Diversity and Distributions, (Diversity Distrib.) (2008) **14**, 47–58

BIODIVERSITY RESEARCH

Ecological and historical factors affecting distribution pattern and richness of endemic plant species: the case of the Maritime and Ligurian Alps hotspot

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ABSTRACT

The aim of this study was to test a method to locate all the foci, centres, and areas of endemism in a biodiversity hotspot in order to understand the influence of ecological and historical factors on the distribution pattern and to identify priority areas for future conservation projects. The study area was the Maritime and Ligurian Alps hotspot.

Analyses were performed on the presence/absence matrix of 36 vascular plant taxa endemic to the study area. For each operational geographical unit, the number of endemic taxa present was counted. Additionally, the weighted endemism value was calculated. Areas of endemism were distinguished using cluster analysis and parsimony analysis of endemicity. The influence of ecological characteristics and historical factors was evaluated using Multi-Response Permutation Procedure and the Nonparametric Multiplicative Regression. The Indicator Species Analysis (INDVAL) method was used to identify the species characterizing the areas of endemism. Our results show the importance and location of four main areas of endemism within the Maritime and Ligurian Alps and explain the distribution pattern of endemic plants. These areas are easily interpreted by historical and ecological factors, and INDVAL indicates which taxa took part in the history of each endemism area.

Keywords

Cluster analysis, geological substrate, glacial refugia, historical factors, Ligurian Alps, Maritime Alps, parsimony analysis of endemism, species richness, vascular plants.

INTRODUCTION

Biogeography is closely tied to both ecology and phylogenetic biology and its main areas of interest are ecological biogeography, i.e. the study of factors influencing the present distribution, and historical biogeography, i.e. the study of causes that have operated in the past (Wiens & Donoghue, 2004). Ecological and historical biogeography therefore applies different concepts in order to explain the distribution of organisms. The former deals with functional groups of species and environmental constraints, whereas the latter focuses on taxonomic groups and historical biogeographical events (Crisci *et al.*, 2006). One of the main objectives of historical biogeography is to investigate relationships between areas. In biogeography, 'areas of endemism' were proposed as crucial units and traditionally defined as areas where numerous species are endemic (Szumik & Goloboff, 2004); however, their definition and delimitation are still controversial (Szumik *et al.*, 2002; Deo & DeSalle, 2006; Moline & Linder, 2006). An alternative to 'areas of endemism' is the 'biotic elements' approach (Hausdorf, 2002) which considers a group of taxa whose ranges are significantly more similar to each other than to those of taxa of other similar groups. The identification of 'areas of endemism' is reputedly remarkable for its application in the development and implementation of conservation strategies (e.g. Platnick, 1992; Morrone, 2000; Whittaker *et al.*, 2005; Crisci *et al.*, 2006; Lamoreux *et al.*, 2006). Recently, the division between historical and ecological biogeography has been considered as an obstacle to the progress of biogeography and some authors have stressed the benefits of integrating these two points of view (Wiens & Donoghue, 2004; Kent, 2006; Posadas *et al.*, 2006). In this context, the present work attempts at filling the gap between these two approaches.

DOI: 10.1111/j.1472-4642.2007.00412.x
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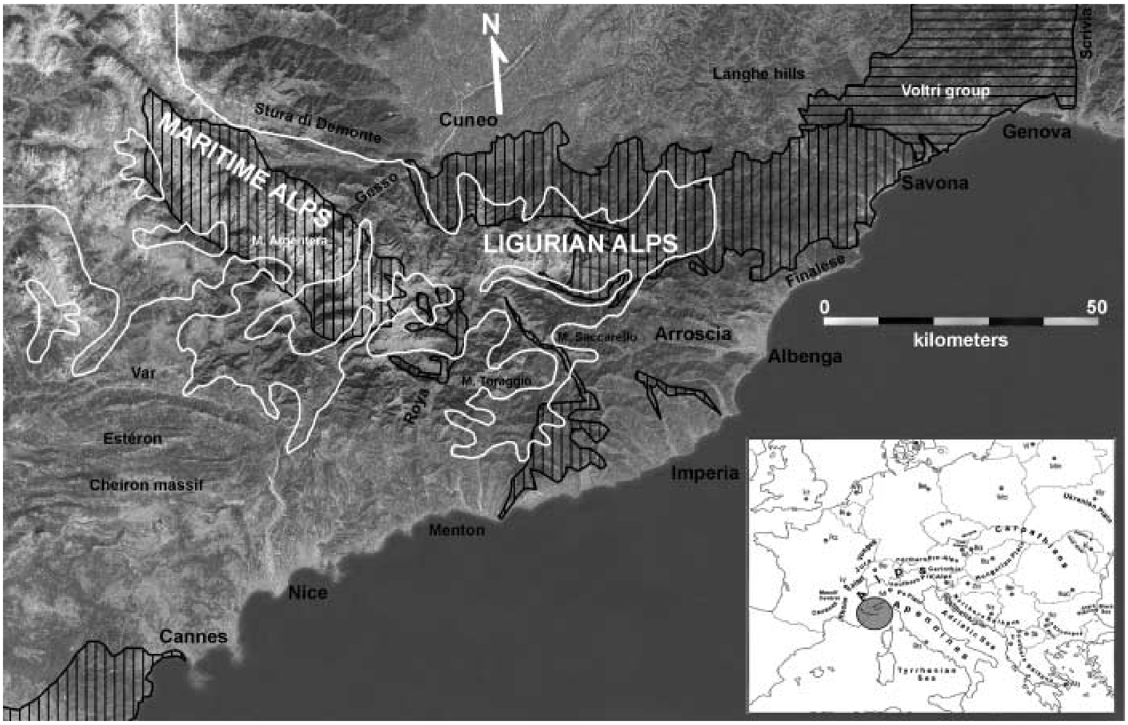

Figure 1 The study area of Maritime and Ligurian Alps. The white line indicates the margin of the Last Glacial Maximum (LGM) during the Würm (*c.* 18 thousand years BP) (synthesis performed by M. Dubar in Diadema *et al.*, 2005). Siliceous outcrops (vertical striped area) and ophiolitic substrate (horizontal striped area) are evidenced. The remnant area corresponds to calcareous outcrops (Novarese, 1931; Taccagna & Franchi, 1934; Sacco & Peretti, 1942; Rouire, 1980; Giammarino *et al.*, 2002).

