Chapter 10

Endemism in Sardinia

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Abstract

The Tyrrhenian islands are known for their highly relictual fauna and flora and are one of the ten Mediterranean hotspots of plant diversity and endemism. There is little detailed information available on species' biogeography, and new species are still being discovered. This chapter is the first to put together information from several groups of organisms endemic to Sardinia (viz. plants, butterflies, amphibians, lizards, and beetles), with a particular focus on butterflies and amphibians. Reviewing recent literature, we describe distributional patterns and point to centers of endemicity, which we compare with the location and extent of existing protected areas in Sardinia, in order to assess their usefulness in protecting endemic species. Further, we discuss the geological history of the Mediterranean basin and relate geophysical events to molecular-based estimates of species' divergence times to investigate when and how Sardinian endemics came to the island and describe scenarios of speciation that might have resulted from vicariance, dispersion, and human transportation. The divergence time estimates we summarize here support that the cladogenetic events leading to the Sardinian lineages of various taxa have occurred after the separation of the Sardo-Corsican microplate from the continental landmass and after the rotation of the Corso-Sardinian plate. Furthermore, there is evidence that the split of many Sardinian taxa has occurred after the marine regressions (± 5 mya). Areas of high endemism generally coincide with mountainous areas. The main centers of endemism in Sardinia are already included in a network of natural parks but these areas have not yet been officially accepted as protected areas by the Sardinian authorities. Giving them official status would be a step towards safeguarding the unique nature of Sardinia.

Keywords: endemism, diversity, butterflies, amphibians, lizards, beetles, plants, evolution, conservation

Introduction

Numerous examples in recent literature show that endemism has high conservation priority (Munguira 1995; Hurtrez-Boussès 1996; Schnittler & Ludwig 1996; Gruttke *et al.* 1999; Médail & Quézel 1999; Cook & MacDonald 2001; Grill *et al.* 2002). Endemic species are often 'specialists' that depend on particular and often localized resources, making them especially

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vulnerable to changes in climate, land use, or habitat management (Munguira 1995). Consequently, increased human pressure will induce greater losses in endemic species than in more widespread biota (Oberdorff *et al.* 1999). This has resulted in increased interest in detecting areas rich in endemics, which are usually termed biodiversity hotspots (Morrone & Crisci 1995; Martín *et al.* 2000; Myers *et al.* 2000). Countries or regions harboring endemic species carry a particular conservation responsibility, as the disappearance of the species from those areas would mean their global extinction. Contrary to general belief, endemic species and regions of high endemism are poorly known even in western Europe (Deharveng 1996). For butterflies, there have been recent efforts to overcome this lack of knowledge, and areas of high endemism and/or species richness in Europe have been defined and pointed out to policy and decision makers as 'Prime Butterfly Areas' (Balletto *et al.* 2003). In the Mediterranean basin, efforts to identify centers of endemicity and species richness revealed that it is one of the world's most important regions of plant diversity, harboring an astounding 20% of the world's total floristic richness in only 2% of the earth's surface (Médail & Quézel 1997, 1999; Médail & Verlaque 1997; Verlaque *et al.* 1997). These studies clearly underline the importance of the Mediterranean region in global conservation.

But the importance of areas of high endemicity goes beyond the straight forward aims of conservation biology. Species with restricted distributions and taxa representing unique lineages within a species flock can be interesting model organisms to investigate the processes of differentiation, speciation, and coevolution, and often provide the key for answers to broader scale biogeographic questions. The study of islands where many endemic species or subspecies evolved has provided fundamental insights into the relationships between geographical patterns and biological processes for famous evolutionary biologists like Darwin, Wallace, Mayr, and Wilson (Drake *et al.* 2002 and references therein).

Islands often hold a large proportion of endemic species (Gómez-Campo 1985; Hurtrez-Boussès 1996; Whittaker 1997). Indeed, the Macaronesian (Madeira and the Canary Islands; see Vargas, this volume) and the Tyrrhenian islands (Balearic Islands, Corsica, and Sardinia) are among the most important hotspots of endemism within Europe (Médail & Quézel 1999). Notably, the Tyrrhenian islands together with the Maritime-Ligurian Alps are known for their high relictual endemism (Médail & Quézel 1999). Island endemics are the most vulnerable of all endemic taxa, as 1) islands are unlikely to offer refuges during ecological change, and 2) island populations are usually limited in size. Generally, all endemic taxa are potentially threatened by hybridization, competition, predation or disease when interacting with introduced taxa. An island is mostly referred to as a stretch of land surrounded by a mass of water isolating it from other land areas. By widening this definition to include areas isolated by habitat unsuitable for the taxon under consideration (Hudson 1998), analogies can be drawn for land patches or refuges that have become isolated through Quaternary Ice-age events, causing populations to differentiate in allopatry. Pleistocene glaciations probably induced insular speciation *sensu lato*. Hence, real islands like the Mediterranean island of Sardinia, provide 'laboratories' *in natura* for the study of evolutionary questions (Caccone *et al.* 1994; Salomon 2001).

Objectives

Endemic species in Europe have received little comprehensive study (Médail & Quézel 1999), and this is especially true for those found in Sardinia. There is little detailed information on the distribution and biogeography of Sardinian endemics, and new species are still being discovered (Rota 1992; Gentili *et al.* 1998; Sabella *et al.* 1998; Selvi 1998; Mossa *et al.* 1999; Bacchetta *et al.* 2000). Here we review published data from several groups of plants, butterflies, amphibians, lizards and beetles, endemic to Sardinia in order to define centers of endemicity and see if these overlap with the existing protected areas in Sardinia. As butterflies and amphibians are the focus of our own research we particularly concentrate on them. Furthermore, we explore the factors that may have promoted Sardinian species to diverge from their continental ancestors or sister species.

