Hotspots within hotspots: Endemic plant richness, environmental drivers, and implications for conservation

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ABSTRACT

Detecting smaller hotspots within larger hotspots could be an essential tool to focus conservation efforts. In this study, we identified hotspots at two scales of analysis within the Mediterranean overall hotspot. Particularly, based on the distribution of endemic-vascular-plant richness (EVPR), we identified micro-hotspots, among the richest floristic territories of the Sardinian and Baetic regions, and nano-hotspots, among the richest 1-km^2 grid cells of Sierra Nevada and Gennargentu massifs, located within these regions. In addition, we explored environmental drivers of EVPR, performing both simple- and multiple-regression models. Our results showed that even in areas previously defined as hotspots, the endemic-plant richness was not uniformly distributed, but rather depended largely on environmental conditions. Relationships between environmental drivers and EVPR have been poorly studied in the Mediterranean context, where we found patterns consistent among scales and regions. Specifically, EVPR was positively linked to altitude and precipitation, particularly in the driest period. Hence, the different levels of hotspots nested in hotspots were organized in a hierarchy. This downscaling approach may help to focus conservation efforts within a given hotspot, e.g. the identification of narrow hotspots could be useful to find gaps in the protected-area networks. Specifically, the identified nano-hotspots are certainly priority sites for plant conservation, since the whole of the nano-hotspots in each region represented less than 1% of the surface area but contained more than 19% of the regional EVPR. Moreover, an examination of both where hotspots are and under what environmental conditions they appear, would enable the detection of specific threats.

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1. Introduction

A central issue in conservation today is to identify biodiversity-rich areas. In this regard, Myers (1988) defined the concept of a biodiversity hotspot. Worldwide, as many as 44% of all vascular plant species and 35% of all species in four vertebrate groups are confined to 25 hotspots comprising only 1.4% of the land surface of the Earth (Myers et al., 2000), a number that was raised to 34 by Mittermeier et al. (2005). As these authors stated, to identify biodiversity hotspots constitutes an effective tool to preserve the most species at the least cost. However, resources are usually scarce, making conservation of an entire global hotspot untenable, and therefore strategies must focus on small areas that represent a maximum diversity and/or endemicity (Murray-Smith et al., 2009).

In addition, identifying priorities at finer scales is an essential way to maximize the effectiveness of conservation investment (Brooks et al., 2006).

In this sense, smaller hotspots within larger hotspots at different scales have been proposed on the basis of plant richness and endemicity (e.g. Murray-Smith et al., 2009; Raes et al., 2009; Kraft et al., 2010). Hotspots have also been identified based on faunal data (e.g. López-López et al., 2011), or combining data on several biological groups (e.g. Schouten et al., 2010). For this hotspot-within-hotspot phenomenon, Fenu et al. (2010) proposed the terms "micro-hotspots" (i.e. endemism-rich areas analogous to biogeographic units) and "nano-hotspots" (i.e. areas lesser than 3 km^2 with an exceptional concentration of endemic species), studying endemic-vascular plants for the Mediterranean island of Sardinia. The "micro-hotspot" term has been also used by Grant and Samways (2011), to identify local hotspots for Odonata, in Kogelberg Biosphere Reserve (Western Cape Province, South Africa).

Most studies identifying hotspots do not use the same criteria proposed at the global scale (Myers et al., 2000), and the

endemicity is often the only criterion used (see also Huang et al., 2012; Kraft et al., 2010), since, for a given territory, endemic species are usually better studied than the complete flora or the threats. In addition, endemic taxa constitute a central group for conservation, since narrowly endemic species are frequently threatened (e.g. Laffan and Crisp, 2003), and because endemism-rich areas are also likely to be species rich (Cowling et al., 2003; Whittaker et al., 2001). In turn, species diversity is positively correlated with diversity at other levels of organization, such as genetic diversity (Chiarucci et al., 2011; Vellend, 2003).

Hence, hotspots are defined at different scales and based on diverse criteria and types of data, their choice being a key issue in the process of hotspot identification. However, it is also crucial to define the boundaries between hotspots and non-hotspots, and this requires the definition of a threshold (Nelson and Boots, 2008). In most cases, a subjective threshold is applied, which often ranges from 1% to 5% of the reference taxa set or grid cells (e.g. Huang et al., 2012; Myers et al., 2000), but it has also been raised to 25% (e.g. García, 2006). The criteria usually applied to identify hotspots are arbitrary, and hotspot selection must be understood in the particular context of each case study (Cayuela et al., 2011).

Evidently, selecting biodiversity hotspots requires data of species distribution, but most of the areas lack complete data sets. Therefore, it is relevant not only to locate hotspots, but also to model the factors that favor a high degree of biodiversity and/or endemicity. A large number of studies have dealt with these issues in recent years, showing that factors such as altitude, precipitation, temperature, and geology, as well as evolutionary history, greatly influence both richness and, in particular, endemic-plant richness (e.g. Jansson, 2003; Vetaas and Grytnes, 2002; Wohlgemuth, 1998). However, the relationships between environmental factors and endemic-plant richness had been poorly studied under the particularities of the Mediterranean Basin (e.g. Casazza et al., 2008; Lobo et al., 2001), on which the present study focuses.

The Mediterranean Basin is one of the global hotspots proposed by Myers et al. (2000) and Mittermeier et al. (2005), within which Médail and Quézel (1997) defined ten hotspots (including the Atlantic islands of Canary and Madeira). The endemic-vascular-plant richness (EVPR) in these hotspots was >2000 species per 15,000 km^2 and within these areas at least 10% of narrow endemics occurred. The high rate of regional endemism is, perhaps, the major characteristic of the Mediterranean flora, with close to 60% of all native taxa being Mediterranean endemics, half of which corresponds to narrow endemic species (Thompson, 2005). Specifically, we focused on two of the Mediterranean hotspots defined by Médail and Quézel (1997): the Baetic–Rifan Complex and the Tyrrhenian Islands (Appendix A), each consisting of several nearby areas that shared great ecological and bioclimatic affinities. As these authors stated, Andalusia and the Rif are grouped together in the Baetic–Rifan Complex, while the Tyrrhenian Islands include the Balearic Islands, Corsica, Sardinia, and Sicily.

