DISTRIBUTION PATTERN AND RICHNESS OF ENDEMIC PLANT SPECIES IN MARITIME AND LIGURIAN ALPS.

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ABSTRACT
In recent years we made an overview of endemic plants (*sunsu lato*) of the Maritime Alps (115 taxa representing 3.2 % of the flora). Ecological preferences and plant life strategies were detected, showing a particular ability of endemics to colonize habitats with low competition and disturbance characteristics. The comparison with other areas of the Mediterranean basin appears to show that the Maritime Alps are really a 'hot spot' owing to the high total number of vascular plants and the high number of endemic plants. Subsequently, looking for any focus, centre and area of endemism, analyses were performed on a presence/absence matrix of 36 vascular plant taxa endemic to the study area. For each operational geographic 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 (PAE). The influence of ecological characteristics and historical factors was evaluated using Multi-Response Permutation Procedure and Non-Parametric Multiplicative Regression. The Indicator Species Analysis (INDVAL) was also used to identify the species characterizing the areas of endemism.
Our results point out the importance and location of four main area of endemism within the Maritime and Ligurian Alps explaining the distribution pattern of endemic plants. These areas are easily interpreted by historical and ecological factors: the NPMR model indicated that the variation in number of endemic taxa is correlated with the thermoclimatic belts and the extent of Würm glaciations. No significant relationship was found between the number of endemism and the soil type. The comparison between the distribution of richness of species and the extension of glaciations, the OGU harbouring the higher number of endemics were in marginal position from the Quaternary glacial sheets. NPMR didn't find models environmental patterns comparing the weighted endemism values
The main focus and centre of endemism of the study area were evidenced inside the Roya Valley areas of endemism. This territory may be considered as a "hotspot within a hotspot", and its statistically well supported identification appears to be very useful for future conservation purposes. Finally, the identification of a "hotspots within a hotspot" as a sum of the previous elements appears to be very useful for future conservation purposes.

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

INTRODUCTION

Ten plant diversity regional hotspots have been proposed within the Mediterranean Basin (Médail & Quézel, 1997), due to their high species richness and endemism.

The great biodiversity of the Mediterranean basin is due primarily to particular climatic conditions, habitat heterogeneity as a result of paleogeographical and historical factors, and varying origins of the flora itself (Quézel, 1985, 1995). Thus, insular, mountain or isolated edaphic systems (i.e. ultrabasic and serpentine rocks) generally appear to be major endemic centres (Quézel, 1985; Stevanovic et al., 2003). Circum-Mediterranean vascular flora owes its taxonomic richness (Médail & Quézel, 1997) to its degree of endemism, varying from 50% (Quézel, 1985) to 59% (Greuter, 1991) depending on the taxonomic interpretations of the authors.

We studied the Maritime and Ligurian Alps, one of the most important hotspots of the Mediterranean Basin (Médail & Quézel, 1997). It is considered as a 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 biogeographic 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). The endemism of the Maritime Alps is the result of an extremely disturbed history (geological and climatic) dating from the mid-Tertiary period (Quézel, 1985, 1995). Due to the moderate impact of the Quaternary glaciation, especially the Würm (Debrand-Passard, 1986), several zones acted as places of refuge, where more favourable thermal conditions (cliffs, formation of nunataks, etc.) helped preserve numerous elements of the Tertiary paleoflora (e.g. *Ballota frutescens* (L.) Woods (Figure 1), *Helianthemum lunulatum* (All.) DC., *Leucojum nicaeense* Ardoino, *Moehringia lebrunii* Merxm. (Figure 2), *Phyteuma cordatum* Balb., *Potentilla saxifraga* De Not.).

Figure 1. *Ballota frutesces* a Tertiary relict of the Roya Valley.

Figure 2. *Moehringia lebrunii* a Tertiary relict of the Roya Valley.

The many geological, edaphic and climatic discontinuities contributed towards the formation of a vast plant and animal diversity, as already reported for the richness distribution of vascular plant species and endemism concentration at other Mediterranean sites (Mariotti, 1990; Lobo et al., 2001; Stevanovic et al., 2003). 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).

