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The plant endemism in the Maritime and Ligurian Alps

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SUMMARY

The Maritime and Ligurian Alps have a flora characterised by a very high number of endemic species in relation to their small geographical extension. This area is considered one of the most important centres of diversification of the Alps and a Mediterranean hotspot of biodiversity. In the last years many studies were performed in order to describe the distribution and phylogeographical patterns of endemism. Despite these studies, Maritime and Ligurian Alps still lack in a broad view about the evolution of endemisms in this area. In this review, we examine the knowledge about the distribution patterns of endemic plant species living in the Maritime and Ligurian Alps in order to identify the evolutionary and biogeographical mechanisms operating on them.

INTRODUCTION

The Mediterranean Basin is one of the world's terrestrial biodiversity hotspots (Quézel 1995, Médail and Myers 2004). This area hosts most of the biodiversity of Europe, but its species richness is threatened by human pressure and climate change (EEA 2010). In particular, habitat fragmentation and global warming have caused changes in the ecosystems structure leaving the ecosystems more vulnerable to invasion by alien species (EEA 2006). For these reasons, there is an urgency to conserve this richness (Blondel and Médail 2009).

The great biodiversity of the Mediterranean Basin is primarily due to particular climate conditions, to habitat heterogeneity as a result of paleogeographical and historical factors, and to different origins of the elements of its flora (Quézel 1985, 1995, Nieto Feliner 2014). Insular, mountain and isolated edaphic systems (i.e., ultrabasic and serpentine rocks) generally appear to be major endemic centres (Quézel 1985, Stevanović 2003, Bacchetta et al. 2013, Sciandrello et al. 2015). Circum-Mediterranean vascular flora owes its taxonomic richness (Médail and Quézel 1997) to its relatively high degree of endemism, varying from 50% (Quézel 1985) to 59% (Greuter 1991) in relation to the taxonomic interpretations of authors.

The Maritime and Ligurian Alps (MLA) are one of the ten hotspots in the Mediterranean area (Médail and Quézel 1997) and they are one of the most relevant biogeographical areas in Europe because of the concentration of endemic taxa (Pawlowski 1970, Martini 1982, Médail and Verlaque 1997, Casazza et al. 2005), and their possible role as long persistence area of species (Merxmüller 1965, Pawlowski 1970) and populations (Garnier et al. 2004). In fact, MLA are considered to be both a major Quaternary refugium (Diadema et al. 2005, Schönswetter et al. 2005) and a suture zone *sensu* Remington (1968) within the Alps (Comes and Kadereit 2003).

This region is geologically and ecologically complex (Fig. 1). Many tectonic units and many lithological types (e.g., calcareous, siliceous, and ophiolitic substrates) are present (Bogdanoff et al. 2000, Rosenbaum and Lister 2005, Bertotti et al. 2006). Furthermore, seven thermo-climatic 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. 2004). The northern part of the MLA is characterised by a temperate climate and it homes a more mesophilous vegetation compared to the southern part (Regione Piemonte 2001, Brunetti et al. 2006). In addition, during the Pleistocene, many glacial events affected this area (Ponel et al. 2001, Ehlers and Gibbard 2004) and repeatedly influenced its geomorphology (Malaroda 2000, Federici and Spagnolo 2004). In this review, we examine the present advances in knowledge about the endemic plants growing in the MLA in order to identify and to describe the evolutionary and biogeographical mechanisms driving the high biodiversity of this area.