Given all the above, in this study we aimed: (1) to identify narrow hotspots nested in broader hotspots, within the Mediterranean Basin, based on the distribution of EVPR; and (2) to explore altitude and climatic factors as drivers of EVPR. Finally, on the basis of the results, different levels of hotspots nested in hotspots were organized in a hierarchy and particular implications for conservation were examined.

2. Methods

2.1. Study areas

Two scales of analysis in two areas were used, specifically studying two regions and within them two massifs (see Appendix A). The regions that we selected were two hotspots in the Western Mediterranean Basin (according to Médail and Quézel, 1997), the first being continental, the Baetic region (included in the Baetic Rifan Complex), and the second one insular, Sardinia (belonging to the Tyrrhenian Islands). The massifs studied were Sierra Nevada (Baetic region) and Gennargentu (Sardinia), both mountains reaching the highest altitudes in their respective regions. The four case studies are characterized by a high environmental variability and high documented biodiversity (below, see the description of the regions and massifs). The delimitation of the study areas was conditioned by the availability of information regarding the presence of endemic vascular plants (both published and our own data), this being crucial to perform the analyses.

2.1.1. Regions

The Baetic region is located in the south-eastern part of the Iberian Peninsula (36.48–38.53°N, 1.88–5.13°W), occupying ca. 33,570 km^2, including the highest peninsular peak (3482 m a.s.l.). Almost the entire Baetic region is located in eastern Andalusia, where 3724 vascular-plant taxa have been identified (Blanca et al., 2009), including 321 Baetic endemics. Within eastern Andalusia, we selected the 11 floristic territories delimited by Blanca et al. (2009; see Table 1) that approximately matched with the Baetic geological region (Vera, 2004).

Sardinia is situated in the western Mediterranean Basin (38.85–41.25°N, 8.13–9.83°E), covering ca. 24,090 km^2, and the maximal altitude reaching 1834 m a.s.l. Sardinian flora comprise 2408 vascular-plant taxa (Conti et al., 2005), 171 being Sardinian endemics (updated from Bacchetta et al., 2012b). Within the island, we also selected 11 floristic territories (Table 1), for which data on endemic taxa have been published or were available (see Appendix B).

2.1.2. Massifs

The Sierra Nevada is located in the south-east of the Baetic region (37.07°N, 3.18°W), where the study area occupies a surface area of 1718 km^2. The number of vascular taxa is approximately 2100, with ca. 12% Baetic endemics (Blanca et al., 2002). This study area largely coincides with the floristic territory named Nevado-Filabres.

The Gennargentu massif, located in the central-eastern Sardinia (40.04°N, 9.34°E), has a surface area of ca. 500 km^2. The flora consists of 948 taxa, with Sardinian endemics being 5.3% (Bacchetta et al., 2013). This massif is almost completely within the Gennargentu floristic territory.

2.2. Data on endemic taxa

To assess endemic vascular-plant richness (EVPR), we used the absolute endemism of each region. Thus, after compiling a list of plant taxa endemic to each region (i.e. regional endemics), we built a presence/absence data matrix for the 22 selected floristic territories (11 in the Baetic region plus 11 in the Sardinian region). The list of Baetic endemics and the presence data were taken from Blanca et al. (2009) and the list of Sardinian endemics was taken from Bacchetta et al. (2012a, 2012b), updated to 171 taxa). The data of Sardinian endemics present in each floristic territory were collected from the available literature (see description of Sardinia above). Literature records were checked for plausibility and completed with our own field surveys. The final data set comprised presence/absence data for 321 Baetic endemics and 171 Sardinian endemics (see Appendix C).

Subsequently, we recorded the endemic-taxa presence in a 1-km^2 grid cell for both massifs. The Sierra Nevada data set was compiled using data from both "Conservation Plan of Threatened Flora of Andalusia" and several field surveys (author's unpublished data). Meanwhile, the Gennargentu data set was compiled almost entirely from the author's field surveys, also adding records from

Table 1
Endemic-vascular-plant richness (EVPR), geographical and environmental variables estimated for each of the floristic territories studied at regional scale, helping to identify micro-hotspots (*).

Floristic territories	Baetic region											Sardinian region										
	NF*	TA*	CA*	RO*	AP	VB	MA	AX	GR	GM	GV	SUP*	IG*	GE*	SUL	SG	EN	SI	LA	Li	CN	GI
EVPRr (n° taxa)	110	103	89	74	65	60	45	21	17	16	3	51	49	48	30	19	13	11	9	9	6	0
EVPRr (%)	34	32	28	23	20	19	14	7	5	5	1	30	29	28	18	11	8	6	5	5	4	0
EVPRl (n° taxa)	71	33	29	32	12	6	4	1	2	6	0	10	15	11	9	2	2	7	2	2	4	0
Surface Area (km²)	2540	1629	3174	3328	2021	3108	2295	1936	3334	3288	6916	406	1164	541	1644	1529	1831	139	49	66	615	43
X (°)	−2.93	−3.67	−2.72	−4.81	−3.07	−2.35	−3.46	−4.44	−3.86	−2.93	−3.84	9.56	8.57	9.34	8.74	9.37	8.63	8.45	9.42	9.16	8.55	8.95
Y (°)	37.15	36.97	38.07	36.78	36.88	37.61	37.57	36.79	37.32	37.55	37.77	40.17	39.44	40.04	39.10	39.38	40.32	39.98	41.23	40.84	40.72	39.76
MinAltitude (m)	528	10	449	0	2	591	413	0	381	380	164	0	0	705	0	0	0	0	0	625	0	494
MaxAltitude (m)	3353	2234	2281	1765	2198	2194	2132	986	1572	1408	1108	1295	1153	1812	1002	962	1007	80	142	1289	505	586
Mean Altitude (m)	1658	1021	1223	706	865	1126	1071	303	827	882	488	596	292	1103	225	327	373	16	15	916	190	558
MinAnPr (mm)	335	317	388	472	274	346	412	372	402	389	386	504	528	698	433	284	565	571	509	752	552	710
MaxAnPr (mm)	1308	899	865	998	834	843	865	708	743	588	761	914	988	1056	873	738	975	612	523	922	787	727
MeanAnPr (mm)	675	547	543	702	447	493	566	553	535	461	514	677	657	882	591	452	756	585	514	841	638	720
MinPrDq (mm)	21	11	26	14	10	28	23	14	20	23	17	32	21	54	18	12	23	23	36	61	25	45
MaxPrDq (mm)	177	88	122	49	98	111	92	28	55	58	55	75	63	94	53	54	69	27	39	83	50	48
MeanPrDq (°C)	67	32	59	23	30	52	38	19	28	35	24	51	32	67	26	30	43	25	36	71	34	47
MinTame (°C)	1.4	7.4	6.7	9.7	7.6	7.5	7.7	13.8	10.9	11.6	13.1	9.8	10.8	7.1	11.7	11.9	11.4	16.3	15.7	9.6	14.2	13.7
MaxTame (°C)	15.9	18.3	16.4	18.4	18.4	15.5	16.9	18.5	17.2	17.0	18.0	16.4	16.8	13.1	16.9	17.7	16.7	16.7	16.3	13.1	16.6	14.1
MeanTame (°C)	10.4	13.7	12.3	15.0	14.4	12.9	13.7	17.0	14.8	14.4	16.5	13.5	15.2	10.9	15.6	15.4	14.8	16.6	16.1	11.6	16.6	13.8
MinTmxWm (°C)	21.7	27.0	26.1	27.5	26.8	26.9	27.7	29.6	30.2	30.1	30.6	23.6	25.0	21.0	26.0	26.2	25.5	28.8	26.7	22.6	27.4	28.0
MaxTmxWm (°C)	32.1	33.0	33.9	32.2	32.3	31.7	34.7	31.2	35.1	34.3	36.0	29.1	30.1	27.2	29.9	29.9	29.8	29.2	27.3	25.9	29.7	28.3
MeanTmxWm (°C)	28.7	31.1	30.9	30.0	30.5	30.2	32.6	30.4	32.9	32.1	33.9	27.0	28.5	24.9	28.9	28.6	28.6	29.0	27.1	24.6	28.9	28.1
MinTmnCm (°C)	−11.4	−5.4	−6.0	−2.6	−5.1	−5.3	−5.2	1.7	−2.0	−1.2	0.0	0.1	0.9	−2.4	1.8	2.0	1.5	6.7	7.2	0.3	4.3	3.6
MaxTmnCm (°C)	4.5	7.5	3.6	8.5	7.7	3.7	4.2	8.4	4.8	4.4	5.5	6.7	74	3.2	7.0	8.7	6.8	7.4	7.5	3.5	7.3	4.1
MeanTmnCm (°C)	−2.3	1.2	−0.6	3.6	2.3	0.3	0.7	6.1	2.0	1.7	3.9	3.8	53	1.0	5.5	5.7	4.8	7.2	7.4	2.1	5.9	3.7