The study area is the Maritime and Ligurian Alps, one of the most important hotspots of the Mediterranean Basin (Médail & Quézel, 1997). It is considered as a major refuge area (Diadema *et al.*, 2005; Schönswetter *et al.*, 2005) as well as a suture zone *sensu* Remington (1968) within the Alps (Comes & Kadereit, 2003). At the crossroads of the Mediterranean Basin and the Alps, this region is one of the most relevant biogeographical areas in Europe due to the endemic concentration of a varied array of taxa (Médail & Verlaque, 1997; Casazza *et al.*, 2005), as well as for its possible role as an ancestral area for some of these species (Merxmüller, 1965; Pawlowski, 1970) or populations (Garnier *et al.*, 2004). Recent molecular investigations of endemic plants belonging to the region showed that vicariance events are probably the most important factor explaining the distribution of these plants in the area (Conti *et al.*, 1999; Diadema *et al.*, 2005; Minuto *et al.*, 2006; E. Conti, pers. comm.).

Hence, spatially detailed biogeographical interpretations of present endemic species distribution in the south-western part of the Alps have been debated for some time and there is a growing amount of material available to detect biogeographical patterns (Zappa, 1994; Casazza *et al.*, 2005; Diadema *et al.*, 2005), which may be of practical use for conservation purposes. Thus, the aim of this study was to detect the patterns of endemism richness and the areas of endemism, based on the analysis of the distribution of vascular endemic plants in order to identify priority areas for conservation. The respective importance of environmental and historical factors influencing patterns of local endemic species richness and distribution within the Maritime and Ligurian Alps was evaluated. The use of Indicator Species Analysis (Dufrêne & Legendre, 1997) applied to biogeographical studies was tested.

METHODS

Description of the study area

The investigated area (Fig. 1) is the Maritime and Ligurian Alps hotspot, located on the border between north-western Italy and south-eastern France (Médail & Quézel, 1997). This 9500 km^2 area extends from the Stura di Demonte River and the Langhe hills in the north to the Mediterranean coast in the south, and from Genoa and the Scrivia Valley in the east to 6°38′ E in the west. Its main geographical characteristics are reported in Fig. 1.

The region is geologically complex (Bogdanoff *et al.*, 2000; Bertotti *et al.*, 2006), with many tectonic units (Rosenbaum & Lister, 2005) and many lithological types (calcareous, siliceous, and ophiolitic substrate) as reported in Fig. 1.

Climatic conditions

Most of the study area is under a Mediterranean pluvioseasonal oceanic or temperate oceanic bioclimate (Vagge, 1999; Rivas-Martínez *et al.*, 2004a), even the south-facing high-altitude slopes, where oromediterranean vegetation shows some affinities with that of other southern Mediterranean mountains (Barbero,

Table 1 INDVAL results (IV) and ecological features of taxa (Aeschimann *et al.*, 2004). s, substrate requirements (Ca, calcicolous; Si, silicicolous); gf, growth form (H, hemicriptophyte; C, chamaephyte; G, geophytes); ab, altitudinal belts (c, coastal; m, mountain; s, sub-alpine; a, alpine); mc, soil moisture contents (mm, very low; m, low; o, medium); ph, preferential and secondary (in brackets) habitats (r, rocky; s, scree; g, grassland; b, bush; w, wood). $^{**}P < 0.005$; NS, not significant. Bold line marks the taxa more characterizing the areas of endemism.