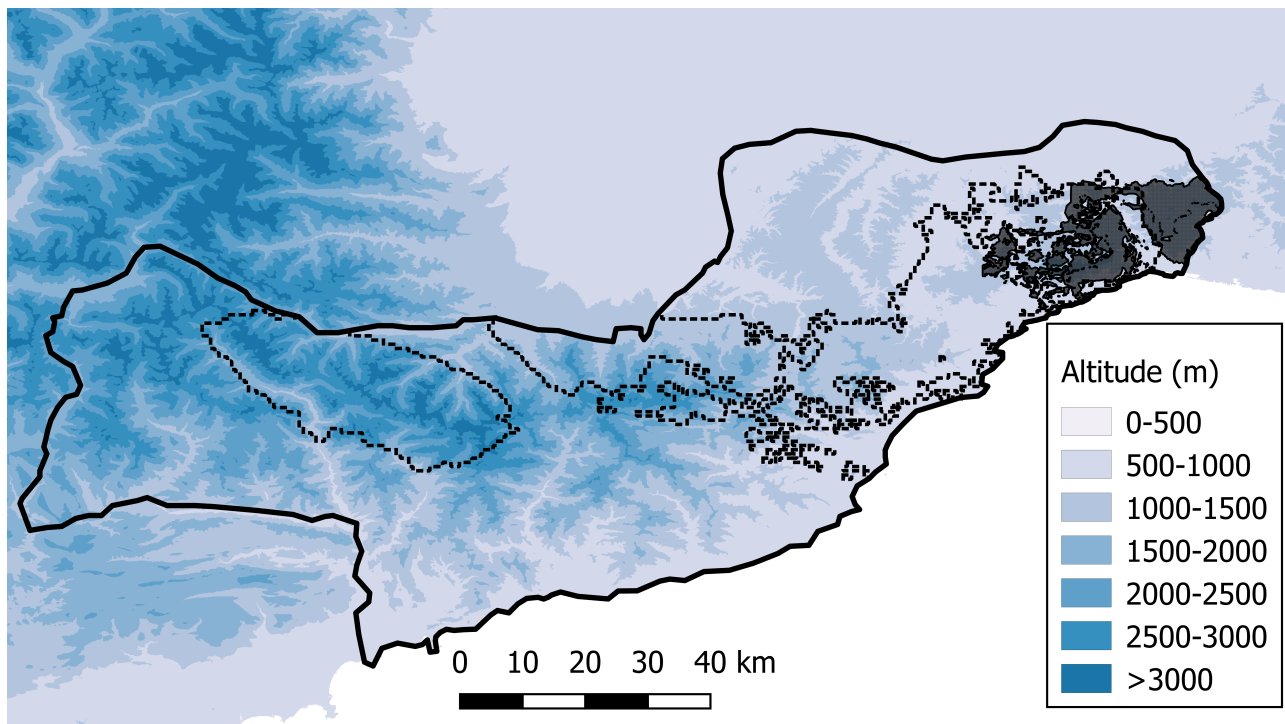


FIGURE 1. Map of Maritime and Ligurian Alps showing major geographic areas. Siliceous outcrops (dotted areas) and ophiolitic substrate (grey areas) are evidenced. The remnant area corresponds to calcareous outcrops. Elevation is showed in a blue scale. Dark blue shows highest altitude while light blue shows lowest altitude.

A PROFILE OF THE ENDEMIC FLORA

In their study about the MLA flora, Casazza et al. (2005) estimated a total number of 3605 taxa, 115 (3.2%) of which were endemic or subendemic (with a small part of their distributional range external to the study sector) to this biogeographical sector. The authors detected other 78 rare plants with a slightly broader distribution but not includable in the previous categories. It should be noted that *Hieracium* and *Taraxacum* genera (Asteraceae) were excluded from the analysis due to the difficulty in identifying such taxa accurately, and to the very different taxonomic treatments adopted in the floristic contributions to this region. The endemisms vs. total species richness ratio indicated that this area has a lower proportion of endemic species than other southern European and Mediterranean regions, because of the high number of total taxa. However, considering the endemic species/area relationship, the MLA do not deviate excessively from the ratios recorded by other interesting floristic areas of the world (Casazza et al. 2005). It was also evidenced that most endemisms grow in high stress level communities, such as screes, cliffs and rocks, at mid and high altitudes and alpine grasslands. In fact, endemic richness peaks (20.56% of the total) in screes and cliff formations (Casazza et al. 2005).

At least a half of the plants endemic to MLA (53%) grows in the mountain belt and occurs mainly in rocky habitats (38%) and in alpine grasslands (12%). On the contrary, few endemisms grow at low elevations (16.68%), mainly in cliffs and rocky grasslands of the maritime belt (13% - Casazza et al. 2005). The high proportion of endemism growing in rocky habitats (63.57%) may be the result of the low aboveground competition that it is known to play an important role in the differentiation of narrow endemic species in the western Mediterranean (Lavergne et al. 2004).