Floristic territories, Baetic region, GV: Guadalquivir, CA: Cazorla, MA: Mágina, GR: Granada, TA: Trevenque-Almijara, GM: Guadiana Menor, VB: Vélez Baza, NF: Nevada-Filabres, AP: Alpujarras, RO: Ronda, AX: Axarquía. Sardinian region, SUL: Sulcis, IG: Iglesiente, SG: Sarrabus-Gerrei, SI: Sinis, SUP: Supramontes, GE: Gennargentu, LA: La Maddalena, CN: Calcareous outcrops in NW Sardinia, EN: Effusive outcrops NW Sardinia, GI: Giara, Li: Limbara. VARIABLES: EVPRr: endemic-vascular-plant richness (regional endemics), EVPRl: endemic-vascular-plant richness (endemic taxa of single areas), X: X coordinate, Y: Y coordinate, Min-: minimum value, Max-: maximum value, Mean-: mean value. Altitude: altitude, AnPr: annual precipitation, PrDq: precipitation of driest quarter, Tame: annual mean temperature, TmxWm: maximum temperature of warmest month, TmnCm: minimum temperature of coldest month.

herbarium specimens (*Herbarium* acronyms: CAG, CAT, FI, SASSA, SS, TO) as well as from seed lots stored at the Sardinian Germplasm Bank (BG-SAR), whenever they included proper geographical information (spatial resolution $\leqslant 1 \, km^2$). Afterwards, we removed duplicate taxon records in each 1-km^2 grid cell to determine EVPR. For the Sierra Nevada in 1949 cells we compiled 6329 records (5426 after removing duplicates) of 132 taxa. Regarding the Gennargentu massif, we compiled a data set with 643 cells and 843 records (644 after removing duplicates) of 43 taxa.

2.3. Environmental data

To model EVPR, we downloaded altitude and bioclimatic variables (environmental drivers hereafter) from the WorldClim database version 1.4 (years 1950–2000; Hijmans et al., 2005), at a resolution of 30 arcsec (ca. 1 km; see Table 1). Specifically, we used the following bioclimatic variables: annual mean temperature, maximum temperature of the warmest month, minimum temperature of the coldest month, annual precipitation, and precipitation of the driest quarter. Subsequently, we ascribed the values of the environmental variables to floristic territories or grid cells, according to the scale of analysis. Thus, within the regions, for each floristic territory, we calculated the total surface areas and subsequently the mean, the maximum, and the minimum values of each environmental variable. In the massifs, we calculated the mean value of the selected variables for each 1-km^2 grid cell. We used QGIS 1.7.4 (Quantum GIS Development Team, 2012) as well as GRASS 6.3.0 (GRASS Development Team, 2012) as GIS software to compute both environmental and floristic data.

2.4. Hotspot selection

We based the hotspot selection on EVPR (i.e. the total number of endemic vascular plants), comparing the number of regional endemic plants present in a given area (floristic territory or 1-km^2 grid cell, accordingly) with those in the complete data set (total number of regional endemics). For better discrimination between the hotspots identified at the regional and at the massif levels, we used the terms "micro-hotspot" and "nano-hotspot" proposed by Fenu et al. (2010). Specifically, at the regional level we selected a given floristic territory as a micro-hotspot whenever it accounted for more than 20% of the total Baetic or Sardinian endemic taxa. Meanwhile, at the massif level, we selected a given 1-km^2 grid cell as a nano-hotspot, within Sierra Nevada or Gennargentu massifs, whenever it accounted for more than 5% of the total regional endemic taxa.

2.5. Modelling environmental drivers of endemic-plant richness

At the regional level, the analyses were made using the data from each region separately, as well as the overall data set (pooling both regions). The modelling process was conducted in two steps; firstly, we performed simple regression analyses in order to assess separately the relationship between EVPR and each environmental variable. Secondly, all potential models resulting from the combination of the variables showing both significant ($P < 0.05$) or marginally significant ($P < 0.09$, for Sardinia) bivariate relationships with EVPR, were run using multiple linear-regression analysis, specifically running ordinary least squares (OLS) models. We selected the models that best explained EVPR variability by means of the corrected Akaike Information Criterion (AICc). The differences between the AIC value of the best model and the values of each model ranked below it (ΔAIC) provide information for evaluating which models in a set are as plausible as the best model. Models with ΔAIC values between 0 and 2 indicate similar support (Burnham and Anderson, 2002).