1. Distributional patterns of endemic species

The Tyrrhenian islands belong to the ten Mediterranean hotspots of plant diversity and endemism defined by Médail & Quézel (1997), where plant richness is >2000 species per 15 000 km^2 and at least 10% of the species are narrow endemics. This high richness is primarily due to paleogeographical and historical factors (Verlaque *et al.* 1997). In the following section we give some examples of distributional and ecological patterns of endemicity in Sardinia (summarized in Table 1) and indicate the main centers of endemism on the island. When we speak of endemics, we consider two different groups: species exclusively endemic to Sardinia and species endemic to Sardinia and Corsica or additional Tyrrhenian islands.

Plants

Echium anchusoides (Boraginaceae) was only recently described (Bacchetta *et al.* 2000) and is endemic to the main siliceous massifs of Sardinia, situated in the mountainous zones of the island. The same is true for the Sardinian oak *Quercus ichnusa* (Fagaceae) (Mossa *et al.* 1999), the Sardo-Corsican thyme, *Thymus herba-barona* (Lamiaceae), the shrub *Santolina insularis* (Compositae), and the perennials *Glechoma sardoa*, and *Lamium corsicum* (Lamiaceae). *Glechoma sardoa* and *L. corsicum* are both endemic to Sardinia and Corsica (Brotzu 1998). In contrast, the Sardo-Corsican endemic plants *Vinca sardoa* (Apocynaceae) and *Ornithogalum biflorum* (Hyacinthaceae) can be found at all altitudes in a variety of habitats, including road margins and the edges of cultivated fields (Brotzu 1998; Sacchetti *et al.* 1999). The perennial herb *Anchusa crispa* (Boraginaceae) occurs in open herbaceous vegetation on low-lying sand dunes (Quilini *et al.* 2001).

Butterflies

Endemic Lepidoptera are usually found at altitudes above 500 meters (Cobolli *et al.* 1995; Biermann 1998; Kleinekuhle 1999). Only three of the 14 Sardo-Corsican endemics are observed at equal frequencies in coastal (sea level) and mountainous habitats (Kleinekuhle 1999; Grill 2002). One of the 14 species, *Hipparchia aristaeus aristaeus*, which is usually known from mountainous areas, has also been recorded on the coast (Cobolli *et al.* 1995). These coastal localities, however, are not its main distributional center. The distribution areas of Sardinian endemics are often strictly related to the composition of the underlying substrate. *Lysandra coridon gennargenti*, for example, strictly follows the distributional pattern of its host plant, *Hippocrepis comosa* (Fabaceae), which is typically found on calcareous grounds and as a consequence, the butterfly is restricted to calcareous outcrops in the 'Barbagia di Seulo' and the 'Supramonte di Orgosolo' mountains. In Sardinia *H. comosa* is most probably the only food plant used by *L. coridon gennargenti*, as the plants used by the continental European populations of *L. coridon*, viz. *Coronilla* sp. and *Astragalus glaucus* (Fabaceae), do not occur in Sardinia. *Hippocrepis comosa* is rather common on other Tyrrhenian islands and the Mediterranean mainland. Individuals of *H. comosa* on Sardinia, however, are much more delicate than those found on the continent with island populations restricted to mountainous areas whereas on the Italian mainland they are found from 0-2900 m a.s.l. (Pignatti 1982). Recognizing the Sardinian form as a distinct endemic taxon could therefore be appropriate.

The Sardinian blue, *Pseudophilotes barbagiae*, is exclusively dependent on *Thymus herba-barona*, the above mentioned Sardo-Corsican endemic thyme species, which grows between 1000 and 2000 m a.s.l (Pignatti 1982); its distribution is thus restricted to a few slopes in the Barbagiae and the Gennargentu mountains, and Mount Limbara. *L. coridon gennargenti* and *P. barbagiae* are among the rarest butterfly species of Europe (Grill 2002). The Sardinian meadow brown, *Maniola nurag*, has its distributional centers around the three main mountainous areas of the island. The endemic hesperid, *Spialia sertorius therapne* has been observed on the Gennargentu, Limbara, and Sette Fratelli mountains (Cobolli *et al.* 1995).

***Table 1**. Distributional patterns of Sardinian and Sardo-Corsican endemics. The geographic extent of species' distribution is shown as well as the altitudes where they occur. S = Sardinia, C = Corsica, T = other Tyrrhenian islands, GS = Gennargentu-Supramonte Massif, SF = Sette Fratelli, LI = Mount Limbara, WC = West-Central Sardinia, CO = Coastal areas.*

		Region						**Altitude**		
Distribution area		**GS**	**SF**	**LI**	**WC**	**CO**	**other**	**<500 m**	**>500 m**	**>1000 m**
Plants										
Echium anchusoides	S	+							+	
Quercus ichnusa	S	+							+	
Thymus herba-barona	S	+								+
Santolina insularis	S	+							+	
Glechoma sardoa	SC	+							+	
Vinca sardoa	SC						+	+	+	
Ornithogalum biflorum	SC						+	+	+	
Anchusa crispa	SC					+		+		
Lamium corsicum	SC	+						+	+	
Butterflies										
Papilio hospiton	SC	+	+	+			+	+	+	
Aglais urticae ichnusa	SC	+	+	+	+				+	
Argynnis elisa	SC	+		+					+	
Argynnis paphia immaculata	SC	+		+					+	
Euchloe insularis	SC	+	+	+	+	+	+	+	+	
Coenonympha corinna	SC	+	+	+	+	+	+	+	+	
Hipparchia aristaeus aristaeus	SC	+				+		+	+	
Hipparchia neomiris	SC	+				+		+	+	
Maniola nurag	S	+	+	+					+	
Lasiomata megera paramegera	SC	+	+	+	+		+	+	+	
Lysandra coridon gennargenti	S	+							+	
Plebejus idas bellieri	SC	+		+					+	
Pseudophilotes barbagiae	S	+								+
Spialia sertorius therapne	S	+	+	+	+				+	
Lizards										
Podarcis tiliguerta	SC	+	+	+	+	+	+	+	+	
Archeolacerta bedriagae	SC	+		+	+		+	+	+	
Salamanders										
Euproctus platycephalus	S	+	+	+				+	+	
Speleomantes supramontis	S	+							+	+
Speleomantes genei	S	+	+					+	+	+
Speleomantes flavus	S	+							+	+
Frogs										
Hyla sarda	SCT				+		+	+		
Discoglossus sardus	SCT				+		+	+		
Cave beetles										
Ovobathysciola grafittii	S				+		+	+		
Ovobathysciola majori	S	+					+	+		
Ovobathysciola gestroi	S	+							+	
Patriziella sardoa	S	+						+		
Patriziella nuragica	S					+		+		
Speonomus lostiai	S				+					
Mammals										
Apodemus sylvaticus	SCT	+	+	+	+	+		+	+	