The knowledge about MLA is still ongoing and during the last decade three endemic and one subendemic new taxa were described: *Viola laricicola* Marcussen (Marcussen 2003), *Moehringia argenteria* Casazza and Minuto (Casazza and Minuto 2008), *Gentiana burseri* Lapeyr. subsp. *actinocalix* Polidori (Polidori 2008), *Arundo donaciformis* (Loisel.) Hardion, Verlaque, Baumel, Juin and Vila (Hardion et al. 2012) and *Aquilegia ophiolitica* Barberis and Nardi (Barberis and Nardi 2011).

THE ORIGIN OF ENDEMISM

Why some species have highly restricted geographic range while closely related species have widespread distributions is a question that has long fascinated ecologists and evolutionary biologists. The identification of different types of plant endemism appeared soon in literature after the first use of this term by De Candolle (De Candolle 1855). Endemic plants were distinguished on the basis of their age (Engler 1882, Cain 1944, Kruckeberg and Rabinowitz 1985, Wherry 1944): paleo-endemisms are ancient or relict elements of a given taxonomic group, often systematically isolated from other taxa; neo-endemisms are more recently evolved and have extant sister taxa. Endemic species were also classified on the base of their ploidy level (Favarger and Contandriopoulos 1961). Polyploid speciation, characterised by duplication of whole genome, played a key role in plant evolution (Soltis et al. 2003, 2009, Fawcett and Van de Peer 2010, Parisod et al. 2010, Balao et al. 2011, Jiao et al. 2011, Mayrose et al. 2011). Recent analyses estimated that all seed plants trace their origins to few polyploidization events (Jiao et al. 2011) and 15% of speciation events involved polyploidization (Wood et al. 2009), occurring both between (i.e., allopolyploidization) and within species (i.e., autopolyploidization). In particular, according to Favarger and Contandriopoulos (1961) patroendemisms are diploid endemisms which have given rise to more widespread polyploids; apoendemisms are polyploid endemisms which have arisen from widespread diploid or lower polyploid parents; schizoendemisms are the result of the range fragmentation of a widespread ancestral taxon producing endemic taxa with the same chromosome number in different parts of the original distribution. Later, Raven (1964) and

Kruckenbergh and Rabinowitz (1985) introduced a new endemism category: edaphic endemism. This category reflects physiological adaptations of plants that allow for colonization, establishment, and growth in toxic soils or soils with few nutrients.

Despite very few studies were addressed to understand the evolutionary history of MLA endemisms, it is possible to assign some of them to the categories previously described. The ancient origin was demonstrated for two endemics *sensu stricto* to MLA using molecular clock: *Saxifraga florulenta* Moretti (Conti and Rutschmann 2004, Szövényi et al. 2009) diversified at the Tortonian/Messinian boundary (about 7 Ma - Comes, 2004; Conti and Rutschmann 2004) and *Silene cordifolia* All. probably differentiated during late Miocene (Sloan et al., 2009). The origin of *Berardia subacaulis* Vill., a species endemic to the SW Alps, was dated to the early Oligocene about 33 Ma (95 % confidence interval 28.95–37.92 Ma) (Barres et al. 2013). Furthermore, *Moehringia lebrunii* Merxm. was assumed to be a taxonomic relict (Merxmüller 1965, Martini 1994) on the basis of morphological features and of its position on an isolated long branch of the phylogenetic tree (Minuto et al. 2006, Fior and Karis 2007).