Afterwards, for each massif (Sierra Nevada and Gennargentu) the modelling process was undertaken in a similar way. We initially explored the bivariate relationships between EVPR and each potential environmental driver, using linear and cubic functions and choosing between the two type models on the basis of the F test. Afterwards, we applied multiple-regression models to determine the relative influence of each environmental variable on EVPR, but seeking to correct for spatial autocorrelation (SAC; influencing only this study level). Different statistical approaches can be used to model geographical patterns in species richness, varying the extent to which they minimize residual spatial autocorrelation (e.g. Diniz-Filho et al., 2008). Specifically, we fitted a lagged-response autoregressive model (ARM), which considers that SAC can affect both response and predictor variables (Dormann et al., 2007). Autocorrelation in EVPR and model residuals was assessed via Moran's I coefficients, that were plotted in the correlogram to show the changes with increasing distance classes. A circular window shape was used.

Simple regression analyses were performed using the R statistical package (R Development Core Team, 2010), while Moran's I and multiple-regression models were performed using SAM v. 4.0 (Rangel et al., 2010).

3. Results

3.1. Identifying micro-hotspots within regions

Within the Baetic region, four floristic territories were designated as micro-hotspots—Nevada-Filabres, Trevenque-Almijara, Cazorla, and Ronda—since each one includes more than 20% of the 321 Baetic endemic taxa (Table 1). These four micro-hotspots contain the 89.72% of Baetic endemics while occupying 31.8% of the Baetic surface area. In Sardinia, micro-hotspots hosting more than the 20% of the 171 Sardinian endemic taxa were Supramontes, Iglesiente, and Gennargentu. Of the all Sardinian endemics, 68.42% appeared within these three micro-hotspots, although the overall surface area accounts for only the 8.9% of the entire island. Besides the highest rate of regional endemic taxa, the micro-hotspots identified host the highest number of narrow endemic taxa inside each region, also, with unique taxa per micro-hotspot ranging from a minimum of 10 (Supramontes) to a maximum of 71 (Sierra Nevada; see Table 1).

3.2. Environmental drivers of endemic-plant richness within regions

Simple regression analysis showed strong relationships between EVPR and many of the predictor variables, particularly in the Baetic region (Table 2, Fig. 1). EVPR was higher at maximum altitudes in both Baetic and Sardinian regions, as well as for the overall data set, with this variable explaining the highest proportion of the variance in all three cases. Also, a significant positive relationship between EVPR and maximum annual precipitation was found in the three data sets.

Similarly, minimum temperature of coldest month and maximum precipitation of driest period had a significant effect on EVPR, although p-values for the latter were marginally significantly for Sardinia ($P < 0.09$). In addition, other significant relationships between EVPR and predictor variables were found, being positive with factors derived from altitude and precipitation but negative with factors linked to temperature (Table 2; Fig. 1). The surface area and some climatic variables (e.g. the minimum values of altitude or annual precipitation, as well as the maximum values of annual mean temperature, maximum temperature of warmest month or minimum temperature of coldest month) had no significant influence on EVPR for any data set.

Table 2
Bivariate relationships between endemic-vascular-plant richness (EVPR) and each potential predictor variable.

Variables	Baetic region			Sardinia region			Both regions		
	F	P	R^2	F	P	R^2	F	P	r^2
Surface area (km²)	3.21	0.1068	0.181	0.62	0.4494	−0.039	0.50	0.4874	−0.024
MinAltitude (m)	0.05	0.8312	−0.105	0.00	0.9506	−0.111	0.32	0.5764	−0.033
MaxAltitude (m)	**24.99**	**0.0007**	**0.706**	**8.34**	**0.0180**	**0.423**	**50.27**	**<0.0001**	**0.701**
Mean Altitude (m)	**10.09**	**0.0112**	**0.476**	1.18	0.3054	0.018	**19.06**	**0.0003**	**0.488**
MinAnPr (mm)	1.02	0.3399	0.002	0.26	0.6215	−0.080	**5.19**	**0.0338**	**0.166**
MaxAnPr (mm)	**14.60**	**0.0041**	**0.576**	**6.07**	**0.0359**	**0.337**	**15.13**	**0.0009**	**0.402**
MeanAnPr (mm)	2.49	0.1488	0.130	0.35	0.5695	−0.069	0.15	0.9050	−0.049
MinPrDq (mm)	0.03	0.8597	−0.107	0.04	0.844	−0.106	1.77	0.1979	0.035
MaxPrDq (mm)	**10.97**	**0.0090**	**0.499**	3.87	0.0806	0.223	**26.05**	**<0.0001**	**0.544**
MeanPrDq (mm)	**8.16**	**0.0189**	**0.417**	0.21	0.6601	−0.086	1.832	0.1910	0.038
MinTame (mm)	**25.36**	**0.0007**	**0.709**	**7.79**	**0.0210**	**0.404**	**47.9**	**<0.0001**	**0.691**
MaxTame (mm)	0.53	0.4869	−0.050	0.01	0.9065	−0.109	0.58	0.4563	−0.021
MeanTame (mm)	**12.71**	**0.0061**	**0.539**	1.02	0.3390	0.002	**8.99**	**0.0071**	**0.275**
MinTmxWm (°C)	**32.79**	**0.0003**	**0.761**	6.06	0.0360	0.336	3.89	0.0626	0.121
MaxTmxWm (°C)	2.92	0.1214	0.161	2.52	0.1468	0.132	0.144	0.7085	0.042
MeanTmxWm (°C)	**10.63**	**0.0098**	**0.491**	2.43	0.1535	0.125	0.11	0.7423	−0.044
MinTmnCm (°C)	**20.47**	**0.0014**	**0.661**	**7.38**	**0.0237**	**0.390**	**42.32**	**<0.0001**	**0.663**
MaxTmnCm (°C)	0.02	0.9005	−0.109	0.00	0.9708	−0.111	0.08	0.7750	−0.045
MeanTmnCm (°C)	**6.40**	**0.0323**	**0.351**	1.22	0.2979	0.022	**16.49**	**0.0006**	**0.424**