Amphibians

The Sardinian mountain newt, *Euproctus platycephalus* (Salamandridae) appears to occur predominantly in the three main mountain ranges: Gennargentu-Supramonte in central Sardinia, Sette Fratelli in the southeast, and Mount Limbara in the north (Lecis & Norris 2003). In this respect it is similar to most endemic butterfly species. The distribution of this endemic newt covers approximately the eastern side of the island, with very few unconfirmed records in the western areas. The genus *Speleomantes* is represented by four species of cave salamanders, which occur in limestone caves and humid rocky substrates: *S. supramontis* in Supramonte, *S. flavus* in Monte Albo, and *S. genei* and *S. imperialis* in the southeast and in the southwest. The Sardinian tree frog *Hyla sarda*, endemic to Corsica, Sardinia, and the Tuscany archipelago, inhabits lowlands and temporary waters all over the island and is locally quite abundant, but probably declining in numbers (Colomo 1999). The Sardinian painted frog, *Discoglossus sardus*, classified as vulnerable, is usually found in stagnant or slow moving waters and is described as widespread (Colomo 1999). Its distribution area covers Corsica and Proquerolles, Port Cros, and the French Hyères archipelago.

Lizards

Archaeolacerta bedriagae (Lacertidae), the Bedriaga's rock lizard, a Sardo-Corsican endemic, seems to occur in areas of Limbara, Marghine, Monte Albo, and Gennargentu, generally in the north and center of Sardinia (Colomo 1999). The insular endemic lacertid lizards, *Algyroides fitzingeri* and *Podarcis tiliguerta*, are described as widespread and common at different altitudes, from sea level to the mountains in both Corsica and Sardinia (Delaugerre & Cheylan 1992; Arnold 2003). Two subspecies, *Podarcis tiliguerta ranzii* and *Podarcis tiliguerta toro*, are both restricted to one little circum-Sardinian island in the north (Molarotto near Olbia) and in the southwest (Toro near Sant'Antioco).

Beetles

The two Sardinian genera of obligate cave-dwelling beetles, *Ovobathysciola* and *Patriziella*, are obviously dependent on cave environments (Caccone & Sbordoni 2001). Recent observations indicate that *Ovobathysciola majori* and *Patriziella sardoa* inhabit numerous caves from sea level to 1000 m elevation in the karst areas of the Supramonte massif (northeast Sardinia) whereas *Ovobathysciola gestroi* is found in the Gennargentu massif. *Ovobathysciola graffitii* and *Patriziella nuragica* have only been found in northwestern Sardinia, near Sassari. *Speonomus lostiai* inhabits a few caves in west-central Sardinia (Caccone & Sbordoni 2001).

2. Speciation molecular divergence, and geological history

Insular speciation usually results from the differentiation between populations settled on an island, and the continental population from which they were isolated (Jacquard 1974; Hudson 1998; Salomon 2001). Diamond (1977) describes three successive stages that can be considered as prerequisites for insular speciation: colonization, settlement, and genetic divergence. Speciation as a consequence of geographical isolation is termed allopatric or geographical speciation. Sympatric speciation results from isolating mechanisms without the involvement of a physical barrier to gene flow. Parapatric speciation takes place when two divergent species have disjunct geographical distributions but there is a contact zone between them, where gene flow is possible.

Estimates of separation times can vary greatly among different genes, and even portions of one particular gene. There is, however, a general consensus that if rates are compared between closely related species for the same DNA region, sequences are very likely to display a clock-like behavior (Caccone & Sbordoni 2001). The existence of well-dated geological events, as is the case for the islands in this study, is a great advantage when trying to calibrate molecular rates in species whose distributions have probably been shaped as a result of these events.

