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Using endemic-plant distribution, geology and geomorphology in biogeography: the case of Sardinia (Mediterranean Basin)

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Research Article

Using endemic-plant distribution, geology and geomorphology in biogeography: the case of Sardinia (Mediterranean Basin)

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The importance of robust systems for classifying biogeographical patterns has been emphasized for its usefulness in designing conservation strategies. For such purposes, the distribution patterns of the endemic flora have often been used. Several studies have identified phytogeographical units within Sardinia (western Mediterranean); however, the main part of the island remains unstudied. Thus, the aim of this study is to lay out a comprehensive biogeographical scheme for Sardinia based on endemic vascular plant distributions, together with geological and geomorphological units. We georeferenced, in a 1-km² grid cell, the presence of 290 vascular endemic taxa from the literature, herbarium specimens and field investigators' research. Sardinia was subdivided into 31 homogeneous units through the integration of geological and geomorphological maps and, subsequently, a presence-absence matrix of endemic taxa in each unit was built. Hierarchical cluster analysis was performed to define two levels of biogeographical units (i.e. sectors and subsectors). For each unit the exclusive and differential endemic taxa were identified. For sectors, indicator species were explored by the Indicator Value (Ind Val) analysis and relationships were analysed by quantitative interaction web. A total of six sectors and 22 subsectors were identified. The highest endemic plant richness was found in the Campidanese-Turritano, Sulcitano-Iglesiente and Supramontano sectors, and in the Gennargenteo, Barbaricino, Iglesiente and Sulcitano subsectors. All sectors were characterized by the presence of exclusive, differential and indicator taxa. The interaction analysis showed the highest uniqueness in endemic flora in the Supramontano and Sulcitano-Iglesiente sectors, which hosted a high number of exclusive endemic species. Mostly mountainous sectors/subsectors had higher endemic-species richness compared with lowland ones. The study showed the relevance of geology and geomorphology, together with accurate data on endemic distribution, to define consistent phytogeographical units. Furthermore, the biogeographical scheme presented here helps to define area-based conservation strategies in Sardinia.

Keywords: conservation, continental island, endemic plant richness, geology, geomorphology, Mediterranean vascular flora

Introduction

Biogeography is a comparative science that attempts to describe and explain spatial patterns of biological diversity on Earth, with respect to its geological history and how these patterns change over time (Lomolino *et al.*, 2006; Parenti & Ebach, 2009). In recent years, the importance of robust systems seeking to classify biogeographical patterns has been emphasized (Whittaker *et al.*, 2005; Mackey *et al.*, 2008; Kreft & Jetz, 2010) for their usefulness in conservation planning (e.g. Mackey *et al.*, 2008 and references therein; Luna-Vega *et al.*, 2013). In this sense, distribution patterns of the vascular flora (e.g. Rivas-Martínez *et al.*, 2002; Moreno Saiz & Lobo, 2008;

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Moreno Saiz *et al.*, 2013), and in particular of endemic flora (e.g. Rivas Martínez *et al.*, 1997; García Barros *et al.*, 2002; Santa Anna Del Conde *et al.*, 2009; Medina-Cazorla *et al.*, 2010; González-Orozco *et al.*, 2013) has often been used to describe biogeographical schemes.

The spatial distribution of endemic species is not random (e.g. Laffan & Crisp 2003; Tribsch, 2004; Casazza *et al.*, 2008; Essl *et al.*, 2009); but is uneven across the world's land areas, with endemic species often being concentrated in specific regions or habitats (Trigas *et al.*, 2012). Several factors shape endemic distribution patterns, such as area, biotic interactions, stochastic events, habitat diversity, isolation and human impact (e.g. Lobo *et al.*, 2001; Willerslev *et al.*, 2002; MacMaster, 2005; Panitsa *et al.*, 2006; Casazza *et al.*, 2008; Duarte *et al.*, 2008). In addition, the current distribution of endemic species on continental Mediterranean

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islands is related to the fact that palaeogeography is the product of colonization events from the mainland during temporary land connections, followed by *in situ* diversification (e.g. Mansion *et al.*, 2008; Salvo *et al.*, 2010). Furthermore, geology and geomorphology are important factors determining endemic distribution patterns (e.g. Tribsch & Schönswetter, 2003; Valente & Vargas, 2013); indeed, bedrock chemistry has been shown to be significant for the delimitation of biogeographical units in several studies on mountain plants of south-eastern France (Médail & Verlaque, 1997), southern Spain (Mota *et al.*, 2002) and the Swiss Alps (Wohlgemuth, 2002), among others.

