost all cases (Fig. 2e), whereas the observed FBD_{CS} between sierras within the same elevational belt was only significant in a few cases.

The observed PBD along the elevational gradient of siliceous Sierra Nevada (four elevational belts) was significantly greater than expected between belt 1 and higher elevations (belts 2, 3 and 4), and also between belts 2 and 4.

Environmental correlates of beta diversity

The first axes of the PCAs for temperature-related and precipitation-related variables explained 87.7% and 65.7% of variance, respectively (negative scores represent high-temperature and high-precipitation regimes). Temperature-related variables had the greatest explanatory power for compositional (CBD), phylogenetic (SES_{pbd}) and functional (SES_{fbdLF} and SES_{fbdCS}) beta diversity across all entities (CBD, 45.5%; SES_{pbd}, 48.6%; SES_{fbdLF}, 39.4%; SES_{fbdCS}, 21.4%; Table 2), whereas precipitation-related variables showed a non-significant relationship in all cases (data not shown). In contrast, variance in the CBD of endemics was related to lithological and geographical distances (14.3% and 27.2% respectively), and to temperature-related variables to a lesser extent (7.2%). Only a small fraction of variance in the SES_{fbdLF} of endemics was explained by temperature-related variables (7.6%), whereas no variables explained significant variance in the SES_{pbd} of endemics.

DISCUSSION

Studies of elevational clines in the diversity and composition of plant assemblages date back to the origins of biogeography (von Humboldt, 1849; Lomolino, 2001). The recent incorporation of phylogenetic and functional information into biogeographical analyses of elevational gradients provides a more complete understanding of the evolutionary and ecological processes that shape plant assemblages, allowing species turnover to be interpreted as a function of adaptation and environmental filtering, and/or speciation in relation to ecological and historical processes (Anacker & Harrison, 2012a; Qian *et al.