Recent studies on *Campanula* (sect. *Heterophylla* – Nicoletti et al. 2014), *Moehringia* (Fior et al. 2006, Fior and Karis 2007) and *Primula* (sect. *Auricula* – Zhang et al. 2004, Casazza et al. 2012) evidenced that the MLA were source of new species (i.e., neoendemisms) during the Quaternary. The recent origin of species belonging to *Campanula* sect. *Heterophylla* is suggested by the weak morphological and genetic differentiation among species (Nicoletti et al. 2014). *Moehringia* has many species endemic to the Alpine chain and its differentiation probably took place during Last Glacial Maximum (LGM), as suggested by the weak genetic differentiation among species (Fior et al. 2006). Another well-studied taxon is *Primula* sect. *Auricula*, one of the largest plant group endemic to the European Alpine System. Range size of *P.* sect. *Auricula* species differs tremendously: some species are widespread, whereas others are limited to narrow areas (Zhang and Kadereit 2004). The section started to diversify significantly during the last Pliocene while diversification slowed down during subsequent glacial cycles of the Pleistocene (Boucher et al. 2015). In this *Primula* section there is strong evidence for allopatric speciation (Kadereit et al. 2004, Boucher et al. 2015) with little ecological divergence, suggesting that these groups represent non-adaptive radiations (Boucher et al. 2015). Close related species originated in glacial refugia may have re-colonized unglaciated areas during the interglacial periods, and they may have come into contact in areas of sympatry (Kadereit et al. 2011). Four species of the section demonstrate the occurrence of these processes in the MLA: *P. auricula* L., *P. hirsuta* All., *P. marginata* Curtis and the narrow endemic *P. allionii* Lois.

Polyploidization within the context of the Pleistocene glacial cycles has been also proposed as an evolutionary driver to the diversification of *Primula* sect. *Auricula* (Casazza et al. 2012). The hexaploid ($2n = 6x = 62, 66$) and dodecaploid ($2n = 12x = 120–128$) populations of *P. marginata* are an example of this process. The hexaploids and the dodecaploids occur respectively in the western and eastern parts of the species range. A recent study suggested an allopolyploid origin of dodecaploid by hybridization, between the narrow endemic *P. allionii* and *P. marginata*, occurred in the Roya Valley, which was free from ice during the LGM (Casazza et al. 2012). Outcrossing test suggested that dodecaploids of *P. marginata* are reproductively isolated from hexaploids (Minuto, personal communication). The reproductive isolation, together with the lack of morphological and ecological distinctiveness of the two cytotypes, suggests that dodecaploids might be considered as crypto-species subendemic to the MLA (Casazza et al. 2012).

The range fragmentation of a widespread ancestral taxon, producing endemic taxa with the same chromosome number in different parts of the original distributional area, was proposed to explain the distribution of the alpine endemic taxa belonging to *Moehringia* sect. *Moehringia* (Fior and Karis

2007) and *Primula* sect. *Auricula* (Zhang et al. 2004, Boucher et al. 2015). *Moehringia* section includes both species endemics to the European Alpine System and widespread species occurring in Northern Hemisphere. The distribution and the phylogenetic analysis of these species suggest that an explosive postglacial speciation took place in the Alps after LGM, resulting in a high number of geographically isolated taxa together with the retention of Tertiary relicts (Fior and Karis 2007). In this context, the endemic species belonging to this section may be considered as schizoendemisms. Another example of schizoendemic species is *Acis nicaeensis* Lledó, A.P.Davis. & M.B.Crespo. The taxon form a monophyletic group together with *Acis valentina* (Pau) Lledó, A.P.Davis. & M.B.Crespo, *A. fabrei* (Quézel & Girerd) Lledó, A.P.Davis. & M.B.Crespo and the newly identify *A. ionica* Bareka, Kamari & Phitos (Lledó et al. 2004, Bareka et al. 2006). All the species are narrow endemics: *Acis valentina* from eastern Spain, *A. ionica* from western Greece and southern Albania, *Acis nicaeensis* from the MLA and *A. fabrei* from Vaucluse (Southern France). The first two sister taxa share the chromosome number $2n=16$ and the last two sister taxa share the chromosome number $2n=18$. These evidences suggest that these pairs of taxa originated from fragmentation of the range of a widespread ancestor.

Among the three species of *Moehringia* endemic to the MLA two occurs on calcareous substrates while one occurs exclusively on siliceous rocks (Martini 1986, Martini 2003, Casazza and Minuto 2008). Others edaphic endemisms are *Viola bertolonii* Pio, *Cerastium utriense* Barberis and *Aquilegia ophiolitica* growing exclusively on ultramaphic rocks in the Voltri groups. Nevertheless, it was recently suggested that the abundance of *C. utriense* was not affected by typical chemical characteristics of serpentine soils, but mainly by physical traits typical of serpentine substrates (Marsili et al. 2009).