The geological and geophysical history

The geological evolution of the Mediterranean region is characterized by the relatively rapid opening of several back-arc basins, generally floored by oceanic crust, within the framework of the Africa-Eurasia collision and Alpine orogenesis (Speranza *et al.* 2002; Blondel & Aronson 1999 and references therein). In the western Mediterranean, the Liguro-Provencal basin, a triangular sea located between the Provencal-Catalan coasts and the Corsica-Sardinia block, opened during the Oligo-Miocene. Basin spreading and the simultaneous eastward migration of the Alpine belt and Corsica-Sardinia-Calabria blocks were probably driven by the eastward retreat of a Ionian/Adriatic slab passively sinking into the mantle (Malinverno & Ryan 1986). Since the middle-late Miocene, further roll-back of the same slab caused spreading of the Tyrrhenian Sea, the southeastward drift of the Calabrian block, and the orogenesis of the Apennines. The Liguro-Provencal spreading took place simultaneously with the eastward drift of the Corsica-Sardinia block, which rotated at least 30º counterclockwise (e.g. Van der Voo 1993, Speranza *et al.* 2002 and references therein). Paleomagnetic investigations carried out in the 1970's on Oligo-Miocene volcanics of Sardinia suggested that the island was separated from the continental landmass about 33 mya, turned by 35° clockwise up to 21-20.5 mya, and then rotated 30° counterclockwise in a few million years (De Jong *et al.* 1969, 1973; Edel 1979, 1980). Since then, the end of the rotation, fixed at 19 myr by Montigny *et al.* (1981) has been subject to controversy (Edel *et al.* 2001; Speranza *et al.* 2002 and references therein). New paleomagnetic and Ar/Ar results support a begin of the rotation around 21-20.5 mya and an end of the rotation at 18-17.5 mya (Deino *et al.* 2001; Edel *et al.* 2001). But there is growing evidence that the rotation did not end before 16 mya and started after 19 mya (Speranza *et al.* 2002). The question of coupling or decoupling between Corsica and Sardinia during drifting was resolved by Vigliotti *et al.* (1990), who showed that after the Permian the two islands rotated as one block. During a period from 18.3 to17.5 mya the marine transgression occurred (Edel *et al.* 2001). At the same time a NE-SW shortening, interpreted as resulting from the collision of the Sardo-Corsican block with Apulia, affected parts of the island. Speranza *et al.* (2002) propose that at 16-19 mya, the lithosphere of a 'paleo-Ionian' oceanic corridor east of Sardinia sunk in the mantle causing a trench retreat and the Liguro-Provencal spreading. Faster subduction beneath Sardinia than beneath Corsica, due to the heterogeneous nature of the subducting plate, has been put forward as a plausible reason to explain the triangular geometry of the Liguro-Provencal basin and the counterclockwise rotation of Sardo-Corsica. About five million years ago, the Mediterranean Sea was almost entirely desiccated, creating connections of dry land between Sardinia and northern Italy and southern France. Sea level oscillations creating land bridges between Sardinia and Corsica continued from Miocene until well into the Pleistocene (5.7 – 0.23 mya) (Arias *et al.* 1980). In the Quaternary, Sardinia could have been in contact with the mainland via Elba as the sea level was up to 120 meters lower than today. During the last glacial maximum, 20 000 years ago, Sardinia was connected with Corsica.

Lizards and amphibians

Lanza (1983) hypothesized that the split among the Sardinian lizards, *Algyroides fitzingeri*, *Archaeolacerta bedriagae*, and *Podarcis tiliguerta* from mainland relatives is related to Premiocenic or Messinian age, while *P. sicula cettii*, could have diverged during the Pleistocene (Lanza 1983). Oliviero (1998) gives preliminary estimates of divergence times based on DNA sequences for *P. tiliguerta* (13 mya) and *P. sicula cetti* (7 mya), suggesting a Messinian age for both species. Ancient taxa such as *Euproctus platycephalus* and *Speleomantes genei* probably originated from ancestors already present on the Sardo-Corsican microplate prior to its detachment from the continent (Lanza 1983). Other ancient taxa such as three of the four Sardinian *Speleomantes* (*S. flavus*, *S. imperialis*, *S. supramontis*) are more closely related to the continental *Speleomantes ambrosii* (Lanza 1983, 1995), indicating that the ancestor of those three species arrived in Sardinia about 5 mya from the Apennines. Jackmann *et al.* (1997), however, infer a close relationship of *S.*

flavus, *S. supramontis*, and *S. genei*, whereas the continental *S. italicus* would be less closely related, and give evidence for a monophyletic origin of the Sardinian *Speleomantes* group.

Caccone and coworkers (1994, 1997) used the split between the Pyrenees and the Corso-Sardinian plate, and the separation of Corsica from Sardinia to calibrate mtDNA (12S and 16S ribosomal RNA and cytochrome *b*) evolutionary rates in newts of the genus *Euproctus*, which comprises three species (with distributions restricted to Corsica, Sardinia, and the Pyrenees). These genetic investigations confirmed records of morphological, anatomical and karyological studies (Bucci-Innocenti *et al*. 1978; Delaguerre & Cheylan 1992): Corsican and Sardinian newts are more closely related to each other than to the Pyrenean newt (Table 2 & 3). This is a sound consequence of a previous speciation event, dated around 29 mya, while the two insular species probably started diverging in Sardinia between 9 and 15 mya (Caccone *et al*. 1994) (Figure 1).

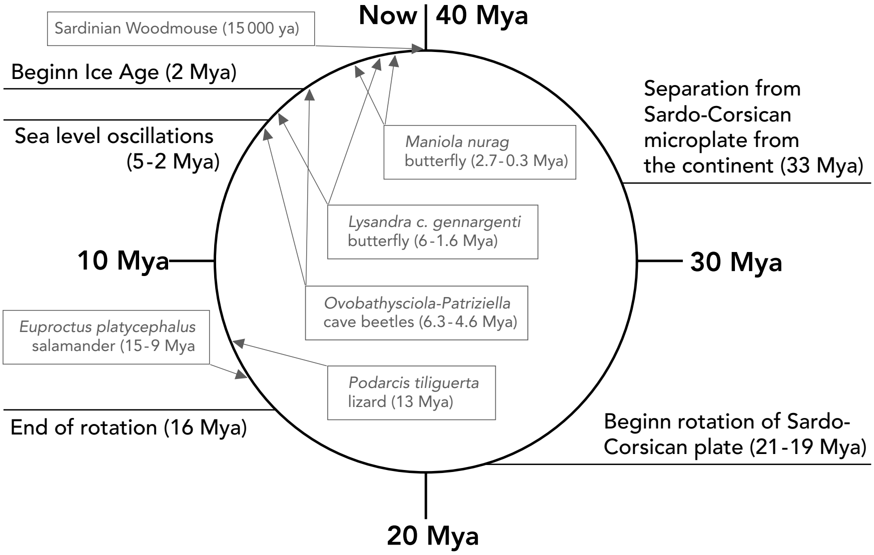

Figure 1*. Time scales of geophysical events in relation to speciation time estimates inferred from molecular data.*