The Mediterranean Basin hosts an especially diverse flora due to its particular palaeogeography, climatic conditions, habitat heterogeneity and the varying origins of the flora itself (e.g. Médail & Quézel, 1997; Thompson, 2005; Blondel & Médail, 2009; Trigas *et al.*, 2012). Specifically, Mediterranean islands and islets are not only singular for their species richness, but also for the high endemicity rates (Rosselló *et al.*, 2009).

Sardinia and its c. 300 circum-Sardinian islands (including four archipelagos), covering 24090 km², are situated in the western Mediterranean basin. The Sardinian flora consists of 2408 taxa (Conti et al., 2005), 171 of which are exclusively endemic (Bacchetta et al., 2012b), the particular geological history of the island being a determining factor of the floristic peculiarities. Thus, before the early Oligocene, Sardinia (and Corsica) was situated adjacent to current southern France, forming a continuous geological entity (part of the so-called Hercynian massif) which subsequently fragmented into microplates that dispersed throughout the western Mediterranean (Alvarez et al., 1974). The tectonic separation of Sardinia from Corsica (which shared great floristic affinity, with 90 Sardo-Corsican endemic taxa; Bacchetta et al., 2012a) began at 15 Ma and was complete by 9 Ma (Cherchi & Montadert, 1982), although episodic contacts occurred (Lambeck & Purcell, 2005; Gover et al., 2009; Salvo et al., 2010). The prolonged isolation and high geological diversity created a wide range of habitats, with high numbers of endemic species, especially on its mountain massifs (Médail & Quézel, 1997).

From a biogeographical standpoint, Rivas-Martínez *et al.* (2002) considered Sardinia to be a subprovince that, together with Corsican and Tuscano-Calabrian subprovinces, constitutes the Italo-Tyrrhenian province. However, owing to the many similarities, other authors have suggested the rank of biogeographical province for Sardinia and Corsica, within an Italo-Tyrrhenian superprovince, which extends over the western coast of the Italian Peninsula, from Liguria to Calabria (Ladero Alvarez *et al.*, 1987; Bacchetta & Pontecorvo, 2005). More recently, Bacchetta *et al.* (2012*a*) proposed to consider Sardinia, Corsica and the Tuscan Archipelago as an independent biogeographical province.

Based on vascular endemic flora, several studies have identified biogeographical units (sector, subsectors and districts) within the island of Sardinia (e.g. Bacchetta & Pontecorvo, 2005; Bacchetta, 2006; Fenu & Bacchetta, 2008; Angius & Bacchetta, 2009; Fenu *et al.*, 2010; Bacchetta *et al.*, 2013); however, the main part of the island (*c.* 85% of the total surface) still lacks a detailed biogeographical study.

Thus, the aim of the present work was to lay out a comprehensive biogeographical scheme for Sardinia based on a spatially detailed and comprehensive dataset of endemic vascular plant distributions, together with geological and geomorphological units. Additionally, we aim to identify the most endemic-rich areas and to explore the relationships among the biogeographical units.