*, 2013). In this study, we explored the compositional, phylogenetic and functional beta diversity of eudicot plant assemblages along elevational belts across multiple disjunct sierras in a western Mediterranean biodiversity hotspot, finding strong phylogenetic and phenotypic structuring of plant lineages along elevational gradients in the range.
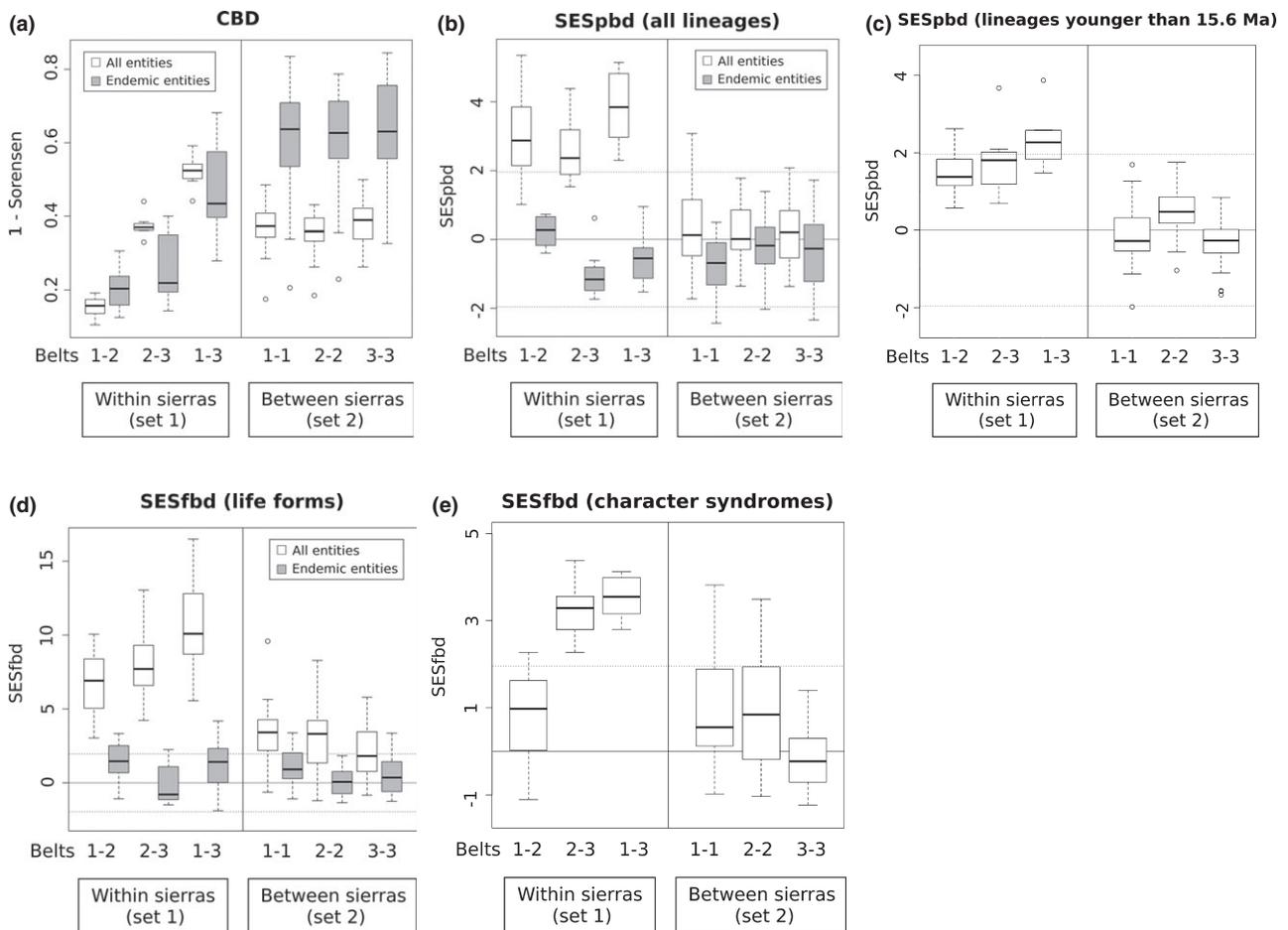
Figure 2 Box-and-whisker plots summarizing compositional (CBD), phylogenetic (SES$_{pbd}$) and functional (SES$_{fbd}$: life forms, SES$_{fbdLF}$; character syndromes, SES$_{fbdCS}$) beta diversity scores (y-axis) among pairwise site comparisons for eudicots of the Baetic sierras of Andalusia. Two types of comparisons of three groups within each are presented: between elevational belts within sierras (set 1, $n = 8$ per group) and between sierras within the same elevational belt (set 2, $n = 28$ per group). Pairwise numbers (x-axis) represent the elevational belts involved in each pairwise site comparison (belt 1, 700–1300 m; belt 2, 1300–1800 m; belt 3, 1800–2700 m). Horizontal dotted lines represent threshold values for significance at −1.96 and +1.96 respectively ($\alpha = 0.05$, two-sided). Horizontal solid lines represent a visual reference line at $y = 0$. The panels represent (a) CBD scores obtained when using all lineages in the dataset (for endemic entities and all entities, respectively); (b) the SES$_{pbd}$ scores obtained when using all lineages in the dataset (for endemic entities and all entities, respectively); (c) the SES$_{pbd}$ scores obtained when using only lineages younger than 15.6 Ma; (d) the SES$_{fbd}$ of life-form scores (for endemic entities and all entities, respectively); (e) the SES$_{fbd}$ of character syndromes scores (woody entities).