Species	IV Cluster analysis	Group Cluster analysis	s	gf	ab	mc	ph	IV PAE	Group PAE
Lilium pomponium L.	40.38**	1	Ca	G	s	mm	(r),s,g,b,(w)	16.15^{NS}	0
Cytisus ardoinoi E.Fourn.	70.00**	3	Ca	C	c	mm	s,b	11.43^{NS}	10
Leucanthemum burnatii Briq. & Cavill.	50.00**	3	Ca	H	c	mm	r,s,(b)	16.33**	0
Galeopsis reuteri Rchb.	18.77**	4	Si	H	s	m	s	11.03^{NS}	8
Gentiana ligustica R.Vilm. & Chopinet	12.12**	4	Ca	H	s	m	(r),s,g,(w)	10.82^{NS}	0
Moehringia lebrunii Merxm.	33.33**	4	Ca	C	m	o	r	11.11^{NS}	15
Scabiosa mollissima Viv.	8.89^{NS}	4	Ca	H	m	mm	r,s,b	8.93^{NS}	10
Phyteuma cordatum Balb.	14.29**	4	Ca	H	m	m	r,(s),g	9.18^{NS}	10
Saxifraga cochlearis Rchb.	60.0**	4	Ca	C	s	m	r	38.57**	10
Moehringia sedoides (Pers.) Loisel.	28.57**	4	Ca	C	s	m	r	25.00**	10
Ballota frutescens (L.) Woods	44.32**	5	Ca	C	m	m	r,(s)	21.77**	10
Potentilla saxifraga De Not.	30.77**	5	Ca	C	c	m	r	28.57**	10
Leucojum nicaeense Ardoino	19.23**	5	Ca	G	c	mm	r,s,(b)	30.00**	13
Leucanthemum discoideum (All.) Willk.	45.24**	6	Ca	H	c	m	(r),s,g,b,w	17.01**	10
Potentilla valderia L.	60.17**	7	Si	C	a	mm	(r),g	40.24**	6
Saxifraga florulenta Moretti	60.36**	7	Si	C	a	m	r,(s)	41.33**	6
Silene cordifolia All.	55.65**	7	Si	H	s	mm	r,(s)	31.06**	6
Viola argenteria Moraldo & Forneris	40.33**	7	Si	H	a	o	r,	30.48**	6
Viola valderia All.	55.86**	7	Si	H	s	o	r,s,g	48.28**	6
Primula allionii Loisel.	28.57**	9	Ca	H	m	m	r,(s)	9.18^{NS}	10
Carduus aemilii Briq. & Cav.	34.62**	10	Ca/Si	H	s	m	s,g	7.14^{NS}	0
Helianthemum lunulatum (All.) DC.	61.54**	10	Ca	C	s	mm	r,s,g	9.92^{NS}	10
Hesperis inodora L.	20.51**	10	Ca	H	m	o	g,b	19.05**	10
Micromeria marginata (Sm.) Chater	35.14**	10	Ca	C	m	mm	r,(s)	15.64**	10
Senecio personii De Not.	17.31**	10	Si	H	s	mm	r,(s)	6.25^{NS}	1
Silene campanula Pers.	34.47**	10	Ca	H	s	o	r	21.43**	10
Campanula fritschii Witasek	26.67**	11	Ca	H	m	mm	r,(s)	20.00**	2
Centaurea jordaniana Moretti ssp. *jordaniana*	44.44**	12	Si	H	m	m	r,w	75.00**	3
Phyteuma villarsii Rich. Schulz	60.00**	12	Ca	H	s	o	r	20.00**	3
Leucanthemum subglaucum De Laramb.	70.00**	13	Ca/Si	H	c	mm	(s),g,b,w	80.00**	5
Limonium cordatum (L.) Mill.	43.75**	14	Ca	H	c	m	r,(s)	18.75**	11
Campanula isophylla Moretti	50.00**	16	Ca	C	c	m	r	66.67**	16
Campanula sabatia De Not.	22.22**	16	Ca	H	c	mm	(r),s	16.67**	16
Centaurea aplolepa Moretti ssp. *aplolepa*	32.14**	16	Ca	H	m	mm	r,b	37.50**	16
Cerastium utriense Barberis	100.00**	18	Si	H	m	o	s,(g)	90.91**	17

1972, 2003). The northern section of the area is characterized by a temperate climate and is home to more mesophilous vegetation (Regione Piemonte, 2001; Brunetti *et al.*, 2006). Seven thermoclimatic belts have been recorded by the Worldwide Bioclimatic Classification System methods (www.globalbioclimatics.org) based on mean temperature and mean precipitations: thermomediterranean, mesomediterranean, meso-submediterranean, supramediterranean, supratemperate, oro-submediterranean, and orotemperate (Rivas-Martínez *et al.*, 2004b). During the Pleistocene epoch, many glacial events affected this area (Ponel *et al.*, 2001; Ehlers & Gibbard, 2004) and repeatedly influenced its geomorphology (Malaroda, 2000; Federici & Spagnolo, 2004), as well as the distribution of animals (Garnier *et al.*, 2004) and plants (Diadema *et al.*, 2005). The ice cover during the last glaciation is reported in Fig. 1 and it is based on an unpublished synthesis by M. Dubar (in Diadema *et al.*, 2005).

Data set and analyses

Species data

One hundred and fifteen endemic taxa *sensu lato* (Casazza *et al.*, 2005) are present in the Maritime and Ligurian Alps. Our analyses were restricted to 36 plant taxa (Table 1), selected according to the following criteria: endemics *sensu stricto* and sub-endemics with very few populations out of the study region (e.g. *Saxifraga cochlearis* and *Viola argenteria*). Apomictic and agamospecies were excluded (Aeschimann *et al.*, 2004; Casazza *et al.*, 2005).

The distribution was inferred from bibliographic information (Mariotti, 1985; Zappa, 1994; Médail & Verlaque, 1997; Casazza *et al*., 2005; and references therein), herbaria, and field surveys (G. Casazza & L. Minuto, unpublished data). Very restricted endemic taxa found in one operational geographical unit (OGU) only were excluded from analysis (*Centaurea jordaniana* ssp. *aemilii*, *C. jordaniana* ssp. *verguinii*, *C. jordaniana* ssp. *balbisiana*, *C. aplolepa* ssp. *gallinariae*, *Micromeria graeca* ssp. *imperica*, *Dianthus furcatus* ssp. *dissimilis*, and *Campanula albicans*). A database was compiled including part of the taxa ecological requirements according to the criteria adopted by Aeschimann *et al*. (2004): substrate requirements, life-form *sensu* Raunkiaer (1934), preferential habitats, soil moisture content, and altitudinal belts. The nomenclature is drawn from Flora Alpina (Aeschimann *et al*., 2004) and Flora d'Italia (Pignatti, 1982).

Richness of species

The taxa were scored as present or absent in each 10 × 10 km cell of an arbitrarily drawn grid (see Appendix S1 in Supplementary Material). The 175 cells containing at least one species were used as OGU for the statistical analyses. For each OGU the number of endemic taxa present was counted. Additionally, we weighted the endemic species (weighted endemism value) using Linder's method (Linder, 2001) that downweights the species by the inverse of their ranges and yields a leptokurtic curve, where the values decrease very rapidly at first, then more slowly (see Appendix S1).