For environmental variables see Table 1. Results of the simple regression analyses, significant P-values in bold (including both significant [$P < 0.05$] and marginally significant [$P < 0.09$] values). R^2: Adjusted R^2, fraction of the total variance explained by the model, but based on the overall variance and the error variance.
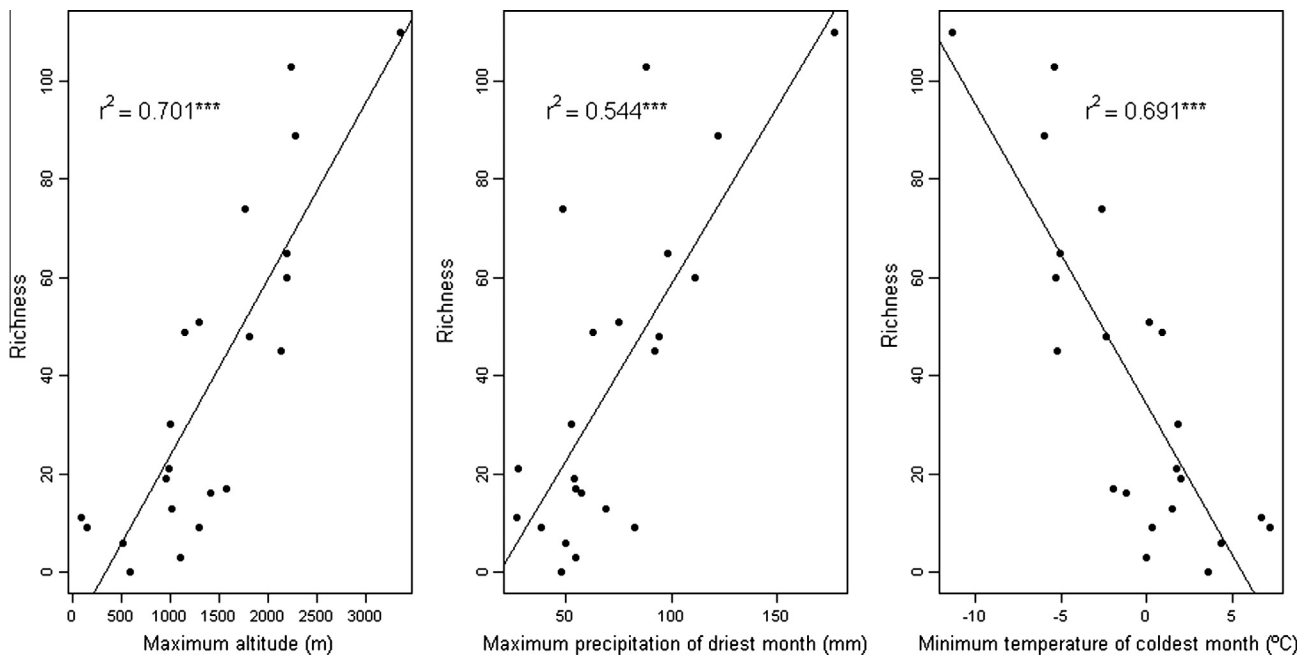

Fig. 1. Linear regressions between the three environmental variables explaining the greatest proportion of endemic-vascular-plant richness, from data sets including both regions.

The three best models according to the AICc values for the Sardinian region consisted of only one variable each (Table 3; maximum altitude, minimum temperature of coldest month, and maximum annual precipitation). However, the model explaining the highest percentage of the total variance in EVPR was the fourth one (59.6%), including two variables: maximum altitude and maximum precipitation of the driest quarter. Regarding the Baetic region, the first models included 9–11 variables, explaining between 99% and 89% of the total variance in EVPR; therefore, we showed the best models that included a low number of variables ($\leqslant 4$), because they also explained a high fraction of the total variance (69–83%) and were easier to interpret. The best models for the overall data set (including both regions) explained around 80% of the total variance in EVPR (Table 3).

3.3. Identifying nano-hotspots within massifs

In Sierra Nevada, 23 nano-hotspots were identified. Altogether, they hosted 29.9% of the Baetic endemic flora, despite that they represented only 0.068% of the Baetic surface area. They were situated mainly in the highest peaks of the western part of Sierra Nevada (e.g. Mulhacén, Cerro de los Machos, Veleta, Tozal del Cartujo, Lavaderos de la Reina, Tajos Negros) and in the highest dolomitic outcrops (Trevenque).