Hence, spatially-detailed biogeographic interpretations of present endemic species distribution in the south-western part of the Alps has been debated for some time and there is a growing amount of material available to detect biogeographic patterns (Zappa, 1994; Casazza et al., 2005; Diadema et al*.*, 2005), which may be of practical use for conservation purposes.

The relationship between habitats and endemic taxa

Since 2004 we worked in evaluating the floristic richness and endemism rate of the Maritime Alps and subsequently we tried to compare the biodiversity level with other hot spots in the Mediterranean Basin. Finally we attempted to analyse the relationship between habitats and endemic/endangered taxa.

The overall number of species in the Maritime Alps is of 3615 taxa, including 115 endemic entities (3.2%). By considering the relationship between the flora and the actual size of the area, the mean percentage of endemics and the number of plants per square kilometre are very interesting by comparison with other Mediterranean hot spots (0.37 species per km^2) (Casazza et al., 2005).

This high plant density and consequent competition appear to play an important role in the ecological and altitudinal distribution of endemics. In view of the high biodiversity, endemics have only been able to remain in extreme habitats, often with very limited interspecific competition. The number of altitude zones occupied by endemics is partly explained by the intense competition: altitudinal narrowing due to increased specialisation. This might be one of the reasons why a high number of endemics live in rocky habitats (62.95%), particularly at high altitudes (34%). This endemic pattern is also the result of the geomorphological and climatic development of this territory (Casazza et al., 2005). The derived biotope mosaic appears to be the main cause of any preservation, isolation and differentiation processes of the flora (Kruckeberg & Rabinowitz, 1985) and particularly explain the conservation role of rocky habitats at high altitudes that were never interested by glaciation effects (nunataks formation) (Debrand-Passard, 1986).

Patterns of endemism

A second part of our 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. Our analyses were restricted to 36 plant taxa (Casazza et al., 2008) and they were based on the most recent biogeographical techniques: cluster analysis and parsimony analysis of endemism.

The respective importance of environmental and historical factors influencing patterns of local endemic species richness and distribution within the Maritime and Ligurian Alps was also evaluated by using the nonparametric procedure Multi-Response Permutation Procedure (MRPP) and Non-Parametric Multiplicative Regression (NPMR) analysis (Casazza et al., 2008).

Figure 3. The upper Roya Valley. View of Tende.

Figure 4. Peillon little village in the hills behind Menton.

The analysis of the patterns of endemic richness in the Maritime and Ligurian Alps distinguished two different kinds of areas (Casazza et al., 2008). As far as the number of endemic taxa/OGU was concerned, the highest values were recorded in the Roya Valley (Figure 3) and in the mountains behind Menton (Figure 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 (Figure 5)and the upper Var

Valley (Figure 6) 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 characterised by both richness and uniqueness; hence, the centres of endemism partly overlap with both these types of biogeographic entities.

Figure 5. S. Lorenzino church near Orco in the Finalese area.

Figure 6. Entrevaux in the upper Var Valley.

The four identified areas of endemism (Casazza et al., 2008) are mainly located in the Maritime Alps, a portion of the SW Alps that was affected by various paleogeographical 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* (Figure 7) survived.

Figure 7. *Viola argenteria* a Tertiary relict of the Argentera Massif.

Figure 8. *Gentiana ligustica* a typical endemism of Maritime and Ligurian Alps.

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 geographic 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* (Figure 8) (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.

The influence of ecological and 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 post-glacial 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 biogeographic studies should cover both components, as recently recommended by many authors (see Morrone 2006).

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 phylogeographic investigations indicate that the genetic architecture of co-distributed taxa was not always shaped by the same historical factors (Schönswetter et al., 2002; Tribsch et al., 2002; Comes & Kadereit, 2003).

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.

REFERENCES

Casazza, G., Barberis, G. & Minuto, L. (2005) Ecological characteristics and rarity of endemic plants of the Italian Maritime Alps. *Biological Conservation*, 123, 361–371.

Casazza, G., Zappa E., Mariotti M.G., Medáil F., Minuto L., 2008 - Ecological and historical factors affecting distribution pattern and richness of endemic plant species: the case of Maritime and Ligurian Alps hotspot. *Diversity and Distribution* 14: 47-58.