Areas of endemism

The presence/absence matrix was analysed with cluster analysis and parsimony analysis of endemism in order to identify the areas of endemism. Cluster analysis was carried out using PC-ORD version 4 statistical software (McCune & Mefford, 1999). Kulczynski index (Shi, 1993) and group average linkage methods were applied. The Kulczynski index has been recently introduced in biogeographical analysis in order to replace the Jaccard coefficient because it is more appropriate for datasets characterized by large differences in the richness of species in different areas (Hausdorf, 2002; Moline & Linder, 2006). Clusters defined at 50% dissimilarity were mapped. A parsimony analysis of endemism (PAE – Rosen, 1988; Morrone, 1994) was carried out using PAUP 4.0 beta 10 for Windows (Swofford, 1998), according to the method described by Moline & Linder (2006). We adopted this method even if it was heavily criticized in the past few years. According to Humpries (2000) PAE only considers the distribution of taxa while ignoring phylogenetic relationships and it a priori assumes vicariance as the main process responsible for the geographical distribution of species (Brooks & van Veller, 2003). For these reasons, PAE is not considered as a true historical biogeographical method by Santos (2005). On the contrary, Posadas *et al*. (2006) states that such criticism is only applicable to PAE variants (PAE based on localities and PAE based on areas of endemism) aiming at elucidating the history of the areas. We therefore used the PAE variant based on quadrates in order to identify areas of endemism rather than their history.

Factors influencing diversity and distribution patterns

The Multi-Response Permutation Procedure (MRPP) was conducted using PC-ORD version 4 software (McCune & Mefford, 1999) and the weight method suggested by Mielke (1984) was adopted. MRPP is a nonparametric procedure used to test the hypothesis of absence of difference between two or more groups. It was performed in order to evaluate the agreement (A) between matrices of the presence/absence of substrate type (calcareous, siliceous, or serpentine), Würm glaciation, or thermoclimatic belts and the groups defined for cluster analysis and PAE. The distance matrix was calculated using the Kulczynski index and Euclidean distance.

Nonparametric Multiplicative Regression (NPMR) analysis (Bowman & Azzalini, 1997; Peterson, 2000; McCune *et al*., 2003) was used to explain the variations in the number of endemic taxa according to the following predictive variables: extent of Würm glaciation, substrate type, or thermoclimatic belts. NPMR was developed on the assumption that species respond simultaneously to multiple ecological factors and that the response to any one factor is conditioned by the values of other factors. NPMR allowed us to abandon simplistic assumptions about overall model form, while embracing the ecological truism that habitat factors interact (McCune, 2006).

The analysis was conducted using HYPERNICHE 1.0 beta version software (McCune & Mefford, 2004). In this study, in particular, the Species Occurrence model was used (Peterson, 2000; McCune *et al*., 2003). This model gives equal weight to all sampling points within the window, while all observations outside the window are given zero weight. NPMR combines two or more predictors to produce a coefficient of determination known as cross R^2 (xR^2). This xR^2 differs from the traditional R^2 because the size of the residual sum of squares can be greater than the total sum of squares and $xR^2 < 0$ (McCune, 2004). A model evaluation was carried out with the Monte Carlo permutation test, by comparing the estimated response variable, obtained from the selected models, to an average estimation calculated by N random permutations among the data set. P-values were also calculated in order to verify the statistical significance of results.

Indicator Species Analysis (INDVAL) is a simple method to find indicator species characterizing groups of samples. It combines information on the concentration of species abundance in a particular group and the faithfulness of occurrence of a species in a particular group. In the case of the presence/absence matrix, abundance was calculated as the ratio of the number of species present in a site group to the total number of species present (Dufrêne & Legendre, 1997). INDVAL analysis was performed using INDVAL version 2.0 for Macintosh (http://mrw.wallonie.be/dgrne/sibw/outils/indval). The significance was calculated using two methods: by computing the weighted distance between randomized values and the observed value (t-test) and by using the rank of the observed value among