In Gennargentu, nine nano-hotspots were detected, representing 0.037% of the Sardinian surface area, but hosting 19.77% of the island's endemic taxa. These were situated in the highest peaks of the massif (e.g. Bruncu Spina, Punta Paolinu, and Punta La Marmora) and in some calcareous outcrops (Monte Bruttu, Tacco di Girgini, and Tacco di Genna 'eragas).
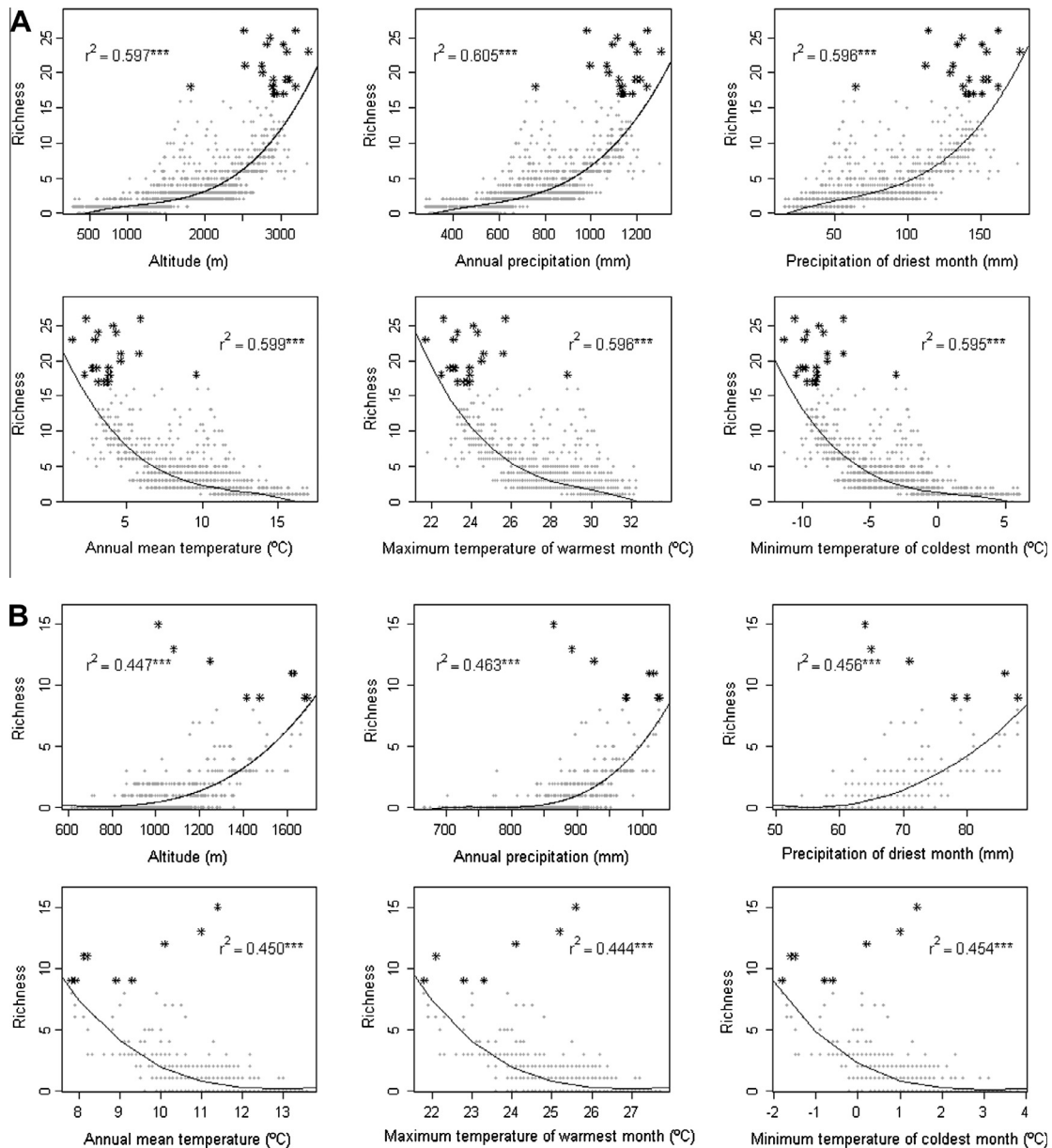
Table 3
Summary of best OLS models explaining endemic-vascular-plant richness by regions, according to AICc values. Models with ΔAIC values between 0 and 2 indicate similar support.

Baetic region				Sardinian region				Both regions			
Variables	R^2	AICc	ΔAIC	Variables	R^2	AICc	ΔAIC	Variables	R^2	AICc	ΔAIC
MinTmxWm	0.785	102.31		MaxAltitude	0.481	97.13		MaxAltitude MeanTmnCm	0.777	192.99	
MinTame	0.738	104.47	2.16	MinTmnCm	0.451	97.75	0.62	MaxAltitude MeanAltitude MinTmnCm	0.806	193.31	0.32
MaxAltitude	0.735	104.58	2.27	MaxAnPr	0.403	98.66	1.53	MaxAltitude MeanAltitude	0.771	193.61	0.62
				MaxAltitude MaxPrDq	0.596	99.64	2.51	MinTame MeanTame	0.768	193.86	0.87
								MaxAltitude MeanAltitude MeanTame	0.799	194.17	1.18
								MaxAltitude MinTmnCm MeanTmnCm	0.798	194.21	1.22
								MaxAltitude MinTmnCm	0.764	194.30	1.31
								MaxAltitude MeanTame MeanTmnCm	0.795	194.59	1.60
								MaxAltitude MinTame MeanTmnCm	0.792	194.88	1.89
								MaxAltitude MeanTam MinTmnCm	0.791	194.98	1.99

AICc is AIC with a correction for finite sample sizes with a greater penalty for extra parameters. For abbreviations of variables see Table 1.

3.4. Environmental drivers of endemic-plant richness within massifs

EVPR showed a clear spatial pattern in both massifs. Higher numbers of taxa were concentrated mainly in the center of the massifs studied and decreased towards the boundaries (Fig. 2). The spatial correlogram confirmed this spatial structure, with Moran's I coefficients being large in the first few km, and decreasing as distances increased (see Appendix D).

EVPR showed strong relationships with all predictor variables for both Sierra Nevada and Gennargentu massifs (Fig. 3). The cubic model was a significant improvement over the linear model in all cases. In general terms, EVPR increased with altitude, annual precipitation, precipitation of driest period, and low temperature. Most of the nano-hotspots identified occurred at the highest altitude, and in the coldest and most rainy cells. However, some nano-hotspots showed a remarkable deviation from the general trends (Fig. 3), specifically Trevenque (Sierra Nevada), Monte Bruttu, Tacco di Girgini, Tacco di Genna 'eragas (Gennargentu), all being calcareous outcrops.

The variance in EVPR explained by environmental variables according to the lagged-response autoregressive models ranging between 47.8% (Sierra Nevada) and 35.7% (Gennargentu), with the six predictor variables being significant in some of the models (Table 4). Residuals from autoregressive models showed little spatial pattern, suggesting that these models were appropriate (Appendix D).

4. Discussion

4.1. Hotspots and environmental drivers

We identified micro-hotspots within the Mediterranean Basin on the basis of their high endemic-plant richness, our results being consistent with previous studies on the Baetic (e.g. Lorite et al., 2007; Mota et al., 2002; Peñas et al., 2005) and Sardinian regions (e.g. Bacchetta et al., 2013; Bacchetta and Pontecorvo, 2005; Fenu et al., 2010). These micro-hotspots, not only host more than 20% of regional endemics, but also a high number of narrow endemics

Fig. 2. Distribution of endemic richness in the Sierra Nevada (A) and the Gennargentu (B) massifs. White crosses symbolize the nano-hotspots identified.

Fig. 3. Bivariate relationships between endemic-vascular-plant richness (EVPR) and environmental variables, for both the Sierra Nevada (A) and the Gennargentu (B) massifs. Stars symbolize the nano-hotspots identified.

which are restricted in distribution to a single micro-hotspot, with the number of taxa per micro-hotspot ranging from 10 to 71. Indeed, this high concentration of endemic species in small areas is a key issue in the Mediterranean Basin (Thompson, 2005). Subsequently, we identified nano-hotspots within two of these micro-hotspots, since the Sierra Nevada and Gennargentu massifs largely coincide with two of the richest floristic territories for endemics. Nano-hotspots were small and extremely rich areas of endemism, they represented less than 1% of the regional surface but contained more than 19% of regional endemics.