According to Jansson (2003), distributional patterns at global scale of several narrow-ranging endemic species are caused by variation in the amplitude of climatic change occurring in time-scale of 10–100 thousand years. The smaller the climatic shifts, the more probable it is that paleo-endemics survive and that diverging gene pools persist without going extinct or merging, favouring the evolution of neo-endemics. The endemism in MLA is probably the result of a moderately disturbed history (geological and climatic) dating from the mid-Tertiary period (Quézel 1985, 1995). Due to the moderate impact of the Quaternary glaciations, especially during the last cold phases (Debrand-Passard 1986), several zones probably acted as refugial areas, where more favourable thermal conditions (cliffs, formation of nunataks, etc.) favoured the survival of numerous elements of the Tertiary paleoflora (Médail and Diadema 2009). The several geological, edaphic and climatic discontinuities, as well as the partial covering of ice sheet, might have favoured the formation of a large plant and animal diversity, as reported for other Mediterranean sites (Mariotti 1990, Lobo et al. 2001, Stevanović et al. 2003). However, further studies are still necessary to understand the causes of restricted geographic range of species endemic to MLA.

THE DISTRIBUTION PATTERNS

The analysis of distribution patterns of the richness in endemic species in the MLA allows the identification of two different types of areas. The highest endemism richness (number of endemic taxa/geographic unit) was recorded in the Roya Valley (at the border between Italy and France; Fig. 1) and in the mountains behind Menton (Casazza et al. 2008). The centres of endemism (measured considering also the rarity of species in an area) were recorded also in the Finalese and in the upper Var Valley, where some narrowly endemic species are present (i.e., *Campanula isophylla* Moretti and *Centaurea jordaniana* Gren. & Godr., respectively). Casazza et al. (2008) evidenced that the current distribution patterns of the endemic taxa reflect the influence of both ecological and historical factors.

An example is the congruence between the detected areas of endemism (i.e., Finalese and Argentera massif; Fig. 1) and their specific bedrocks. Conversely, glaciations seem to have had a certain influence on plant distribution but their effect was weakened by postglacial migrations. The possibility of the plants to migrate was affected by environmental factors, but also by capability of plants to disperse into and to recruit available and empty patches as well as by their competitive abilities when spreading into already occupied areas.

Ecological factors

Some edaphic and environmental adaptations have been recorded among the endemic species of the MLA. For example, *P. marginata* prefers high altitude rocky calcareous habitats, abundant precipitation, low moisture retention at soil level and marked temperature range between winter and summer seasons (Casazza et al. 2013). Species distribution model describes *P. marginata* at equilibrium with the environment, suggesting that any future climate changes might cause limitations for the survival of the species.

As previously debated, the substrate plays a role in determining the range of other endemic species. An example is *Cerastium utriense* endemic to the ophiolitic area near Voltri (Marsili et al. 2009; Fig. 1). Other examples are the species endemic to the Argentera Massif (i.e., *Saxifraga florulenta*, *Viola argenteria* Moraldo & Forneris and *Silene cordifolia*) whose range roughly corresponds to the crystalline massif, confirming the strict link between soil and distribution range.

Historical factors

Médail and Diadema (2009) evidenced that the local ‘biogeographical stasis’ of plant species or populations in Mediterranean Basin is linked to the capacity of the mountain range to provide a wide array of microhabitats. Under unfavourable conditions, the complex microtopography of the MLA may have allowed the persistence of plant species in locations with climatic conditions that contrasted with the average climatic envelope of the region.

Some important survivors of Tertiary flora in the MLA are: *Saxifraga florulenta* (Conti and Rutschmann 2004, Szövényi et al. 2009), *Silene cordifolia* and *Berardia subacaulis*. During the glacial cycling of the Quaternary, all these species probably maintained their populations at high altitudes where the mountains were free from the glacial sheet. In *S. florulenta* the weak genetic divergence between genetic groups suggests that their separation took place more recently, and that the species survived the Pleistocene glaciations *in situ* (Szövényi et al. 2009). This hypothesis was also recently supported by species distribution models (Patsiou et al. 2014). A similar genetic pattern was detected in *Silene cordifolia* (Casazza et al. unpublished data) and it seems to confirm that this region may have held multiple micro-refugia during the Pleistocene glaciations.