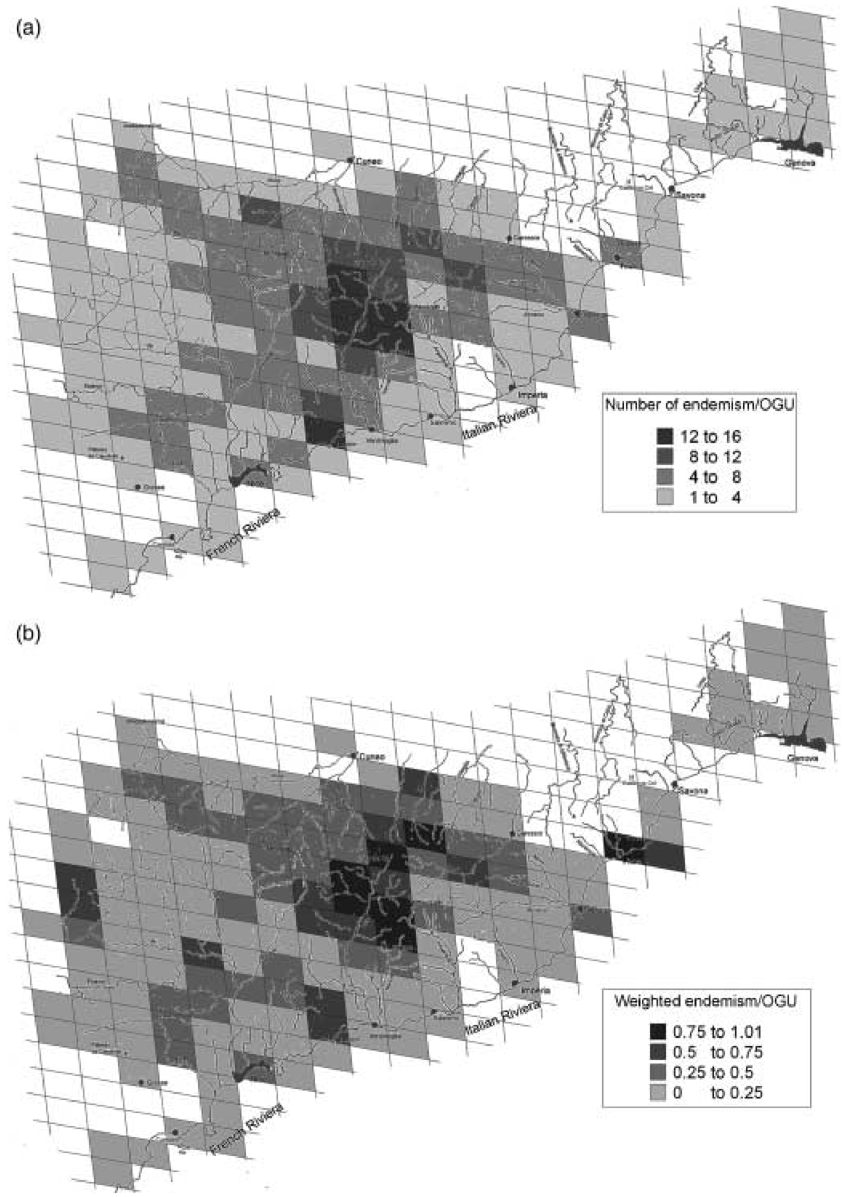

Figure 2 Graphical representations of the richness of endemism (a) and of the weighted endemism value (b). OGU, operational geographical units.

the decreasingly ordered randomized value distribution; randomization was achieved using 999 random interactions and five seeds for random number generator. The significance level was set at $P < 0.05$.

RESULTS

Patterns of richness and distribution of endemic plants

Richness of species

The greater concentration of taxa/OGU is generally present along the ridge of the Maritimes Alps and a portion of the Ligurian Alps. The highest values, ranging between 10 and 16 taxa/OGU, were recorded in the upper part of the Roya Valley and in the southern mountain area behind Menton (Fig. 2a). The weighted endemism value pointed to the importance of the two previous areas and of two other small areas: the Finalese and the upper Var Valley (Fig. 2b).

Cluster analysis and PAE

Cluster analysis (see Appendix S2 in Supplementary Material) revealed the existence of 18 clusters (Table 2) that were progressively numbered and mapped in Fig. 3(a). INDVAL analysis performed on the cluster analysis results (Table 1) showed that only seven clusters include at least two species (3, 4, 5, 7, 10, 12, and 16), while six are characterized by only one taxon (1, 9, 11, 13, 14, and 18).

PAE (see Appendix S1) showed the presence of 17 areas (Table 2) without a hierarchical definition; they were progressively numbered and mapped in Fig. 3(b).

Table 2 Geographical denomination and environmental features of the clusters of cluster analysis (CA) and the parsimony analysis of endemism (PAE). For each cluster are reported: geomorphology (a, alluvial plain; c, cliffs; cs, coasts; g, gorges; h, hills; m, mountains); substrate (Ca, calcareous; si, siliceous; Oph, ophiolites); thermoclimatic belt (Tm, thermomediteranean; Mm, mesomediterranean; Msm, meso-submediterranean; Ssm, supra-submediterranean; St, supratemperate; Osm, oro-submediterranean; Ot, orotemperate).

Clusters			Geomorphological and ecological features		
CA	PAE	Geographical area	Geomorphology	Substrate	Thermoclimatic belt
1	1	Upper Var Valley	m	Ca	Osm
	4	Var Valley	g	Ca	Msm
	7	Esteron Valley	c	Ca	Osm
2	4	Esteron Valley/Cagne Valley	g	Ca	Msm
11	2	High mountain of Var Valley	m	Ca	Ssm
12	3	Vaire and Coulomp Valley	c	Ca	Ssm
3		Cheiron Massif	c	Ca	Mm
4	10	Upper Roya Valley	g	Ca	Osm
5	10	Mountains behind Menton	c	Ca	Osm
	15	M. Saccarello/M. Toraggio	m	Ca	Osm
6	12	Hills between Var and Impero	h	Si	Mm
	14	M. Acuto – Rocca Barbena	c	Ca	Ssm
7	6	M. Argentera group	m	Si	Ot
8	9	Hills between Cuneo and Garessio	h	Si	St
9		Low Gesso valley	c	Ca	St
10		Ligurian Alps	m	Ca	St/Ssm
13	5	Arroscia Valley	a	Ca	Mm
14	13	Coast between Ventimiglia & Nice	cs	Ca	Mm
	11	Coast between Nice and Cannes	cs	Ca	Tm
15		Capo Mele	cs	Ca	Mm
16	16	Finalese	c	Ca	Mm
18	17	Voltri group	m	Oph	St

INDVAL analysis performed on the PAE results (Table 1) shows that only four clades are characterized by at least two species (3, 6, 10, and 16), while eight are characterized by only one taxon (1, 5, 8, 11, 13, 14, 15, and 17).