Materials and methods

Floristic data

The checklist of Sardinian endemic vascular plants was taken from Bacchetta et al. (2012a, b) by selecting the 290 endemic taxa (Appendix S1, see online supplemental material, which is available from the article's Taylor & Francis Online page at http://dx.doi.org/10.1080/ 14772000.2014.894592), which were Sardinian (183 taxa, including 12 new endemic taxa described in Sardinia in the last years) and Sardo-Corsican (90 taxa), as well as taxa also present in the Tuscan Archipelago (17 taxa). We georeferenced the presence of endemic taxa from the available literature (105 studies with 3980 records on 216 taxa), as well as from herbarium specimens conserved in several botanical museums (CAG, CAT, FI, RO, SASSA, SS, TO) and from the Sardinian Germplasm Bank (BG-SAR) database (1158 records on 171 taxa). Finally, 53 450 records on 139 taxa, from the authors' field research (including unpublished data), were incorporated into the database. The final dataset included 2431 records (on 106 taxa) accurately georeferenced, as well as 51019 records georeferenced to 1-km² grid cells (of 43 widespread endemics). All records were checked for plausibility by the authors.

Definition of biogeographical units

Initially, a presence–absence matrix was built by ascribing the georeferenced data of endemic taxa to geological units of Sardinia (60 171 units; Carmignani *et al.*, 2001). Afterwards, we removed duplicate taxon records in each unit. Preliminary hierarchical clustering showed that considering each geological unit independently led to uninterpretable results with regard to geographical coherence, as reported in previous studies (e.g. Reyjol *et al.*, 2007). Accordingly, basic geological units were grouped into homogeneous polygons through the integration of geological (Carmignani *et al.*, 2001) and geomorphological maps of Sardinia (Ulzega, 1988), with a minimum surface area of 780 km²; some limits were adjusted using elevation or other cartographic sources (e.g. hydrographic and land-use maps). Thus, small units were grouped according to similar or identical geological substrates being part of a common structure, regarding origin or topographical features (e.g. mountain range, valley), using a GIS software. Subsequently, a new presence–absence data matrix was built from the total 31 polygons and the 59 232 records on endemic taxa (31 polygons × 1566 records, after removing duplicates). Spatial information was processed using QGIS 1.7.4 (Quantum GIS Development Team, 2012).

The data matrix was analysed by a hierarchical cluster analysis using 'hclust' function, included in the R vegan package (Oksanen *et al.*, 2012). Euclidean distance and arithmetic averages were used as clustering options, since they provided interpretable results. This analysis was performed following the procedure successfully tested by other authors (Reyjol *et al.*, 2007; Reygondeau *et al.*, 2012), by selecting two cut-off levels to define two levels of biogeographical units (sectors and subsectors hereafter). The resulting units were named in relation to local toponymy, according to the system proposed by Rivas Martínez *et al.* (1997).

The indicator species of the identified sectors were explored by the IndVal (Indicator Value) procedure (Dufrêne & Legendre, 1997), using the 'indval' function, which is included in the R labdsv package (Roberts, 2012). This function identifies the most characteristic taxa of each unit, i.e. taxa found mostly in a single unit and present in the majority of sites belonging to that unit. In addition, the endemic taxa that were mostly but not entirely restricted to a sector or subsector, i.e. a species might be found in one or two non-adjacent geological units outside its primary sector, were identified (differential taxa hereafter) following a similar approach used in previous studies (e.g. Laffan *et al.*, 2013).

Finally, to show relationships among Sardinian endemics and sectors, a graphic quantitative interaction web was produced using the R bipartite package (Dormann *et al.*, 2009). All statistical analyses were performed using the R statistical package (R Development Core Team, 2012).

Results

A total of six biogeographical sectors and 22 biogeographical subsectors were identified (Figs 1-2). Only in the Gennargenteo sector was no subsector identified.

Although the surface area varied among units (for sectors as well as subsectors; Table 1), the highest endemic plant richness was found in the Campidanese-Turritano (166 taxa), Sulcitano-Iglesiente (129 taxa), Supramontano (117 taxa) and Gennargenteo (116 taxa) sectors. At the subsector level, the highest endemic plant richness was found in the Gennargenteo (116 taxa), Barbaricino (98 taxa), Iglesiente (83 taxa), Sulcitano (82 taxa) and Supramontano (79 taxa) subsectors. An exceptionally high number of endemic taxa in relation to its small surface area was found in the Tavolarino subsector (44 taxa in a surface area of c. 9 km²; Table 1).