Beta diversity patterns

The observed phylogenetic and functional beta diversity in life-forms (PBD and FBD$_{LF}$, respectively) for all entities and the observed functional beta diversity in character syndromes (FBD$_{CS}$) among elevational belts within sierras (set 1) were generally higher than expected, although the compositional beta diversity (CBD) within sierras was similar or even lower than between sierras. This pattern suggests a strong ecological structuring of lineages, life-forms and character syndromes along elevational gradients in the mountain areas of the Baetic ranges. The close relationship between lineage and functional turnover is likely to be due to the strong phylogenetic signal in the distribution of life-forms and character syndromes across the phylogeny. The significant PBD between elevational belts was mainly attributable to

differences in phylogenetic diversity (PD) among elevational belts (Fig. 3) both for all lineages and for lineages younger than 15.6 Ma, which implies a loss of relatively deep lineages (compared to the average age of the constituent lineages in each case) from low to high elevations.

The observed FBD$_{LF}$ for all entities was higher than expected among elevational belts within sierras and, to a lesser extent, between sierras within the same elevational belt. This suggests strong phenotypic structuring with elevation (Giménez Luque et al., 2004) and some phenotypic structuring between the different sierras across the study area. Thus, lineages containing many therophytes (e.g. Caryophyllaceae, Boraginaceae, Papaveraceae, Fabaceae–Fabeae and Fabaceae–Trifolieae) are abundant at low elevations, whereas those containing many chamaephytes (e.g. Lamiaceae, Fabaceae–Genisteae, Cistaceae) and especially hemicryptophytes (e.g.
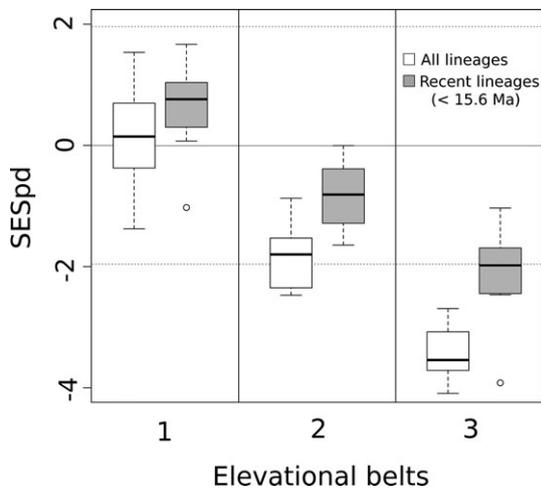
Figure 3 Box-and-whisker plot of the standardized effect-size values of phylogenetic diversity (SES$_{pd}$) for eudicots within elevational belts across the Baetic sierras of Andalusia, for all lineages and for lineages younger than 15.6 Ma. Horizontal dotted lines represent threshold values for significance at −1.96 and +1.96 respectively ($\alpha = 0.05$, two-sided). Horizontal solid line represents a visual reference line at $y = 0$.

Apiaceae, Asteraceae) become increasingly dominant at higher elevations (Melendo *et al.*, 2003; Giménez Luque *et al.*, 2004). Despite debate about the extent to which phylogenetic signal equates to phylogenetic niche conservatism (Ackerly, 2009; Wiens *et al.*, 2010), the strong phylogenetic signal reported for life-forms, combined with the non-random PBD among elevational belts within sierras, provides further evidence for the combined role of phylogenetic niche conservatism and habitat filtering in shaping plant assemblages (Webb *et al.*, 2002; Siefert *et al.*, 2013).

The observed FBD$_{CS}$ was also generally higher than expected among elevational belts within sierras, particularly between comparisons involving the highest sites, and occasionally greater than expected between sierras within the same elevational belt. This pattern might be explained by the predominance of the non-sclerophyllous syndrome at the highest elevations and the ecological restriction of the less diverse

sclerophyllous syndrome to low elevations. Many of these sclerophyllous lineages (e.g. *Coriaria*, *Ilex*, *Myrtus*, *Osyris* and *Pistacia*) are the extant representatives of the past flora that existed under Tertiary climatic conditions (Herrera, 1992; Postigo Mijarra *et al.*, 2009; Verdú & Pausas, 2013) and are well-represented in the Baetic ranges, where they have persisted through the Quaternary ice ages (Finlayson & Carrión, 2007). Although many of these ancient taxa are endozoochorous (a putatively efficient dispersal mechanism), and are generally widespread throughout the Northern Hemisphere (Herrera, 1992), they are mainly found in low-elevation woodland habitats of mild climate. It is thus likely that the significant FBD$_{CS}$ and PBD pairwise comparisons among elevational belts within sierras are partly driven by the combined role of strong habitat filtering and phylogenetic niche conservatism among these Tertiary taxa (Rodríguez-Sánchez & Arroyo, 2008). The pattern is also driven in part, however, by the differential sorting of more recently diverged lineages, because most of the observed PBD pairwise comparisons between elevational belts 1 and 3 within sierras remain significant even when considering only the youngest lineages (Fig. 2c).

Finally, the limited analysis of PBD in the tallest range (siliceous Sierra Nevada) shows a similar pattern of high values between lowest and highest belts. There was no clear-cut phylogenetic differentiation between belt 3 and the unique belt 4 in this range, suggesting that these belts share the same or closely related entities.

Environmental correlates of beta diversity

Climatic differences based on temperature-related variables explained a high fraction of the total variance in compositional (CBD), functional (SES$_{fbdLF}$ and SES$_{fbdCS}$) and phylogenetic (SES$_{pbd}$) beta diversity of all entities, whereas geographical and lithological distances better explained CBD of endemics. The strong influence of temperature-related variables reflects the importance of elevational gradients in explaining beta diversity patterns within the Baetic ranges, where temperatures decrease with increasing elevation and there are no clear-cut rules for precipitation (for details, see Appendix S3 and Körner, 2003, 2007).