Areas of endemism

The combination of cluster analysis and PAE results showed four different geographical areas (Fig. 4) characterized by at least two taxa with a significant INDVAL. These areas can be considered as areas of endemism within the Maritime and Ligurian Alps hotspot. The Finalese is characterized by three calcicole species living on cliffs: *Campanula isophylla*, *Campanula sabatia*, and *Centaurea aplolepa* ssp. *aplolepa*. The Argentera massif is characterized by *Potentilla valderia*, *Saxifraga florulenta*, *Viola valderia*, *Silene cordifolia*, and *Viola argenteria*, silicicolous species mainly living in rocky habitats. The upper Var Valley is characterized by two species with different ecological features: *Centaurea jordaniana* ssp. *jordaniana* and *Phyteuma villarsii*. While PAE includes the entire Roya Valley, cluster analysis divides it into low and upper Roya Valley. The former is characterized by *Ballota frutescens* and *Potentilla saxifraga*, the latter by *Moehringia sedoides* and *Saxifraga cochlearis*. All of these are calcicole species living on cliffs but at different altitudes.

Factors influencing richness and distribution patterns

Local richness of endemism

The NPMR model (Table 3) showed that the variation in number of endemic taxa is correlated with the thermoclimatic belts and the extent of Würm glaciation. No significant relationship was found between the number of endemisms and substrate type. The combined models of the previous variables showed a remarkable increase of xR^2 only in the two-variable model (Würm and thermoclimatic belts). However, when the distribution of richness of species (Fig. 2) and the extent of glaciation were compared (Fig. 1), the OGUs harbouring the higher number of endemics were on the edge of the Quaternary glacial sheets. The comparison of weighted endemism values and predictive variables by NPMR did not reveal any specific pattern.

Distribution patterns

MRPP analysis (Table 4) evaluates the agreement between the matrix of ecological or historical factors and the groups obtained by cluster or parsimony analysis. A better congruence exists with the clusters of cluster analysis. No influences have been recorded by including the Würm glaciation extent. This finding was

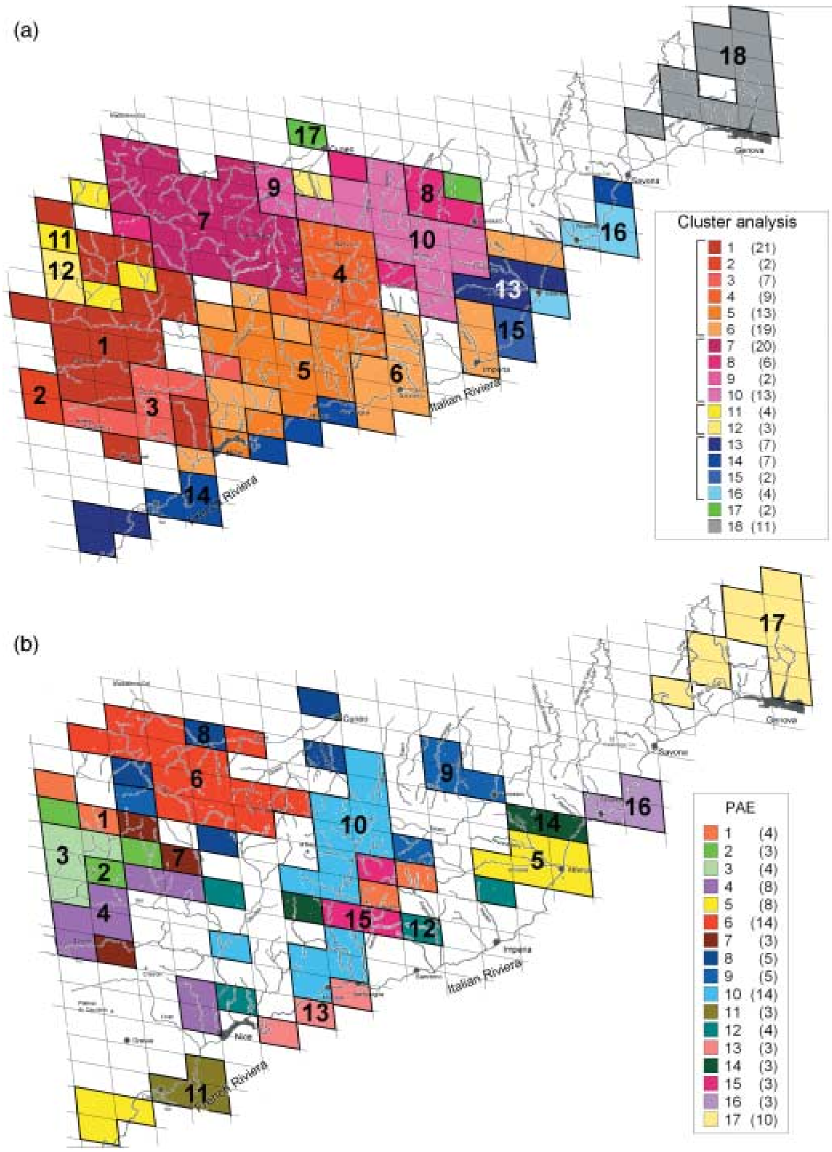

Figure 3 Biogeographical analysis of Maritime and Ligurian Alps hotspot. (a) Graphical representation of cluster analysis, different tones of colour are reported according to the hierarchy of clusters. (b) Graphical representation of parsimony analysis of endemicity; Argentera group (6), Voltri groups (17), Roya Valley (10), Finalese (16), alluvial plains near Cannes and near Albenga (5), upper Var Valley (2, 3), Côté d'Azur (11, 13).