All sectors were characterized by the presence of exclusive endemic taxa, ranging from two to 33 taxa, as well as by differential endemic taxa, ranging from two to 23 taxa (Table 1). The sector with the highest number of exclusive species was the Sulcitano-Iglesiente (33 taxa), followed by the Campidanese-Turritano (31 taxa) and Supramontano (14 taxa) sectors. Also, exclusive taxa were present in all subsectors, except in Nuorese and Ogliastrino (Table 1), reaching a maximum of six (Sulcitano, Turritano and Marghino-Logudorese), seven (Iglesiente and Maddalenino) or eight taxa (Gennargenteo).

By applying indicator-species analysis, we found that some species had a significant preferential distribution in some sectors (Table 1). Specifically, four sectors included at least seven indicator species (Barbaricino, Sulcitano-Iglesiente, Supramontano and Gennargenteo), while Goceano-Logudorese and Campidanese-Turritano were characterized by only one taxon (Table 1).

The quantitative interaction web between sectors and endemic taxa is presented (Fig. 3). The black bar width is proportional to Sardinian endemic richness of the sectors (left bars) or to the frequency of endemic taxa in the sectors (right bars). This graph shows the floristic relationships among sectors; in particular the Sulcitano-Iglesiente and the Supramontano are the most different from each other (maximum distance), with the greatest endemic uniqueness. In addition, this analysis highlights that all sectors were characterized by the presence of exclusive and differential endemic taxa (see Table 1 for details), whereas species such as *Vinca sardoa*, *Oenanthe lisae*, *Quercus ichnusae*, *Santolina insularis* and *Dianthus sardous* were among the most frequent in the sectors (Fig. 3).

Discussion

The study showed the relevance of geology and geomorphology to define consistent phytogeographical units, since the identified units hosted both exclusive and shared endemic taxa. In particular, six biogeographical sectors and 22 subsectors were defined for Sardinia and the circum-Sardinian small islands (including four archipelagos). This is the first study available to define biogeographical units at a small scale on a Mediterranean islands system, based on accurate distribution pattern of endemic vascular flora.

The biogeographical scheme identified in this study, on the basis of all the Sardinian endemics, was congruent

	Prob.	0.0093 0.0075 0.0052 0.0130 0.0050 0.0050 0.0193	0.0455	0.0069
	Ind_Val	0.6667 0.6667 0.6349 0.5000 0.5000 0.3389	0.3363	0.7143
·	Indicator species	Hieracium soleirolianum Potentilla rupestris ssp. corsica Myosotis soleirolii Ramunculus cordiger ssp. cordiger ssp. cordiger Festuca morisiana Trisetaria gracile	Portulaca sardoa	Genista valsecchiae
01 01 01100 1110 111711, 1 1 0 1	Differential species (*)	Phalaris rotgesti, Irisetaria gracile	Genista salzmannii; Phalaris roigesti ^t ; Potentilla crassinervia ^b ; Trisetaria gracile ^b ; Anthyllis hermanniae ssp. ichnusae ^c ; Sagina pilifera ^c	Borago morisiana; Echium anchusoides; Galium corsicum; Genista salzmanni; Ileris integerrima; Polygala sardoa; Santolina corsica; Silene morisiana; Dianthus mossanus ^{a,e} ; Linaria ar cusangelt ⁵ ; Dianthus mossanus ^{a,e} ; Linaria ar cusangelt ⁵ ; Cardua si roigesit ⁶ ; Filago tyrrhenica ^{h,e} ; Sachys salisi ⁶ ; Phleum sardoum ^c ; Buphthahuum inutoides ^d ;
	Exclusive species (*)	Armeria sardoa. ssp. genargentea; Centaurea magistrorum; Cynoglossum barbaricinum; Diandhus genargenteus; Genista pichi- sermolliana; Lamyropsis microcephala; Orobanche denudata; Ruta lamarmora e	Dianthus ichnusae ssp. ichnusae ^c ; Dianthus ichnusae ssp. toddet ^e ; Limonium acutifolium ssp. bosanum ^c ; Limonium acutifolium ssp. cornusianum ^c ; Lavatera plazzae ^c , Romulea limbarae ^b ; Rubus arrigonit ^c , Rubus limbarae ^b	Anchusa formosa ⁴ , Anchusa littored ⁵ , Anchusa montelinasana; Armeria sulcitana; Astragalus maritinus ⁵ , Asrragalus regulenins, Astragalus verrucosus ⁵ , Bellium crassifolium var. canescens ⁴ , Cephalaria big azzii ⁴ ; Charybdis glaucophylla; Dianthus morisianus ⁶ ; Genista arbusensis; Genista bocchieri ⁴ ; Genista insularis ⁴ ; Genista avina ⁶ ; Genista insularis sep. insularis ⁴ ; Genista avina ⁶ ; Genista sulcitana ⁶ , Genista sulcitana ⁶ , Genista valeecchiae; Helichrysum montelinasanum; Lavatera
ai amina. 7 204	No. end.		58 58 66	82
	Area (km ²)		3894 1887 2954	1371
operaprintati anno 14	Subsector		Nuorese (a) Gallurese (b) Marghino- Logudorese (c)	Sulcitano (a)
01 m 010	No. end.	116	104	129
eo 1161 10110	Area (km ²)	721	8643	2897
10 III 11 III	Sector	Gennargenteo	Goceano- Logudorese	Sulcitano- Iglesiente