Table 2 Proportion (%) of the variance in compositional (CBD), phylogenetic (SES$_{pbd}$) and functional (SES$_{fbd}$: life forms, SES$_{fbdLF}$; character syndromes, SES$_{fbdCS}$) beta diversity for eudicots of the Baetic sierras of Andalusia explained by temperature-related variables, lithology and geographical distance using the matrix multiple regression method of Lichstein (2007). Correlated variation and residual unexplained variance are reported.

Metric	Taxa	Temperature	Lithology	Geographical distance	Correlated	Unexplained
CBD	All	45.5***	3.7**	8.3**	0.0	43.7
CBD	Endemic	7.2**	14.3***	27.2***	6.7	44.6
SES$_{pbd}$	All	48.6***	1.8**	4.7**	5.3	39.7
SES$_{pbd}$	Endemic	< 1.0	3.7	4.9	0.0	92.1
SES$_{fbdLF}$	All	39.4***	< 1.0	2.0*	2.9	55.0
SES$_{fbdLF}$	Endemic	7.6***	< 1.0	< 1.0	< 1.0	90.9
SES$_{fbdCS}$	Woody	21.4***	< 1.0	< 1.0	1.7	75.1

Significant variables at ***$P < 0.001$, **$P < 0.01$, *$P < 0.05$.

The SES$_{pbd}$ of endemics was only weakly explained by the environmental variables considered in this study. Divergence in the results for endemic entities from those for all entities is not surprising given that existing evidence suggests that endemic diversity does not necessarily mirror the diversity patterns apparent in the regional pool of which they are a part (Molina-Venegas *et al.*, 2013). Here, CBD of all entities was explained well by climatic variables, whereas lithological and geographical distances better explained the CBD of endemics. This stresses the importance of substrate specialization and/or geographical isolation in driving local speciation in the Baetic ranges (see Molina-Venegas *et al.*, 2013 for further discussion). In addition, unlike CBD, the SES$_{pbd}$ of endemics was only weakly correlated with lithological distance, suggesting little phylogenetic signal in substrate specialization among endemics. This implies that edaphic specialist endemics have evolved from multiple lineages, highlighting the role of substrate in promoting differentiation in the Baetic ranges (Mota *et al.*, 2002) and in Mediterranean climate regions in general (Anacker *et al.*, 2011; Anacker & Harrison, 2012b).

The recent Neogene uplift of the Baetic sierras started in the Tortonian age, around 8 Ma (Braga *et al.*, 2003). Between 8.5 and 7.2 Ma, the Baetic range constituted a set of small islands separated by narrow marine channels and small basins (Rodríguez-Fernández & Sanz de Galdeano, 2006). Since that time, the Baetic ranges have undergone regional uplift at a maximum rate of 0.5 mm yr^{-1} (Braga *et al.*, 2003), which ultimately led to the isolation of populations and incipient speciation, followed by ecological divergence (Wiens, 2004). The ecological characteristics of the endemic species further support the role of substrates and geographical isolation as drivers of diversification among the sierras of the range (Melendo *et al.*, 2003; Giménez Luque *et al.*, 2004; Mota *et al.*, 2008). Furthermore, there is phylogenetic evidence of higher speciation rates associated with the non-sclerophyllous syndrome (Verdú & Pausas, 2013), which is overrepresented at high elevations within the Baetic ranges. In fact, the high degree of endemism in Mediterranean-type ecosystems has been proposed to be the result of differential speciation and extinction rates during the Quaternary (Cowling *et al.*, 1996). Nevertheless, further phylogenetic, biogeographical and ecological genetics analyses focusing on disparate lineages found across the Baetic ranges will help to improve our understanding of diversification patterns and mechanisms among Mediterranean biodiversity hotspots.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Methods for compilation of species checklists.
Appendix S2 Binary traits defining character syndromes, multiple correspondence analysis coordinates and life forms.
Appendix S3 PCA1 scores of the temperature and precipitation related variables within elevational belts across sierras.

BIOSKETCH

Rafael Molina-Venegas studies patterns, causes and consequences of the spatial distribution of compositional, phylogenetic and functional diversity of vascular plant assemblages in the Baetic–Rifan hotspot (southern Iberian Peninsula and northern Morocco), the main topic of his current PhD project (EVOCA research group at http://grupo.us.es/grnm210/web/).

Author contributions: R.M.V. and J.A. conceived the ideas; R.M.V. and A.A. collected the data; R.M.V., J.S. and S.L. contributed to the analyses of the data, which was led by R.M.V.; and all authors contributed to the writing, which was led by R.M.V.

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