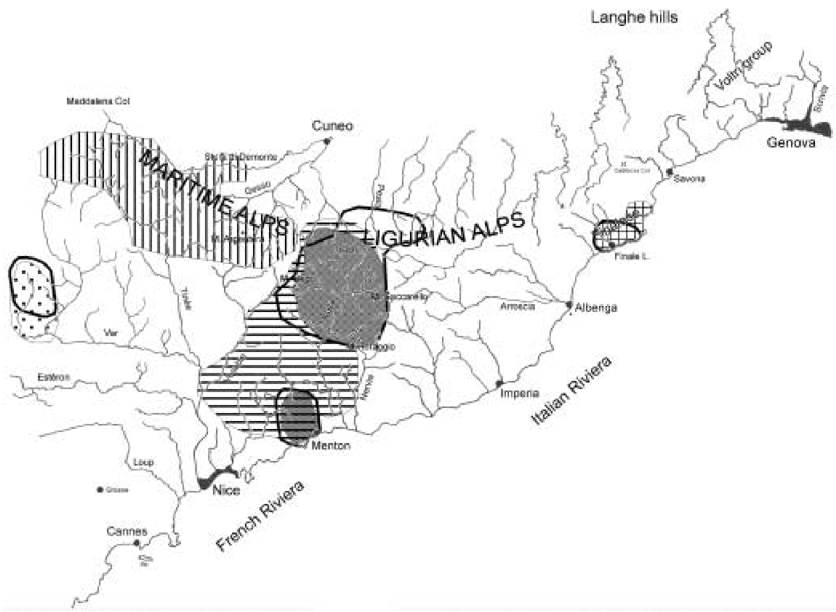

Figure 4 Synthetic representation of the distribution of areas of endemism (horizontal striped areas – Roya Valley, vertical striped areas – Argentera massif, squared areas – Finalese and spotted areas – upper Var Valley), centres of endemism (bold lines), and foci of endemism (grey plots).

Table 3 Results of Nonparametric Multiplicative Regression (NPMR) (xR^2) analysis performed in order to evidence any links between the taxa number per OGU and the ecological and historical factor.
NPMR analysis

Response variable	xR^2	xR^2 change	Predictive variable	Predictive variable	Predictive variable
Number of taxa/OGU	0.013*		Soil		
Number of taxa/OGU	0.140**		Würm		
Number of taxa/OGU	0.189**		Thermoclimatic belts		
Number of taxa/OGU	0.227**	0.038	Würm	Thermoclimatic belts	
Number of taxa/OGU	0.236**	0.009	Würm	Soil	Thermoclimatic belts

$^{**}P < 0.005$; $^{*}P < 0.01$.

Table 4 Results of Multi-Response Permutation Procedure (MRPP) analysis (A) performed in order to evidence any links between the groups of cluster analysis and PAE and ecological and historical factor. $^{**}P < 0.005$; $^{*}P < 0.01$.
MRPP analysis

	A (with glacial extension)		A (without glacial extension)	
	Kulczynski	Euclidean	Kulczynski	Euclidean
Cluster analysis	0.325**	0.408**	0.413**	0.420**
Parsimony analysis	0.200**	0.270**	0.217**	0.280**

further tested by comparing the ecological features of the taxa identified by INDVAL for the same clusters (Table 1). The hilly region from Estéron Valley to Imperia (clusters 1–6, red and orange in Fig. 1) corresponds to the mountain region including the supramediterranean and oromediterranean belts. These clusters are characterized by calcicole and mountainous taxa living in the hill or mountain belt and having greater hygrophilous requirements (1–3, red). The Maritime Alps (7 and 9) and Ligurian Alps (8 and 10) clusters (pink) are characterized by shrubby or herbaceous plants, silicicolous in the former and generally calcicole in the latter; these species are typical of mountain or sub-alpine altitudinal belts, living both in rocky and in grassland habitats. The French and Italian Riviera clusters (13–16) correspond to the coastal area within the thermomediterranean and mesomediterranean belts and they are characterized by calcicole hemicryptophytes plants mainly living on the cliffs of the coastal belt; *Leucanthemum subglaucum* is an exception in the alluvial plains (13) being a silicate-tolerant plant. The Voltri ophiolitic group cluster (18) corresponds to the supra-temperate belt and is characterized by the serpentine *Cerastium utriense* only.

The importance of geological differences must be emphasized: the Roya, Vésubie and Argentina Valleys (4–6) belong to the Briançonnais tectonic unit and are separated from the upper Var and Estéron Valleys belonging to Helvetic nappes (1–3). The Argentera crystalline group (7), belonging to the External crystalline massifs, is distinguished from the Ligurian Alps (8–10) that belong to the Briançonnais unit. Similarly, the coastal belt is divided into two main areas: the Quaternary alluvial plains near Cannes and Albenga (13) and the calcareous or dolomitic areas on the Riviera (14–16).

DISCUSSION

Areas of endemism in the Maritime Alps

By analysing patterns of endemic richness in the Maritime and Ligurian Alps, two different kinds of areas can be distinguished.

As far as the number of endemic taxa/OGU was concerned, the highest values were recorded in the Roya Valley and in the mountains behind Menton (Fig. 4). These locations were defined as foci of endemism, because they harbour a higher number of endemic taxa belonging to the hotspot. The centres of endemism measure (weighted endemism) are also sensitive to the rarity of species in an area, and many widespread species might yield a higher value than a small number of narrowly range-restricted species (Linder, 2001). For this reason, the Finalese and the upper Var Valley (Fig. 4) where some narrowly endemic species (*Campanula isophylla* and *Centaurea jordaniana*) are present have to be added to the two previously mentioned areas. While a focus of endemism is defined according to richness only, centres of endemism are characterized by both richness and uniqueness; hence, the centres of endemism partly overlap with both these types of biogeographical entities.

The four areas of endemism identified in this study are mainly located in the Maritime Alps, a portion of the SW Alps that was affected by various palaeogeographical and historical events (Malaroda, 2000; Rosenbaum & Lister, 2005). A glacial sheet covered the area throughout the Quaternary, as geologically demonstrated by the glacial circles found in the Argentera massif area (Federici & Spagnolo, 2004) and by glacial moraine deposits (Malaroda et al., 1970). The patchy ice cover created many potential refugia (Ponel et al., 2001; Ehlers & Gibbard, 2004) mainly in the peripheral zone on the edge of the glacial sheet. The same phenomenon probably took place in the Argentera massif as well, where some relicts of the Tertiary flora like *Saxifraga florulenta* (Conti & Rutschmann, 2004), *Potentilla valderia*, and *Viola argenteria* survived. This is further confirmed by the INDVAL value, showing that these species characterize this area of endemism.