Butterflies and beetles

Recently, Caccone & Sbordoni (2001) used COI divergence rates to estimate the time of isolation of cave beetles of the genera *Ovobathysciola*, *Patriziella*, and *Speonomus*. They estimated divergence times of 16-10 myr among the three *Ovobathysciola* species (*O. grafittii*, *O. majori*, *O. gestroi*), 6.3-4.6 myr for the split between *O. grafittii* and the two *Patriziella* species, and 4.5 to 3.7 myr for the split between *P. sardoa* and *P. nuragica*, all endemic to Sardinia (Table 2 & 3). The species assemblage of cave-dwelling beetles in Sardinia might be explained as the result of vicariance (Caccone & Sbordoni 2001). This assemblage probably began its diversification in a first step due to the separation of Sardinia from the continental landmass, and in a second step after the dramatic changes brought about by sea level oscillations (up to 1000 meters) in the middle and late Miocene (16-5 mya), which separated northern Sardinia from central and southern Sardinia (Steininger & Rögl 1984). These changes might have enhanced the isolation of the ancestral forest-dwelling populations of cave beetles, which then retreated to the wet habitats in the karstic caves of Sardinia. Also the climate changes in the Pliocene (5-2 mya), when the climate switched to cooler and drier conditions, forcing warm and humid subtropical forests to gradually change into a savanna-like vegetation (LaGreca 1998), could have forced some populations into the humid environment of caves where they became isolated from their ancestral forest dwelling populations (Caccone & Sbordoni 2001).

In Lepidoptera, the first expansion events vigorously influencing the European fauna occurred in the Pliocene, when Near Eastern and Balkan species started to invade Europe (10-1 mya. Before the Pliocene, the European fauna was predominantly tropical (Leestmanns 1965; Kleinekuhle 1999). The migration route probably went from central Asia, to the Near East, and Greece, which at this point was still connected to Africa, and from there via Sardinia and Corsica to Tuscany (Leestmanns 1965; Kleinekuhle 1999). During the last glacial maximum, Sardinia was much less affected than Corsica, so that thermophilic species survived in Sardinia, while cold-adapted species could persist in Corsica (Kleinekuhle 1999). This might have enhanced differentiation of a number of endemic species, which during the postglacial warming retreated to higher altitudes. Similarly, it has been suggested that the endemic taxa of the genus *Erebia* in the Alpine region and Scandinavia have arisen due to differentiation within glacial refugia (Roos & Arnscheid 1979; Kleinekuhle 1999). Sardinian examples of endemics, which most likely evolved as a result of Ice-age events are *Aglais urticae ichnusa* (Nymphalidae) and *Hipparchia aristaeus aristaeus* (Satyridae), both endemic to Sardo-Corsica, and related to *Aglais urtica* and *Hipparchia semele* (Satyridae) (Kleinekuhle1999). The latter two species are long-distance dispersers, but probably orientate their routes on determined features of the landscape and appear to be reluctant to cross large sea areas, explaining why they never reinvaded Sardinia or Corsica. Other Sardinian species most probably originate from central Asia. According to Leestmanns (1965), *Argynnis elisa* (Nymphalidae), *Hipparchia neomiris*, *Coenonympha corinna* (Satyridae), and *Papilio hospiton* (Nymphalidae) originated from the Asiatic species *Argynnis clara*, *Hipparchia digna*, Asiatic taxa of the genus

Coenonympha and *Papilio sikimensis* respectively. More recent studies however, conclude a closer relationship between *Papilio machaon saharae* and *Papilio hospiton* (Pierron 1990, 1992).

Table 2. *Examples of species pairs: genetic differences between closely related species/subspecies based on allozyme markers and mtDNA.*

Species	***Podarcis muralis*** **(Italian mainland)**	***Lysandra coridon appenina*** **(Central Italy)**	***Lysandra coridon caelestissima*** **(Central Spain)**	***Maniola jurtina*** **(Austria, France, Spain)**	***Ovobathysciola grafittii*** **(Sardinia)**	***Anillochlamys bueni*** **(Pyrenees, Spain)**	***Speonomus delarouzei*** **(Pyrenees, Spain)**	***Speonomus bruckii*** **(Pyrenees, Spain)**	***Speonomus hygrophilus*** **(Pyrenees, Spain)**	***Apodemus sylvaticus*** **(France)**	***Apodemus sylvaticus*** **(Belgium)**
Lizards											
Podarcis tiliguerta (Sardinia, Corsica) Capula 1996	0.181-0.318*										
Butterflies											
Lysandra coridon gennargenti (Sardinia) Marchi *et al.* 1996		0.434*	0.337*								
Maniola nurag (Sardinia) Grill *et al.* in prep.				0.065-0.089*							
Cave beetles											
Ovobathysciola grafittii (Sardinia)						0.828**					
Ovobathysciola majori (Sardinia)					0.327**	0.617**					
Ovobathysciola gestroi (Sardinia)					0.390**	0.597**					
Patriziella sardoa (Sardinia)					0.146**	0.655**					
Patriziella nuragica (Sardinia)					0.160**	0.755**					
Speonomus lostiai Caccone & Sbordoni 2001							0.772**	0.710**	0.860**		
Woodmouse											
Apodemus sylvaticus (Sardinia) Michaux *et al.* 1996										0.001-0.002*	0.003-0.007*

* Nei's genetic distances based on allozyme markers.
** Based on mtDNA.

Table 3*. Divergence time estimates of closely related species in millions of years (myr) or years (y).*

Species	***Podarcis* spp. (continental mainland)**	***Euproctus montanus* (Corsica)**	***Lysandra coridon appenina* (Italy)**	***Lysandra coridon caelestissima* (Spain)**	***Maniola jurtina* (Austria, France, Spain)**	***Ovobathysciola grafittii* (Sardinia)**	***Patriziella sardoa* (Sardinia)**	***Apodemus sylvaticus* (France, Belgium)**
Lizards								
Podarcis tiliguerta (Sardinia, Corsica)	13 myr							
Podarcis sicula settii (Sardinia)	7 myr							
Salamanders								
Euproctus platycephalus		9 -15 myr						
Butterflies								
Lysandra coridon gennargenti (Sardinia)			6 -1.6 myr	6 -1.6 myr				
Maniola nurag (Sardinia)					2.7 - 0.3 myr			
Cave beetles								
Ovobathysciola majori (Sardinia)						16 -10 myr		
Ovobathysciola gestroi (Sardinia)						6.3 - 4.6 myr		
Patriziella nuragica (Sardinia)							4.5 - 3.7 myr	
Woodmouse								
Apodemus sylvaticus (Sardinia)								15 000 y