Besides micro- and nano-hotspots hosting the highest EVPR, we modelled environmental factors favoring this plant index. We found that the maximum EVPR in Mediterranean areas was linked to the highest altitudes, and subsequently to the minimum temperatures, as well as to greatest precipitation values (especially in the driest period). We found similar patterns at both the massif and region levels, as well as in both insular and continental areas. Nonetheless, environmental factors explained a higher percentage of the total

variance in EVPR for Baetic than for Sardinian data, since Baetic areas comprise a broader environmental range (i.e. altitude, temperature, precipitation). In mountain systems throughout the globe, general biodiversity often declines from middle to high altitudes (Sanders and Rahbek, 2012) while the percentage of endemic species usually increases with altitude (e.g. Essl et al., 2009; Steinbauer et al., 2012;Vetaas and Grytnes, 2002). However, regional endemic richness showed a hump-shaped pattern across the elevational range in many studies (e.g. Nogué et al., 2013), this pattern being found also in a Mediterranean context (Trigas et al., 2013). Nevertheless, our results showed that the absolute number of endemic taxa increased with altitude, in agreement with other studies exploring plant richness in Southern Europe (e.g. Lobo et al., 2001; Moreno Saiz and Sainz Ollero, 1992), where more isolated higher altitudes support a degree of endemism higher than that in Northern Europe (Myklestad and Birks, 1993). High levels of narrow-range taxa at high altitude in mountain ranges have been linked to isolation, since conditions are suitable for speciation and refuge for elements origi-

Table 4
Lagged-response autoregressive models results for both the Sierra Nevada and the Gennargentu massifs.

AICc R^2	Sierra Nevada 8266.15 0.448			Gennargentu 2253.781 0.357		
Variables	b	t	P	b	t	P
Altitude (m)	3.124	2.586	0.01	−2.003	−3.191	0.001
AnPr (mm)	1.633	5.684	<.001	−0.997	−6.684	<.001
PrDq (mm)	0.731	3.191	0.001	1.591	8.15	<.001
Tame (°C)	1.773	1.556	0.12	−1.811	−2.295	0.022
TmxWm (°C)	−0.42	−2.049	0.041	1.014	4.111	<.001
TmnCm (°C)	3.284	4.662	<.001	−1.089	−2.196	0.028

Partial regression coefficients of the multiple-regression model: b, t statistics, and associated P-values for endemic-vascular-plant richness regressed against environmental factors.
Variables: Altitude: altitude (mean), AnPr: annual precipitation (mean), PrDq: precipitation of driest quarter (mean), Tame: annual mean temperature (mean), TmxWm: maximum temperature of warmest month (mean), TmnCm: minimum temperature of coldest month (mean).

nating from lineages distributed at higher latitudes, presumably reflecting responses to past climate change (Bell et al., 2010; Nogué et al., 2013).

In addition, we found a positive relation between EVPR and precipitation, as in some other studies (e.g. Gillespie et al., 2013), with precipitation during the driest period being a key factor explaining richness in our study. This trend is similar to that observed for altitude, since aridity generally decreases with altitude in the Mediterranean Basin (Walter and Breckle, 1991). In fact, it is well known that summer drought typical of the Mediterranean climate is a main factor for the specific development of plants as well as for the general heterogeneity and distribution of the vegetation (Pons and Quézel, 1998).

Nevertheless, part of the EVPR variability was not explained on the basis of altitudinal and/or climatic factors; e.g. some of the nano-hotspots were not found at the highest altitude (see figures exploring bivariate relationships at the massif level). In both massifs, they corresponded to calcareous outcrops within the siliceous matrix that predominates in both the Sierra Nevada and the Gennargentu massifs. These cases agree with studies reporting higher endemicity rate or general richness, on calcareous bedrock than on other types of bedrock (Essl et al., 2009; Wohlgemuth, 1998). In turn, local relationships between plant diversity and type of bedrock or soil pH are related to evolutionary history (Chytrý et al., 2003; Ewald, 2003). Actually, climate and geological history greatly contribute to the distribution patterns of endemics (Jansson, 2003; Ohlemüller et al., 2008). Therefore, although a substantial proportion of regional variation in EVPR can be explained statistically in terms of a few environmental variables, it is not simply the current states of the factors that are relevant but also their historical dynamics (Gaston, 2000). In this regard, Médail and Diadema (2009) found a clear correspondence between glacial "refugia" and hotspots in the Mediterranean Basin.

4.2. Hotspots within hotspots: proposal of a hierarchy and implications for conservation

We identified narrow hotspots nested in broader hotspots, within the Mediterranean Basin. Also preceding studies identified areas holding a high biodiversity within global hotspots, from intermediate scales (e.g. Kraft et al., 2010; Murray-Smith et al., 2009; Reyes-Betancort et al., 2008), to finer scales (⩽10 × 10 km; e.g. Raes et al., 2009). However, regardless of the scale of study, the term "hotspot" has been applied, with few exceptions (Fenu et al., 2010; Grant and Samways, 2011). It was practical in our

study to use the terms "micro-hotspot" and "nano-hotspot" for better discrimination of the two levels of hotspots identified. They were, in turn, nested in broader hotspots, which could also be named using other standard prefixes, already applied to classification in some biology fields (e.g. Ellenberg, 1973; Lascelles et al., 2012; Sarr et al., 2005). In this regard, the Mediterranean Basin, which is one of the 25/34 world hotspots (Mittermeier et al., 2005; Myers et al., 2000), could be named "mega-hotspot", within which the Baetic–Riffan Complex and the Tyrrhenian Islands (Médail and Quézel, 1997) could be categorized as "macro-hotspots", while Baetic region and Sardinia would be "meso-hotspots". These terms, proposed to our case studies, could be also applied to other approaches and territories (see Fig. 4).