The Roya Valley is an area of endemism located in the calcareous bedrocks of the Col de Tende, which separates the Maritime from the Ligurian Alps. It is characterized by calcicole plants, but other taxa are also present and show their distributional limits in this area (e.g. *Campanula sabatia*, *Cytisus ardoinoi*, and *Campanula fritschii*). The variability in substrate and the diversity in habitats and climatic conditions might explain the coexistence of alpine and more thermophilous plant species within a small geographical area. Moreover, being on the edge of the ice sheet, the Roya Valley was a major peripheral refugium where dynamic processes on plant population occurred: divergence (ultimately leading to speciation), migration, or extinction (Hewitt, 1999; Hampe & Petit, 2005). The first event is demonstrated by polyploidy of *Primula marginata* in south-eastern populations (Pignatti, 1982) or by the genetic diversity of *Gentiana ligustica* (Diadema *et al*., 2005) and *Moehringia sedoides* (Minuto *et al*., 2006). Migration and extinction processes might be seen in the fragmented distribution area of some species, such as *Primula allionii* (Martini *et al*., 1992). Some species, such as *Moehringia lebrunii*, probably are relict plants that survived several dramatic historical events (Martini, 1994).

The high mountains bordering the Roya Valley in the north and east may have acted as a physical barrier causing the discontinuities and making this the most important suture zone of the Maritime Alps (Kropf *et al*., 2002; Grassi *et al*., 2006).

According to INDVAL values, the Finalese area of endemism is mostly characterized by *Campanula isophylla*. This plant was not influenced by glacial events but its speciation probably dates back to the Cenozoic (Martini, 1982), when an adaptation to the specific substrate present in the area was developed.

Ecological vs. historical factors

Statistical analyses show that the groups selected by cluster analysis and PAE can be explained by the type of substrate and by thermoclimatic belts. Therefore, the present distribution patterns of the investigated endemic taxa reflect the influence of ecological factors. One such example is the congruence between areas of endemism (Finalese, Argentera massif) and the corresponding specific bedrocks. Conversely, glaciations seem to have had a lower influence on plant distribution and their effect was weakened by postglacial migrations. These events were influenced by environmental factors, but also by the plants' capabilities to disperse into and to recruit in available and empty patches as well as by their competitive abilities when spreading into already occupied areas. Glaciations have a strong influence on taxa richness. In fact, the two major areas of endemism within the hotspot are located in spatially limited areas where historical factors showed their influence. This finding is in agreement with Morrone's suggestion (2001) that 'areas of endemism' represent historical entities.

The interaction between ecological features and historical events, influencing the distribution pattern of endemic taxa in the Maritime and Ligurian Alps, further confirms that biogeographical studies should cover both components, as recently recommended by many authors (see Morrone, 2006).

INDVAL is a very useful tool for biogeographical investigations because, on the one hand, it allows identification of the species characterizing an area of endemism, and on the other, it indicates how much the distribution area of a given taxon overlaps with the area of endemism. For these reasons, in an area of endemism, INDVAL makes it possible to recognize taxa that are influenced by the same historical and ecological factors. For instance, the upper Roya Valley (cluster 4 in cluster analysis) is significantly characterized by *Moehringia lebrunii* (33.33) and *Saxifraga cochlearis* (60.0). Their INDVAL values are quite different and can be interpreted as follows: the entire distribution area of *Moehringia lebrunii* is included in the upper Roya Valley, but it covers only a few OGUs. The distribution area of *Saxifraga cochlearis* overlaps quite completely the area of endemism, even if some of its populations are recorded outside the upper Roya Valley cluster. *Saxifraga cochlearis* is probably more representative of the history of the entire area of endemism than *Moehringia lebrunii*, the latter being limited to a very small part of the area. Since INDVAL considers the relationship between the distribution area of taxa and a geographical area, it might be a useful tool for the development and implementation of a procedure combining the alternative notions of biotic elements and areas of endemism.

The Maritime Alps have been interpreted as a contact zone (Kropf *et al*., 2002; Garnier *et al*., 2004; Diadema *et al*., 2005), but recent molecular phylogeographical investigations indicate that the genetic architecture of codistributed taxa was not always shaped by the same historical factors (Schönswetter *et al*., 2002; Tribsch *et al*., 2002; Comes & Kadereit, 2003). For this reason further phylogeographical studies on the Maritime Alps are needed.

This hotspot is rich in both species number and endemic taxa (Médail & Verlaque, 1997; Casazza *et al*., 2005). As already stated empirically by Pawlowski (1970), large numbers of endemic taxa are found in the regions with the oldest flora. This concept completely fits with the Maritime and Ligurian Alps hotspot, where the low impact of glaciations allowed some Tertiary flora plants to survive, but it also induced dynamic processes like plant population divergence and speciation.

ACKNOWLEDGEMENTS

The authors thank Marc Dufrêne for helpful suggestions on how to use INDVAL statistics and Janos Podani for critical discussion of statistical analyses. Finally, we are grateful to the anonymous reviewer for helpful comments on the manuscript.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Appendix S1 Matrix based on presence/absence of taxa.

Appendix S2 Cluster analysis and PAE dendrograms.

This material is available as part of the online article from: http://www.blackwell-synergy.com/doi/abs/10.1111/j.1472-4642.2007.00412.x
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