Table 1. Main characteristics of the biogeographical units identified for Sardinia. Abbreviations: No. end. = Number of endemic *taxa*: Prob. = Probability.

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(continued)

Prob.		0.0001	0.0121	0.0212	0.0092	0.0079	0.0169	0.0194	0.0175	0.0181	0.0284	0.0352
Ind_Val		0.7108	0.6599	0.5728	0.5714	0.5714	0.4864 0.4286	0.4286	0.4286	0.4286	0.3710	0.3529
Indicator species		Genista morisii	Bellium crassifolium	Plagius flosculosus	Verbascum plantagineum	Charybdis glaucophylla	Bryoma marmorata Genista sulcitana	Limonium tigulianum	Helichrysum montelinasamum	Armeria sulcitana	Limonium suicitanum Stachys corsica var. micrantha	Erodium corsicum
Differential species (*)	Clinopodium sandalioticum ⁴ ; Dianthus insularis ⁴ ; Gensisa sardoa ⁴ ; Leucojum roseum ⁴ ; Veronica verna ⁶ , Viola corsica ssp. limbarae ⁶											Alyssum tavolarae; Limonium contoritrameum ⁴ ; Centaurea horrida ^{bu} ; Clinopodium sandalioticum ⁴ ; Dianthus insularis ^{be} ; Phleum sardoum ⁶ ; Salvia desoleana ⁶ Barbarea ruptcola ⁴ ; Carduus Barbarea ruptcola ⁴ ; Dianthus mossanus ⁴ ; Hypericum amulatum ⁴ , Linaria arcusangel1 ⁴ ; Narcissus supramontanus ssp.
Exclusive species (*)	riloba ssp. pallescens ⁴ ; Limonium carisae; Limonium insulare ^b ; Limonium merzmuelleri ssp. merznuelleri ssp. merznuelleri ⁴ , Limonium sulcianum; Limonium sulcianum; Limonium sulcianum; Limonium sulcianum; Limonius serdoa; Sesleria insularis ssp. morisiand; Silene merrinoli; Verbascum plantagineum	2										Anchusa crispa ssp. maritima ^c ; Anchusa sardoa [®] , Asperula deficens ^b Astragalus thermensis ^e ; Centaurea corensis ^e ; Conchicum arenasii; Colchicum arenasii; Arenasii; Colchicum arenasii; Colchicum aren
No. end.		47	59	83	56							49
Area (km ²)		415	339	321	361			-			_	775
Subsector		Antioco– Carlofortino (h)	Guspinese-	Iglesiente (d)	Linisico (e)			-				Ogliastrino (a)
No. end.												166
Area (km ²)			_	-		-		-	_			9365
Sector												Campidanese- Turritano