Comes, H.P. & Kadereit, J.W. (2003) Spatial and temporal patterns in the evolution of the flora of the European Alpine System. *Taxon*, 52, 451-462.

Conti, E., Soltis, D.E., Hardig, T.M. & Schneider, J. (1999) Phylogenetic relationships of the silver saxifrages (*Saxifraga*, sect. *Ligulatae* Haworth): Implications for the evolution of substrate specificity, life histories, and biogeography. *Molecular Phylogenetics and Evolution*, 13, 536-555.

Conti, E. & Rutschmann, F. (2004) Molecular dating analyses support the pre-Quaternary origin of *Saxifraga florulenta* Moretti, a rare endemic of the Maritime Alps. Poster contribution, IXth IOPB meeting “Plant Evolution in the Mediterranean Climate Zones”. Valencia, 16–19 May 2004, p. 114.

Debrand-Passard, S., 1986. Synthèse Géologique du Sud-est de la France. Vol. 2. Atlas. *Mémoires du Bureau de Recherches Géologiques et Minières* 126. Paris.

Diadema, K., Bretagnolle, F., Affre, L., Yuan, Y.M. & Médail, F. (2005) Geographic structure of molecular variation of *Gentiana ligustica* (Gentianaceae) in the Maritime and Ligurian regional hotspot, inferred from ITS sequences. *Taxon*, 54, 887-894.

Ehlers, J. & Gibbard, P.L., eds. (2004) *Quaternary Glaciations - Extent and Chronology, Part I: Europe*. Developments in Quaternary Science, Vol. 2a. Amsterdam, Elsevier.

Federici, P.R. & Spagnolo, M. (2004) Morphometric analysis on the size, shape and areal distribution of glacial cirques in the Maritime Alps (Western French-Italian Alps). *Geography Annal*s, 86A, 235–248.

Garnier, S., Alibert, P., Audiot, P., Prieur, B. & Rasplus, J.-Y. (2004) Isolation by distance and sharp discontinuities in gene frequencies: implications for the phylogeography of an alpine insect species, *Carabus solieri*. *Molecular Ecology*, 13, 1883–1897.

Grassi, F., Labra, M., Minuto, L., Casazza, G. & Sala, F. (2006) Natural hybridization in *Saxifraga callosa* Sm. *Plant Biology*, 8, 243-252.

Greuter, W., 1991. Botanical diversity, endemism, rarity and extinction in the Mediterranean area: an analysis based on the published volumes of Med-Checklist. *Botanika Chronika* 10, 63-79.

Hampe, A. & Petit, R.J. (2005) Conserving biodiversity under climate change: the rear edge matters. *Ecology Letters*, 8, 461-467.

Hewitt, G.M. (1999) Post-glacial re-colonization of European biota. *Biological Journal of the Linnean Society,* 68, 87-112.

Kropf, M., Kadereit, J.W. & Comes, H.P. (2002) Late Quaternary distributional stasis in the submediterranean mountain plant *Anthyllis montana* L. (Fabaceae) inferred from ITS sequences and amplified fragment length polymorphism markers. *Molecular Ecology,* 11, 447-463.

Kruckeberg, A.R., Rabinowitz, D., 1985. Biological aspects of endemism in higher plants. Annual *Review of Ecology and Systematics* 16, 447-479.

Lobo, J.M., Castro, I., Moreno, J.C., 2001. Spatial and environmental determinants of vascular plant species richness distribution in the Iberian Peninsula and Balearic Islands. *Biological Journal of the Linnean Society*, 73, 233–253.

Malaroda, R., Carraro, F., Dal Piaz, G. B., Franceschetti, B., Sturani, C. & Zanella, E. (1970) Carta Geologica del Massiccio dell’Argentera alla scala 1:50 000 e Note Illustrative. *Memorie della Società Geologica Italiana*, 9, 557–663.

Malaroda, R. (2000). Neotettonica e glacialismo nella parte meridionale dell’alta Val Vésubie (Alpes Maritimes, Francia). *Atti della Accademia Nazionale dei Lincei, Rendiconti, Classe di Scienze Fisiche, Matematiche e Naturali*, 9, 143-150.

Mariotti, M.G., 1990. Floristic connection between the Sardo-Corsican dominion and the Ligurian area. *Atti Convegni Accademia Nazionale dei Lincei* 85, 429-448.