For the Sardinian Blue butterfly, *Lysandra coridon gennargenti*, there is genetic and morphological evidence that it is specifically different from the continental *Lysandra coridon* (Marchi *et al.* 1996; Jutzeler *et al.* 2003). Marchi *et al.* (1996) suggest an allopatric speciation event. They found evidence for an absence of gene flow with the continental populations, indicated by the presence of alternative fixed alleles at several enzymatic loci (*Aat*, *Gpi* and *Pgm*) and significant differences in allele frequencies at other loci, distinguishing the Sardinian population from *L. c. apennina* and *L. caelestissima*. The genetic differentiation of *L. c. gennargenti*, measured using Wright's F_{ST}-

values (0.129-0.923) and Nei's genetic distances (0.337-0.434) indicate that the Sardinian populations evolved as an independent lineage, facilitated by isolation and the strict dependence of the butterflies on specific biotopes. Marchi *et al.* (1996) also found a reduction of genetic variation (Polymorphism = 17.6 %, Heterozygosity = 0.024) with respect to the continental populations (P > 52 %, H greater than or equal to 0.170). Values of Nei's genetic distances (Table 2) between the Sardinian subspecies and the populations of continental Italy, are higher than those found between geographically isolated populations of *L. coridon* from continental Italy, and comparable to or even higher than distance levels found between other endemic taxa that are considered separate species. Our own data on genetic differentiation between *Maniola jurtina* and *Maniola nurag* based on allozyme markers (Grill *et al.*, unpublished work), for example, shows smaller genetic distances (0.065-0.089) although these two butterflies are considered to be different species (Table 2). This suggests that they probably diverged in more recent times than *L. c. gennargenti.* Based on sequence data from two regions of the mtDNA (cytochrome oxidase subunit I and cytochrome *b*) and the assumption of a mutation rate of 1.1% to 1.2%/myr in arthropod mtDNA (Brower 1994; Gaunt & Miles 2002), which translates to about 2.3% sequence divergence/myr, divergence time between *M. nurag* and *M. jurtina* was estimated to be 1.1 to 1.2 myr (Grill *et al.,* unpublished work). However, these numbers are only indicative of the degree of differentiation, and there is no general rule for the relationship between genetic distance and taxonomic status (Menken & Ulenberg 1987; Orr 2001).

Maniola nurag as an example for ecologically induced speciation?

Maniola jurtina, the meadow brown butterfly, has been shown to be closely related to *M. nurag* in allozyme-genetic analyses (Thomson, 1987; Grill *et al.*, unpublished data). The two species are phenotypically similar but nevertheless can usually be distinguished by their wing patterns. However, there is some overlap for individuals flying late in the season, and in exceptional cases, genital preparation might be the only way for determination. Both species fly in Sardinia but have only minor overlap in distribution area and flight period. *M. nurag* emerges a couple of weeks after *M. jurtina*, and has only been found above 500 m a.s.l. whereas *M. jurtina* is most abundant at sea level but can occasionally be observed up to 1000 m a.s.l. (Grill 2001). Adults of *M. nurag* are on the wing from May to September depending on altitude and local weather conditions, *M. jurtina* flies in Sardinia from late April to June. At lower altitudes *nurag* females aestivate during the hottest part of the summer (Tolman & Lewington 1997; Kleinekuhle 1999; Grill 2001). A similar aestivation behavior has been observed in southern populations of the pan-European species *M. jurtina* (Scali & Masetti 1973). *M. nurag* is probably better adapted to the particular conditions in the Sardinian mountains, with extremely dry and hot conditions during Mediterranean summers, and large temperature oscillations between day and night. Body size is smaller than in *M. jurtina*, the body is more compact and darker, and the upper side of both fore- and hindwings are brighter in the endemic species (Grill *et al.* 2004). UV-photographs of wing patterns do not reveal any differences between the two species. In both, the eyespot pupil is bright and visible, as generally observed in satyrids (S. Bryant, pers. comm.). Differentiation between the two species could be related to larval food-plant choice. The larvae of *M. jurtina* feed on a wide range of grass species including *Poa pratensis*, *Festuca rubra*, *F. arundinacea*, *Agrostis stolonifera*, *A. canina*, *Bromus erectus*, *Brachypodium pinnatum*, *Holcus lanatus*, *Avenula pubescens*, and *Anthoxanthum odoratum* (Tolman & Lewington 1997). The island endemic is probably more specialized in its diet, perhaps feeding on grasses that flower relatively late in spring, thus offering oviposition sites that are still green when most other vegetation is already dry.

Ecological and evolutionary isolation in *Euproctus platycephalus*

The three species in the genus *Euproctus*, *E. platycephalus* (Sardinia), *E. asper* (Pyrenees), and *E. montanus* (Corsica) share various morphological, reproductive, and ecological traits, such as the presence of a sixth toe on the male hind legs, the mating behavior (males actively search for females and hold them, curving body and tail in order to manipulate their spermatophores into the female cloaca in an almost real amplexus), and the typical habitat (although the Sardinian *E. platycephalus* seems to occur at lower altitudes than the other two). All three species live in streams, springs, pools or small lakes in mountainous areas. However, the Pyrenean, Corsican and Sardinian mountain ranges differ in geology and climate, so that apparently similar sites might actually be very different as a result of differing environmental conditions. Pyrenean and Corsican mountains are on average higher than Sardinian ridges, and a large part of the area is still covered by *Pinus* and *Quercus* forests. In Sardinia, centuries of deforestation, stock breeding, and fires have gradually changed landscape and microclimate, especially in the center and south of the island (mountains of Gennargentu and Sette Fratelli), where the largest part of the land is currently covered by Mediterranean '*macchia*'. In the Gennargentu mountain system, typical landscape consists of bare or bushy slopes with *Alnus glutinosa* creating gallery forests along water courses. Lecis & Norris (2004b) found evidence for a lack of gene flow between the *E. platycephalus* populations from the three Sardinian mountain ranges, Limbara, Gennargentu, and Sette Fratelli, although the same mtDNA clades are present in all of them.