Similarly, widespread species such as *Euphorbia spinosa* L. (Zecca et al. 2011), *Arabis alpina* L. (Ansell et al. 2008) and *Saxifraga callosa* Sm. (Grassi et al. 2009) survived glacial age in refugia within the MLA too. The phylogeographical pattern based on molecular data of *Euphorbia spinosa* (Zecca et al. 2011) supports the hypothesis of long-term separation of the north-western (Maritime Alps, Sardinia, Corsica, North Apennines) and south-eastern (South Apennines and Balkan area) lineages; together with the estimated divergence time this result suggests the survival of the species into at least two glacial refugia during the Quaternary glaciations. The existence of these two allopatric lineages is probably the result of isolation in different glacial refugia, likely due to the LGM cooling and the complex topography of the Italian peninsula.

Vicariance events due to the glacial sheet extinction may explain the genetic structure of some plants endemic to MLA, like *Gentiana ligustica* R.Vilm. & Chopinet (Diadema et al. 2005, Christe et al. 2014). Indeed, a molecular study suggested that the genetic structure of *G. ligustica* is the result of isolation and genetic drift occurred during glaciation (Diadema et al. 2005). A similar pattern is showed by *Moehringia sedoides* (Pers.) Cumino ex Loisel.: in this species, the combination of ecological and historical factors has probably induced the fragmentation and the reduction in size of populations, affecting their genetic diversity (Minuto et al. 2006).

The biogeographic interpretation of disjoint occurrences in the northern Apennines recorded in some species (e.g., *Primula marginata* and *Saxifraga cochlearis* Rchb.) might represent a residue of the ancient extent during the glaciation or the results of long-distance dispersal stochastic events reaching a narrow suitable area. On the contrary, both the lack of morphological distinctiveness and the genetic analysis suggest that the disjoint Corsican populations of *V. argenteria* may have originated by a rare long-distance dispersal of seed by birds rather than by vicariance due to Corsica-Sardinia microplate disjunction (15 Ma). Future studies on this matter are still necessary.

CONSERVATION ISSUES

Endemism and rarity are not interchangeable. Species may be endemic to an area and yet occur at levels of abundance greater than those of other species found here. In accordance with this observation, 47.7% of the endemic and subendemic plants in the MLA have locally abundant populations (Casazza et al. 2005). Naturally rare species, however, with populations not declining but restricted in size or range may be vulnerable to large-scale or unpredictable threats despite their current stable status (Mace et al. 2008). Furthermore, narrow endemic species having geographically restricted distributions have been considered rare at worldwide level (Ferreira and Boldrini 2011).

In MLA, habitat loss as a result of human impacts was mainly confined to lowland areas (Ortu et al. 2003). Even if only few endemic species are localized at low altitude, in the rapidly changing landscape shaped by anthropogenic alterations, it is important to predict species extinction risk as result of habitat loss and reduced genetic connectivity among populations (Gilpin and Soulé 1986). The term “extinction vortex” indicates the positive feedback cycle involving small and/or fragmented isolated populations, generating a loss of genetic diversity (mainly due to inbreeding) and reducing their adaptability, survival and reproduction (Frankham et al. 2010). In front of the high anthropogenic pressure, the lowland endemic species need conservation plans based on deeper genetic knowledge. In particular, this information is critical in determining whether a species requires human-assisted exchange of individuals to prevent inbreeding and loss of genetic diversity (Frankham et al. 2010). Currently, a conservation plan based on genetic knowledge is available only for *Campanula sabatia* De Not. (Nicoletti et al. 2012). This species is considered vulnerable according to the IUCN criteria due to the decline of populations induced by the anthropogenic pressure (Marsili et al. 2010). Another lack in the biodiversity conservation plans concerns the monitoring activities. Most of monitoring activities carried out until now have been aimed to clarify aspects of the species ecology or populations biology but unfortunately have not triggered specific and timely conservation activities (see Diadema et al. 2004a, 2004b, 2007, Minuto et al. 2012).