Hence, the different levels of hotspots nested in hotspots, were organized in a hierarchy, which consists of nano-hotspots within micro-hotspots, micro-hotspots within meso-hotspots, meso-hotspots within macro-hotspots, and macro-hotspots within mega-hotspots. Certainly, within the same system there is a gradual decrease in the surface area from mega- to nano-hotspots, and consequently, higher rates of biodiversity would be progressively hosted within smaller areas, this being a key feature for conservation. However, it has little meaning to establish concrete limits or intervals for each level, since hotspots are identified from very different approaches (regarding taxonomic groups, biodiversity indicators, thresholds, etc.), as has been expounded in the Introduction. Moreover, it would not be feasible to set spatial limits from the broadest level, and thus the surface area of the world hotspots ranges widely (Myers et al., 2000).

Nevertheless, this preliminary proposal for a hotspots hierarchy has a practical application, with the narrowest levels being particularly relevant for specific conservation purposes. Thus, to make nature-conservation planning more efficient, it should take into account not only ecological but also administrative criteria for the hotspots at lower scales. With regard to our case study, while a "macro-hotspot" such as Tyrrhenian Islands include areas from different countries (Spain, France, Italy), the "meso-hotspot" of Sardinia is in a single administrative unit (Italy). Analogously, while Baetic–Riffan Complex (macro-hotspot) includes Spanish and Moroccan territories, the Baetic region (meso-hotspot) is only within Spain, which facilitates the implementation of conservation policies.

The identification of narrow hotspots could be useful to find gaps in the protected-area networks. In this regard, quantifying endemism for regions at local to global scales can provide useful results for assessing the representation of protected sites, which may have implications for identifying priority areas for conservation (e.g. Laffan et al., 2013). In our case study, most of the micro-hotspot surface area corresponds to protected areas, considering European Sites of Community Importance (SCI), National Parks, as well as regional protected areas, with the percentage of the total protected surface in micro-hotspots being similar for both regions (ca. 60%). In particular, both the Sierra Nevada and Gennargentu massifs are National parks as well as SCI. Moreover, all nano-hotspots identified on Sierra Nevada are within zones of maximum protection, following the approved national-park planning. In this sense, since the Gennargentu National Park planning has not yet been defined, the nano-hotspots identified may be helpful for its future definition. However, this is a matter not only of conservation purposes, but also of data resolution and funding available, these factors being crucial in the decision making process (Wilson et al., 2007).

Moreover, an examination of both where hotspots are and under what environmental conditions they appear would enable the detection of specific threats, which is a priority in conservation (Brooks et al., 2006). Thus, the fact that the nano-hotspots identified are located often in high peaks in Mediterranean mountains, makes them particularly vulnerable to climatic change. It has
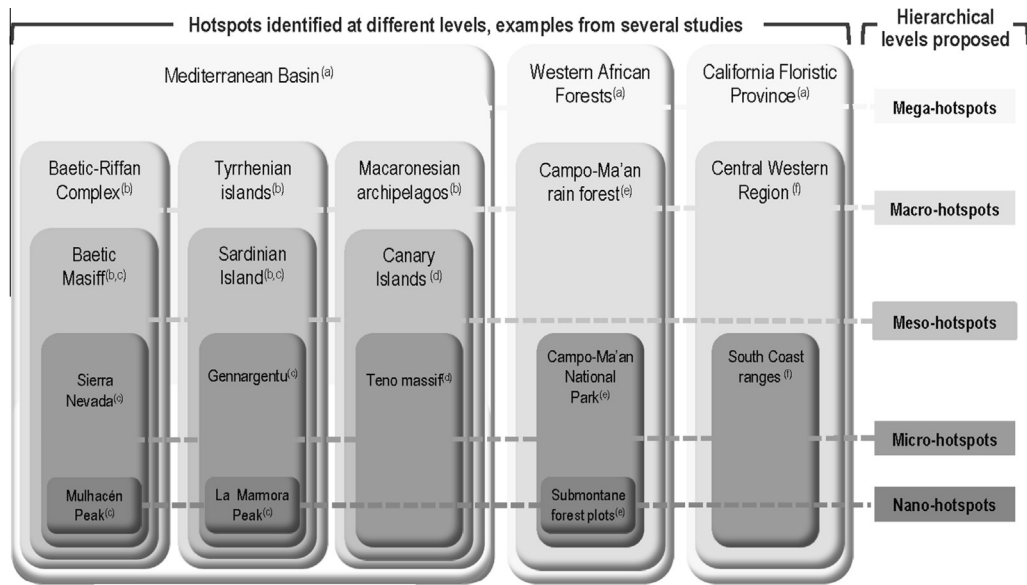
Fig. 4. Hierarchy proposed to organize different levels of hotspots nested in hotspots; examples from some previous studies as well as from our own results. Superscript letters show the specific studies in which hotspots were identified. (a) Myers et al. (2000), (b) Médail and Quézel (1997), (c) Present study, (d) Reyes-Betancort et al. (2008), (e) Tchouto et al. (2006), (f) Kraft et al. (2010).

been confirmed that rapid increases in temperature are driving migrations of species to higher elevations (Le Roux and McGeoch, 2008); however, high-mountain endemic species cannot adopt the strategy of vertical migration (La Sorte and Jetz, 2010). Specifically, in Sierra Nevada the models performed by Benito et al. (2011) predict a potential loss of suitable high-mountain habitats before the middle of the century, even under the most optimistic scenarios simulating climatic changes. The model predictions have been supported by empirical evidence. For example, Pauli et al. (2012) studying recent changes in vascular-plant richness across Europe's major mountain ranges, showed that species moved upslope on average, with the loss of endemic species being particularly severe in Mediterranean mountains. Therefore, Mediterranean nano-hotspots, and consequently micro-hotspots, are probably losing biodiversity. Similar patterns have also been found or predicted in other mountains beyond the European context (Pickering et al., 2008; Williams et al., 2003). Apart from climate change, other threats could be detected by identifying the narrow hotspots for EVPR (human intrusions and disturbance, invasive alien species, agricultural intensification, etc.), on which to focus economical resources and monitoring efforts.

4.3. Conclusions

Our results showed that even in areas that are noted for their high biodiversity (hotspots), the endemic-plant richness is not uniformly distributed, as we expected, but depends largely on environmental conditions. Specifically, we found that drivers such as altitude and precipitation, and particularly precipitation of the driest period, favor EVPR in the Mediterranean Basin. Consequently, it was possible to identify hotspots within hotspots, which can be organized in a hierarchy. This downscaling approach may help to focus conservation efforts at different scales within a given hotspot, with the identification of hotspots corresponding to narrowest levels being particularly relevant for conservation.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2013.12.007.

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