Mammals

Sadly enough, in Sardinia as well as in Corsica most indigenous land mammals have disappeared. Human activities brought about the extinction of most of the autochthonous mammalian fauna and the gradual introduction of more than 25 taxa, which form the present wild and domestic fauna. Such a complete turnover has also been recorded on other Mediterranean islands. These extinctions include *Prolagus sardus* (Lagomorpha, Leporidae), known from subfossil remains found on Corsica, Sardinia, and adjacent small islands (Vigne 1992). *Prolagus* could possibly have reached Sardinia during the desiccation of the Mediterranean during the Miocene (Schüle 1993). Its origin seems to be in Mongolia from where its ancestors reached Corsica and then Sardinia. Skeletal remains indicate that *Prolagus* was still present on Corsica and Sardinia less than 2000 years ago (Vigne 1992). The final report of a living population was made in 1774 by F. Cetti, who observed, *"giant rats whose burrows are so abundant that one might think the surface of the soil had been recently turned over by pigs"* on the island of Tavolara of northeastern Sardinia. It probably attained a length of 200-250 mm but must have undergone rapid evolutionary changes following the arrival of humans on Corsica and Sardinia about 9000 years ago (Vigne 1992). These modifications include an increase in the size of the skull but a reduction of the post cranial skeleton. In Neolithic times *Prolagus* was an important part of human diet in Sardinia, testified by the great amount of skeletons found in human-inhabited caves, like the Grotta di Corbeddu near Oliena. While it apparently survived longer than other extinct, mice-like, insectivorous mammals of the Mediterranean islands (*Nesiotites*, *Tyrrhenicola*, *Rhagamys*), its final extinction seems to have been caused by human predation. Another species that probably became extinct due to human influence is the giant deer *Megaceros*. All extant wild ungulates on the Mediterranean islands are feral domestic animals, or continental game introduced during the Neolithic or later, and none of them have Pleistocene ancestors (Schüle 1993).

The largest mammal on the island is *Cervus elaphus corsicanus*, the Sardinian form of the European deer. It is smaller, darker and more delicately built than continental deer and restricted to three main regions, *viz.* Capoterra, Sette Fratelli forest, and the World Wildlife Fund park of Monte Arcosu. The Sardinian deer is protected by regional legislation and is a target species in the Italian Natura 2000 network. Most of the other mammals presently living on the island have been introduced by man, albeit perhaps hundreds of years ago (Blondel & Vigne 1994; Michaux *et al.* 1996). The Tyrrhenian form of the wood mouse, *Apodemus sylvaticus milleri*, also has an anthropogenic origin. Allozyme data suggest that all the Tyrrhenian wood mice and those of peninsular Italy have a common origin but differ from the northwestern subspecies, *A. sylvaticus sylvaticus*. The Tyrrhenian mice are well isolated from those living on the western edge of the Alpine chain, including the eastern

Pyrenean beech forest. They invaded the islands via the route of Etruria to Elba and Corsica. This hypothesis is in agreement with archaeological evidence of relations between island and mainland populations of Neolithic humans (Klein Hoffmeiyer *et al.* 1986; Michaux *et al.* 1996). According to this theory, wood mice would have colonized the islands as 'lifters' on human boats. The island-specific alleles of Corsican and Elban *Apodemus* are completely absent in Sardinian mice. This indicates that Sardinia was invaded directly from Italy without the detour across Elba and Corsica (Michaux *et al.* 1996).

3. Reflections on conservation issues in butterflies and salamanders

Island species and particularly endemics, are intrinsically more vulnerable to extinction than more widespread species. Habitat destruction, and/or competition with newly introduced species may have severe effects on islands biodiversity. Low genetic variability, resulting from inbreeding or genetic drift has often been reported to decrease species' fitness, and consequently make them more vulnerable (Keller *et al.* 2002). Hybridization and consequent genetic assimilation might be additional threats.

A well known example where natural hybridization is frequent are the butterflies *Papilio machaon* and *Papilio hospiton* (Aubert *et al.* 1996, 1997). Laboratory crosses show that hybrids are not sterile. However, genetic assimilation does not seem to be a threat for *P. hospiton* as developmental perturbations impair the viability of further hybrid progenies.

A recent assessment of endemic Sardinian butterflies suggests that the lycaenids, *Pseudophilotes barbagiae* and *Lysandra coridon gennargenti*, are the only two butterfly species classified as 'vulnerable' according to the IUCN threat categories (Grill *et al.* 2002). However, the two more conspicuous but probably less threatened species *Papilio hospiton* and *Argynnis elisa*, are listed in Appendix II of the Bern Convention, which, since 1988 legislates for the protection of invertebrates at a European level. *Papilio hospiton* is also listed in Annex II of the European Habitats Directive (Council Directive 92/43/EEC).

Maniola nurag could become vulnerable as a result of its complicated life-history. Oviposition only takes place after a female diapause during the hottest part of the summer. Female butterflies need large amounts of nectar before laying their eggs, so the timing of oviposition is probably related to the availability of thistles as high quality nectar resources (D. Jutzeler, pers. comm.). As a consequence, female survival over the summer diapause is a crucial factor for the viability of *M. nurag* populations. This particular ecological characteristic makes the species very susceptible to human-induced changes of their habitat (as shown for *M. jurtina*) (Scali 1971) and might become a particular concern if the climate warms. Under a warmer climate scenario, imagos would emerge earlier in spring but resume activity later in autumn. The consequence would be a prolonged aestivation phase that would increase the risk of female death before oviposition. Another effect could be that with increasing temperature, individuals from intermediate altitudes move higher up the mountain slopes. But due to the island situation these areas would only serve as a limited refuge. Although *M. jurtina* performs the same female diapause in its southern European populations, this species is much less vulnerable than *M. nurag* on a global scale. First, *M. jurtina* is much more widespread and abundant, and second, it does not aestivate in the northern part of its range (Scali 1971; Tolman & Lewington 1997).