Martini, E. (1982) Lineamenti geobotanici delle Alpi Liguri e Marittime: endemismi e fitocenosi. *Lavori della Società Italiana di Biogeografia n.s.*, 9, 51-134.

Martini, E. (1992) Recherches géobotaniques sur *Primula allionii* Loisel., espèce endémique exclusive des Alpes Maritimes. *Biogeographia*, 16, 131-139.

Martini, E. (1994) Ricerche geobotaniche su *Moehringia lebrunii* Merxm. e *Primula allionii* Loisel. Endemismi ristretti delle Alpi Marittime. *Revue Valdôtaine d'Histoire Naturelle*, 48, 229-236.

Médail, F. & Quézel, P. (1997) Hotspots analysis for conservation of plant biodiversity in the Mediterranean Basin. *Annals of the Missouri Botanical Garden*, 84, 112–127.

Médail, F. & Verlaque, R. (1997) Ecological characteristics and rarity of endemic plants from southeast France and Corsica: implications for biodiversity conservation. *Biological Conservation*, 80, 269–281.

Merxmüller, H. (1965) *Moehringia lebrunii*, une nouvelle espèce connue depuis longtemps. *Le Monde des Plantes*, 347, 4-7.

Minuto, L., Grassi, F. & Casazza, G. (2006) Ecogeographic and genetic evaluation of endemic species in the Maritime Alps: the case of *Moehringia lebrunii* and *M. sedoides* (Caryophyllaceae). *Plant Biosystems,* 140, 146-155.
Morrone, J.J. (2001) Homology, biogeography and areas of endemism. *Diversity and Distributions*, **7**, 297–300.
Morrone, J.J. (2006) *La vita fra lo spazio e il tempo. Il retaggio di Croizat e la nuova biogeografia*. Medical Books, Palermo.
Pawlowski, B. (1970) Remarques sur l'endémisme dans la flore des Alpes et des Carpates. *Vegetatio,* 21, 181-243.
Ponel, P., Andrieu-Ponel, V., Parchoux, F., Juhasz, I. & Beaulieu de J.-L. (2001) Late-glacial and Holocene high-altitude environmental changes in Vallée des Merveilles (Alpes–Maritimes, France): insect evidence. *Journal of Quaternary Science*, 16, 795–812.
Quézel, P., 1985. Definition of the Mediterranean region and the origin of its flora. In Gomez-Campo, C. (Ed.), Plant Conservation in the Mediterranean Area. Dr W. Junk Publisher, Dordrecht. *Geobotany* 7, 9-24.
Quézel, P., 1995. La flore du bassin méditerranéen: origine, mise en place, endémisme. *Ecologia Mediterranea* 21, 19-39.
Remington, C.L. (1968) Suture-zones of hybrid interaction between recently joined biota. *Evolutionary Biology*, 2, 321–428.
Rosenbaum, G. & Lister, G.S. (2005) The Western Alps from the Jurassic to Oligocene: spatio-temporal constraints and evolutionary reconstructions. *Earth-Science Reviews,* 69**,** 281-306.
Schönswetter, P., Tribsch, A., Barfuss, M. & Niklfeld, H. (2002) Several Pleistocene refugia detected in the high alpine plant *Phyteuma globulariifolium* Sternb. & Hoppe (Campanulaceae) in the European Alps. *Molecular Ecology*, 11, 2637–2647.
Schönswetter, P., Stehlik, I., Holderegger, R. & Tribsch, A. (2005) Molecular evidence for glacial refugia of mountain plants in the European Alps. *Molecular Ecology***,** 14, 3547-3555.
Stevanović, V., Tan, K., Iatrou, G., 2003. Distribution of the endemic Balkan flora on serpentine. I. – obligate serpentine endemics. *Plant Systematic and. Evolution*. 242: 149–170.
Tribsch, A., Schönswetter, P. & Stuessy, T.F. (2002) *Saponaria pumila* (Caryophyllaceae) and the ice age in the European Alps. *American Journal of Botany*, 89, 2024–2033.
Zappa, E. (1994) *L'endemismo vegetale nelle Alpi Liguri e Marittime*. PhD Thesis, University of Pavia.