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 Table 1. (Continued)

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Table 1. (Continu	(pəi									
Sector	Area (km ²)	No. end.	Subsector	Area (km ²)	No. end.	Exclusive species (*)	Differential species (*)	Indicator species	Ind_Val	Prob.
			Tavolarino (b) Turritano (c) Sarrabense (d) Maddalenino (e) Campidanese (f) Nurrense (g) Sinisico (h)	9 645 645 5031 81	44 52 41 53 41 59	Limonium merxmuelleri ssp. oristanum ^c , Limonium multifurcatum ^e Limonium pulvinforme ^e ; Limonium reviraneum ssp. Limonium reviraneum ssp. caralitanum ^c , Limonium ursanum ^e , Limonium ursanum ^e , Limonium var. tuberculata ⁱ , Polygala var. tuberculata ⁱ , Srophularia morisi ^e , Senecio vulgaris var. tyrrhenum ^e , Silene ichnusae ^s	cunicularium ^{4.e.} ; Silene valsecchiae ^{4.e.} ; Stachys salisif ^e Genista sardoa ⁸ ; Limonium laetum ⁸ ; Orobanche australis ⁸			
Barbaricino	1294	116	Sarcidanense (a)	489	67	Anchusa capellii ^b ; Helianthemum morivianum ^a	Orobanche australis ^a ; Socina vilitard ^b	Helianthemum morisianum	1.000	0.0008
	-		Barbaricino (b)	806	98		nugun punjeru	Solenopsis minuta ssp.	1.000	0.0012
			-					corsica Ophrys ortuabis	0.8750	0.0032
								Colchium gonarei	0.8750	0.0030
								Ophrys funerea	0.7933	0.0025
								Hypericum scruglii	0.7640	0.0058
								Iberis integerrima	0.7636	0.0051
			-					Dianthus insularis Amiilaria mircorensis	0.7500	0.0024
			_					Cymbalaria muelleri	0.7059	0.0056
								Galium glaucophyllum	0.6269	0.0135
								Ranunculus cymbalarifolius	0.5793	0.0195
								Helichrysum saxatile ssp.	0.5285	0.0235
-								saxatile Anchusa capellii	0.5000	0.0480
								Crepis caespitosa	0.5000	0.0467
								Cistus creticus var. corsicus	0.4972	0.0353
								Campanula forsythii	0.4668	0.0377
								Borago pygmaea	0.4548	0.0190

(continued)

Table 1. (Contin.	(pən									
Sector	Area (km ²)	No. end.	Subsector	Area (km ²)	No. end.	Exclusive species (*)	Differential species $(^*)$	Indicator species	Ind_Va1	Prob.
								Biscutella morisiana Limonium morisianum Romulea requienii	0.4546 0.4138 0.2884	0.0387 0.0495 0.0420
Supramontano	1348	117	Supramontano (a)	162	62	Aquilegia cremnophila [*] ; Aquilegia nuragica ^b ; Astragalus gennarii ^c ; Brassica tyrrhena; Centaurea filiformis ssp. ferulacea ^b ; Centrantus amazonum; Festuca alfrediana ssp. alfrediana [*] ; Genista cadasonensis ^b ; Genista toluensis; Lactuca longidentata; Limonium coraliforme ^c ; Narcissus supramontanus ssp. supramontanus ssp.	Hypericum scruglii ^a ; Stachys corsica var. micrantha ^b ; Carduus fasciculiflorus ^c	Lactuca longidentata	0.6955	0.0070
			Oroseino (b)	240	61	5		Anthyllis hermanniae ssp. ichnusae	0.5877	0.0193
			Baronico (c)	946	73			Centranthus amazonum	0.5000	0.0068
								Genista toluensis	0.5000	0.0082
								Brassica tyrrhena	0.5000	0.0094
								Colchicum actupii	0.5000	0.0063
								Ophrys panattensis	0.4500	0.0069
								Micromeria cordata	0.4298	0.0171
								Limonium protohermaeum	0.4048	0.0198
								Cerastium supramontanum	0.3971	0.0182
								Limonium hermaeum	0.3696	0.0262
(*) Different letters	indicate that ti	his taxon is ex	xclusive or differential	of the corresp	ondent subsec	stor.				