As for amphibians, the Sardinian newt is the only species in the genus *Euproctus* for which there is high conservation concern: it is classified by the IUCN as a critically endangered species due to deterioration of its freshwater stream habitat (IUCN 2000). Recent studies have pointed out a contraction in the mountainous range inhabited by the species, as newt populations are no longer present in some localities that some years ago were still occupied (Lecis & Norris 2003). *E. platycephalus* is fully aquatic, and consequently the severe droughts in Sardinia during the last decade caused a strong decline of populations and numbers of individuals. Other threats to this endemic urodele might be the introduction of brown trout, *Salmo trutta* , illegal fishing methods, water pollution and other anthropogenic disturbances (Lecis & Norris 2004a). Long term detailed field surveys would be required to investigate the actual extent of population decline. In the genus *Speleomantes*, all four Sardinian species are rare, *S. flavus* is classified as vulnerable, *S. flavus*, *S. genei*, *S. imperialis*, *S. supramontis*, are considered to be at a lower risk.

4. Conclusions and perspectives

Although this overview is far from being complete, we think it points to some general distributional and ecological patterns of Sardinian endemics and how they have evolved. Divergence time estimates from various sources suggest that the cladogenetic splits leading to the Sardinian lineages have occurred well after the separation of the Sardo-Corsican plate from the continent. Many taxa seem to be younger than the marine regressions in Miocene (5 mya), and may even have arisen during the severe climatic changes of the latest Ice Age (Figure 2).

In Sardinia, areas of high endemism generally coincide with mountains (Table 1, Figure 2). For butterflies, areas of maximum endemism also coincide with areas of maximum species richness (Biermann 1998; Kleinekuhle

1999). This is probably due to the high proportion of endemics among the entire biotic community of Sardinia (25% for butterflies) (Kleinekuhle 1999). Butterfly species richness reaches a maximum in the Gennargentu massive and decreases from east to west and towards the lowlands, and reaches its minimum at the coast. The patterns of endemicity in Sardinia seem to be in agreement with what has been shown for the Iberian Peninsula (Martín *et al.* 2000) and the general European pattern (Balletto 1995). But as indicated in those studies, it is expected that each taxonomic group follows a different pattern related to its individual ecological characteristics or dispersal ability. As yet, estimates of total numbers of species endemic to Sardinia are only available for a few taxonomic groups. Consequently, these last conclusions remain preliminary, and it might as well be that Sardinian mountain massifs generally have higher species richness and endemic species just follow this pattern.

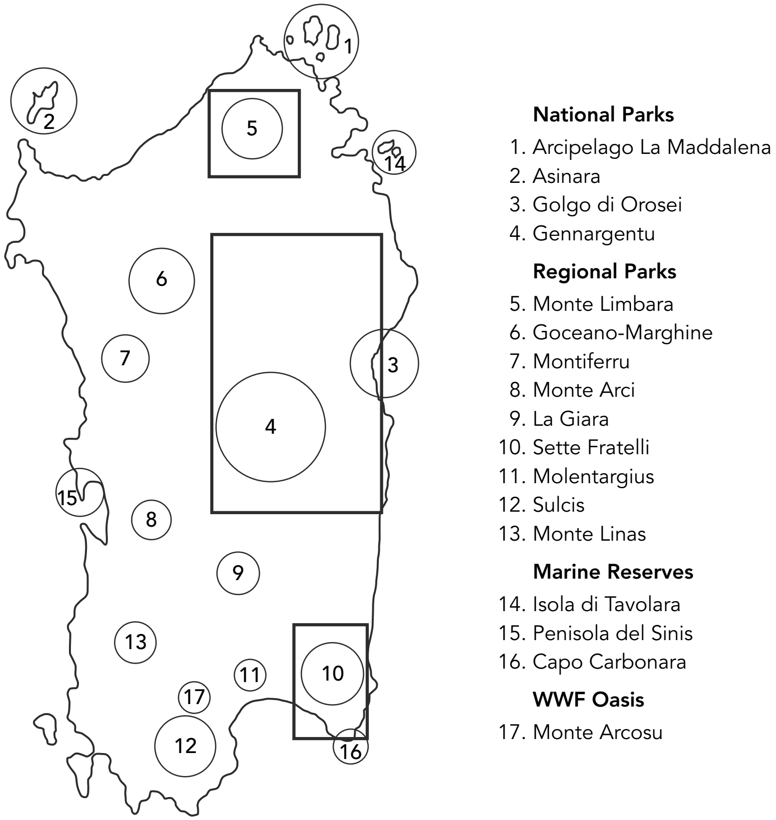

Figure 2*. Existing network of protected areas in Sardinia. Centers of endemicity are indicated with rectangles.*

Considering that most developmental efforts of the tourism industry take place in coastal areas, the concentration of endemic species at higher altitudes might help protect them from the negative effects of increased human pressure. Nevertheless, giving those areas extra protection status is surely not superfluous. There are several protected areas in Sardinia (such as national and regional parks, WWF Oasis, marine reserves, and sites designated as 'Relevant Natural Areas'), however, many political and economical problems need to be resolved before the protection of these areas can be implemented. Given the high number of endemic species in Sardinia, it is necessary that designated reserves and parks do not only exist on paper but conservation and management of the island's unique habitats and species are implemented in practice. This requires increasing the awareness of local people, promotion of field surveys and publication of updated atlases.

Three main centers of endemism, namely the Limbara, Gennargentu, and Sette Fratelli mountains are already included in a network of natural parks that have been proposed to become protected areas but have not yet been officially accepted as such by the Sardinian authorities (Figure 2). Giving them equal status as the already established marine reserves in Villasimius, Asinara, and the Maddalena islands would be a further step to safeguard the unique nature of Sardinia.

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