A recent study predicted that 36–55% of alpine plants species will lose more than 80% of their suitable habitat by 2070–2100 (Engler et al. 2011). According to these predictions of climate change models the SW Alps (including MLA) will face a significant decrease (-41%) in summer precipitation till the end of the 21st century with related impacts on the hydrological cycle and water supply (EEA 2009). Furthermore, species rich areas are more prone to habitat loss. In fact, it has been demonstrated

that the amount of habitat loss is positively related with the pooled endemic species richness and with the richness of endemic vascular plants, snails, and beetles (Dirnböck et al. 2011). The tree line expansion will disproportionately reduce habitats of high-altitude species and will aggravate extinction risks under future climate change (Dirnböck et al. 2011). Most of the endemic species of MLA occur at high altitude. As a consequence, these species might be mainly prone to the effect of climate change and they might be useful indicators of climate change effects. However, whether and which species will be forced upslope in a warmer climate is still debated. In fact, increasing elevation the vegetation is closer to the ground and therefore the decoupling from atmospheric conditions generally increases with increasing elevation (Scherrer and Körner 2010). Furthermore, the complex microtopography of the MLA might decouple climatic conditions in plant species locations from climatic conditions at coarse scale, as supposed during past unfavourable periods (Patsiou et al. 2014).

Plant phenology and plant-insect interactions may also change as a result of climate changes and human activities. Climate change may lead not only to warmer temperatures but also to increased snowpack at high elevations. Snowpack may affect flowering time driving rearrangement in plant communities (Inouye et al. 2002, Keller & Körner 2003). Furthermore, climate changes have the potentiality to act in concert with existing environmental alterations negatively affecting plant-pollinator networks (Phillips et al. 2010). As observed by Minuto et al. (2013) in *Primula allionii*, even if currently there is no evidence of imminent threats, changes in plant-pollinator interactions due to climate change might increase inbreeding, resulting in an increased extinction risk. For these reasons, future study on reproductive biology and plant-insect interaction in endemic species located at high altitude might give useful information to assess their conservation status.

The two main threats recorded in MLA are urbanization and land use change (Noble & Diadema 2011). In particular, urbanization affects mainly the coastal areas and it is probably the greatest threat for endemic species (Noble & Diadema 2011). Unfortunately, the lack of comprehensive integration of ecological, biological and demographic data for the majority of MLA endemisms prevents our capability to perform an actual assessment of conservation status of species. This information is available only for few species mainly threatened by urbanization and landscape fragmentation existing in the coastal areas, as *Acis nicaeensis* (Diadema et al. 2004a).

CONCLUSION

Centres of endemism represent areas of special evolutionary history (Jetz et al. 2004) and have important conservation implications (Mittermeier et al. 2005). The MLA may be considered a hotspot of biogeographic and evolutionary research and they provide excellent settings where to explore mechanisms of evolutionary diversification, since these processes remain poorly understood. Given the various diversification mechanisms hypothesised for MLA, the time is now overdue for applying explicit hypothesis testing to this system, using novel approaches. These approaches offer the opportunity to address some gaps in the study of endemism in this area:

a) The temporal component of the diversification mechanisms. Did diversifications occur mainly during Quaternary glaciation?

b) The role of glaciation. Because of the mild impact of Quaternary glaciation, how have it affected the diversification and the pattern of genetic diversity of species?

c) Modes of speciation. Because of the few studies addressed to understand the mechanism of speciation in this area. Is vicariant speciation the main mechanism of speciation in the MLA as supposed for many endemisms?

In the same time, it is also necessary to better study the causal factors of rarity and narrow range as well as the functional role of endemic species within ecosystems in order to understand if they possess unique traits that might have disproportionate ecosystem-level effects if they went extinct (Mouillot et al. 2013).

Developing effective conservation strategies should rely on improved understanding of the nature of the threat to species, and how it interacts with their ability to confront stress. The rich history of ecological and evolutionary studies, together with relevant climate data and with appropriate evolutionary and ecological theory and modelling, has the potential to transform the way we assess vulnerability of species. More appropriate conservation actions will result from taking into account all these previous aspects.

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