Fig. 1. Dendrogram derived from hierarchical cluster analysis showing two cut-off levels to define sectors and subsectors, as well as geological features. Characteristics of each geological unit, according to Carmignani *et al.* (2001): (0) Metalimestones and metasandstones of Lower Cambrian; (1) Oligocene-Miocene calcalkaline volcanic cycle; (2) Carboniferous quartzites and granites; (3) Coastal metalimestones and metasandstones of Lower Cambrian; (4) Ordovician-Carboniferous metasandstones and metasiltstones; (5) Coastal Ordovician metasandstones; (6) Quaternary conglomerates, sand and mud deposits; (7) Tertiary basalts and limestones; (8) Quaternary conglomerates, sand and mud deposits; (10) Post Middle Eocene-Lower Miocene continental and marine deposits; (11) Cenozoic continental and marine deposits; (12) Basaltic plateaus and rhyolitic uplands of Pliocene lying on post Middle Eocene-Lower Miocene marls, sands and siltstones; (13) Triassic-Cretaceous carbonatic shelf deposits; (14): Palaeozoic paragneisses and alkaline metagabbroes; (15) Coastal granites; (16) Para-Sardinian islands of granitic origin; (17) Para-Sardinian island of dolomitic origin; (18) Hercynian granitic basement; (19) Hercynian metamorphic complex; (20) Upper Cretaceous dolomitic uplands; (21) Upper Cretaceous carbonatic mountains; (22) Upper Cretaceous dolomitic uplands with a Devonian-Carboniferous terrigenous basement; (23) Middle Cambrian-Lower Odovician micaceous metasandstones and quartzites; (24) Upper Carboniferous-Permian tonalitic granodiorites; (27) Hercynian granitic mountains; (28) Upper Cretaceous carbonatic coast; (29) Oligo-Miocenic andesites and ignimbrites spaced out by Miocenic silty and sandy marls; (30) Paragneisses and Pliocenic rhyolite.

with the results of partial studies carried out in some floristic territories within the island (Bacchetta & Pontecorvo, 2005; Bacchetta, 2006; Fenu & Bacchetta, 2008; Angius & Bacchetta, 2009; Fenu *et al.*, 2010; Bacchetta *et al.*, 2013), although some minor differences at the subsector level were found.

Several units were well defined, not only because of the endemic flora that they shared, but also because they owned a high number of exclusive, differential and indicator endemic taxa. On the contrary, the definition of other units was less conclusive (i.e. the Campidanese-Turritano sector and their subsectors), since they are characterized by scarcity of exclusive or indicator endemic taxa. This result could be due to geology, geomorphology and historical constraints (e.g. Jansson, 2003; Casazza *et al.*, 2008), but also to be a territory with high level of anthropic alteration (which can cause the loss of endemic plants) or still not thoroughly investigated.



Fig. 2. Biogeographical regionalization in sectors (a) and subsectors (b) of Sardinia based on the distribution of endemic vascular plants.

Our results show that the mountainous subsectors maintain higher endemic species richness compared with lowland ones. Higher endemic-species richness in the mountainous areas could be attributed to increased ecological isolation, altitudinal range or higher habitat diversity (Médail & Quézel, 1997; Thompson, 2005; Fenu *et al.*, 2010; Trigas *et al.*, 2012; Bacchetta *et al.*, 2013; Cañadas *et al.*, 2014). In addition, these areas have a high level of naturalness and low human pressure.

Island geology has been recognized to be a strong determinant of species numbers (Kreft *et al.*, 2008). In this sense, for example, in the Sulcitano-Iglesiente sector the complex palaeogeography (these areas have constituted islands for long periods) and geological history (i.e. Palaeozoic limestones and dolomites in the Iglesiente subsector, Palaeozoic autochthonous siliceous rocks such as metapelites, metacalcites and metasiltites in the Sulcitano subsector; see Carmignani *et al.*, 2001), have played a key role in the evolution of endemic richness (Bacchetta, 2006).

In addition, the Sulcitano-Iglesiente, Gennargenteo and Supramontano sectors include several areas that were identified as Mediterranean putative refugia (*sensu* Médail & Diadema, 2009) with high endemic richness (Fenu *et al.*, 2010; Bacchetta *et al.*, 2013). The less drastic climate changes on large Mediterranean islands during the Quaternary could promote the local persistence of high plant richness and the co-existence of distinct genetic lineages (Valiente Banuet *et al.*, 2006; Medail & Diadema, 2009). The quantitative interaction graph separates, according to their endemic flora, the south-western part of Sardinia (Sulcitano-Iglesiente sector) from the central territories of the Island (Gennargenteo and Supramontano sectors). Thus, these sectors have a complex geological history and prolonged insularity and include several putative Mediterranean refugia.

The high endemic richness in the Tavolarino subsector deserves special attention. An anomalous species richness on smaller islands, in comparison with larger ones, has been identified and this phenomenon has been described as the 'small island effect' (Panitsa *et al.*, 2006). The debate over this effect is not yet resolved (Triantis *et al.*, 2012), although the case of the Tavolarino subsector could be useful to test whether the small islands deviate from the common pattern of species–area relationship (Panitsa *et al.*, 2006). In addition, the carbonate substrates and the



Fig. 3. Quantitative endemic-sector interaction web. Left bars represent sectors and right bars represent endemic taxa. Linkage width indicates the presence of each endemic taxon in each sector. Exclusive endemic taxa of each sector (given in Table 1) were grouped and showed using the following abbreviations: **ESI** (Exclusive of Sulcitano-Iglesiente sector), **ECT** (Exclusive of Campidanese-Turritano sector), **EGL** (Exclusive of Goceano-Logudorese sector), **EB** (Exclusive of Baronico sector), **EG** (Exclusive of Gennargenteo sector) and **ES** (Exclusive of Supramontano sector). Plant names are given in Appendix S1.

island altitude, higher than the other circum-Sardinian islands and comparable to the cliffs of Orosei Gulf, could strongly govern endemic richness. Similarly, the Sinisico subsector, consisting mainly of carbonate substrates, deserves particular attention because these substrates constitute an ecological island with a wide range of habitat variability (Fenu & Bacchetta, 2008).

The definition of biogeographical units on a fine scale, which is considered a fundamental step in biogeography in recent decades (Hengeveld, 1999; Di Virgilio et al., 2013), gained key support from tools such as geographical information system (GIS). The GISs make possible the creation of geodatabases with detailed information on taxa distribution and other key variables in biogeographical studies, such as geology and geomorphology. Moreover, the use of different tools such as the Indval Analysis, which enable the identification of indicator taxa in geographical units (Casazza et al., 2008: Casazza & Minuto, 2009), can help in biogeographical analysis. Similarly, the bipartite network diagram, showing the relationships among Sardinian endemic taxa and biogeographical sectors, used for the first time in this type of study, may represent a powerful tool to summarize the biogeographical scheme of a territory. These tools are a valuable help to obtain useful information for biogeographical units, identifying key taxa for conservation within the units. In fact, conservation guidelines have been improved over recent decades by applying biogeographical methods and principles (Whittaker et al., 2005). Since the identification of priorities at finer scales is essential to ensure the implementation of conservation measures (e.g. Brooks et al., 2006; Cañadas et al., 2014), the biogeographical scheme presented here helps to identify area-based conservation strategies in a floristic hotspot such as Sardinia.

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