

Modern taxonomic and biogeographic approaches to biodiversity in the Mediterranean area

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ABSTRACT

I review here examples of recent progress in the taxonomy and biogeography of Mediterranean taxa. Morphological approaches have still much to offer, as shown by a study of the Sicilian species of the wingless weevil genus *Pseudomeira* Stierlin, 1881 (Coleoptera Curculionidae). A systematic analysis of molecular markers, however, is revealing a huge number of previously unsuspected cryptic species, as in the scarab genus *Pachypus* Dejean, 1821 (Coleoptera Pachypodidae). Other molecular studies have revealed very deep phylogeographic structure in the Corsican brook salamander; the presence of six or more species hitherto lumped under *Rumina decollata* (Linnaeus, 1758) (Pulmonata Subulinidae), in a snail genus in which biparental and uniparental reproduction coexist; the conservation of the same male pheromone in vicariant species of the scarab beetles of the genus *Osmoderma* Lepeletier et Serville, 1828 (Coleoptera Cetoniidae); the interplay of vicariance and dispersal events in giving rise to the different taxa of the land snail genus *Chilostoma* Fitzinger, 1833 (Gastropoda Helicidae) inhabiting the Greek islands. Further examples of modern biogeographic studies are a morphometric analysis revealing the preferential localization of steep slopes of phenetic diversity of seven butterfly species groups in the Tuscan archipelago and across the Strait of Messina; a research on tenebrionid beetles showing that present distribution patterns are not completely explained by postglacial recolonization from Pleistocenic refugia; a comparative analysis of the diversity of patterns (explained in part by vicariance, in part by dispersal) in the biota on the two shores of the Strait of Gibraltar. A study on the ocellated lizards provides a nice analysis of climatic niche evolution throughout speciation. Finally, a comparative study of mtDNA from spurge hawkmoths collected between 1884 and 1986 has demonstrated the complete disappearance, within one century, of a lineage from a former area of sympatry with what now appears as its vicariant.

KEY WORDS

dispersal; ecological niche; molecular taxonomy; taxonomic methods; vicariance.

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INTRODUCTION

The terrestrial and freshwater biota of the Mediterranean area have long attracted the attention of zoologists and botanists. Their study has always

been a challenging but eventually rewarding task for the taxonomist confronted with a sometimes explosive fragmentation of isolated populations whose taxonomic rank, either specific or subspecific, continues to trouble us to date, as well as for

the biogeographer looking for an interpretation of present-day distributions in the light of past events, including palaeoclimatic history.

There is plenty of lineages within which ongoing speciation is worth investigation. But there are also persisting traces of palaeogeographic and palaeoecological events, suggesting for example areas of glacial refugium and routes of (re)colonization. There are distribution patterns that would support a vicariance paradigm in biogeography alongside others supporting dispersal instead.

In the last few decades, the study of the Mediterranean biota has been often addressed by means of new research tools, especially those of molecular systematics, but also other approaches, for example those of multivariate morphometrics, have contributed and are still contributing to an evolving appreciation of biodiversity in the Mediterranean area.

In the following, I will review a few recent studies, beginning with examples of accurate evaluation of species diversity in critically difficult genera, due to the careful application of different taxonomic approaches, either morphological or molecular. Next, I will move into the spatial dimension of biological diversity, thus giving examples of studies addressing the dispersal vs. vicariance dichotomy, the localization of refugia or the subtle interpopulation relationships revealed by phylogeography. I will provide examples focussing on the evolution of Mediterranean biota in geological times as well as others revealing instead dynamic changes in very recent time, virtually in the present.

MORPHOLOGY TO MOLECULES

Since the advent of molecular systematics and especially since the development of cheap and highly efficient sequencing techniques, many authors have expressed critical or at least sceptical attitudes in respect to the usefulness of purely morphological analyses in taxonomy, and especially in the reconstruction of phylogeny. This criticism is arguably justified in some groups, but it is simply wrong as a general rule. Specialists generally know where to look for reliable taxonomic traits, they also know that their study may require operationally challenging and time-consuming work. Coleopterists, for example, know well that the aedeagus (the main component of the male copulatory organ) is

generally diagnostic at the species level, even in groups with very uniform external morphology; in some groups, additional information (occasionally even more diagnostic than the morphology of the aedeagus) can be found in the female reproductive apparatus, especially in the sclerotized spermatheca. A very good example of taxonomic study based on a careful study of genital structures is Bellò & Baviera's (2011) revision of the Sicilian species of *Pseudomeira* Stierlin, 1881 (Coleoptera Curculionidae), a genus of wingless weevils whose members are nearly undistinguishable on external morphology, but are confidently set apart by examining the last two abdominal tergites, plus aedeagus, tegmen and spiculum gastrale of males, and ovipositor, spiculum ventrale and spermatheca of females. The importance of using female characters is exemplarily demonstrated by this study because, of the 18 Sicilian species now recognized in the genus, six are parthenogenetic and thus represented by females only.

An obvious superiority of many taxonomic studies based on morphology in respect to most of those based on molecules is the much better sampling, both in terms of localities and as number of specimens. For example, Bellò & Baviera (2011) examined over 2000 specimens from 116 localities, a sampling that allowed them to find a number of species new to science.

It must be acknowledged, anyway, that because of the rapidly increasing efficiency and the also rapidly decreasing cost of DNA sequencing, molecular studies are also increasingly based on extensive sampling. Results are often puzzling and sometimes astonishing. A case in point is the current progress with the taxonomy of the scarab genus *Pachypus* Dejean, 1821 (Coleoptera Pachypodidae), insects of extremely reduced vagility, due in particular to the wingless condition of the females. To the first-described species, *P. candidae* (Petagna, 1787), recorded from Southern Italy, Latium, Elba, Sardinia, Corsica, old taxonomists were able to add only *P. caesus* Erichson, 1840, from Sicily, and *P. demoflysi* Normand, 1936, only known from Cap Serrat in Tunisia and Annaba in Algeria. The picture, however, has changed rapidly since Sparacio (2008) recognized the Sardinian representatives of this genus as belonging to a new species, *P. melonii* Sparacio, 2008. In Sardinia, however, another, morphologically quite different species was described soon there-

after, *P. sardiniensis* Guerlach, Bazzato et Cillo, 2013 (Guerlach et al., 2013). It was not difficult then to suspect that the overall taxonomic articulation of the *Pachypus* populations in the Tyrrhenian area is possibly more complex than accepted thus far. The study of two markers (Cox1 and 16S) of the mitochondrial DNA of an extended sample from many localities of Italy and Sardinia (Ahrens et al., 2015) has revealed indeed a huge genetic diversity, suggesting the presence of up to 42 species!

PHYLOGEOGRAPHY

With their study of the Corsican brook salamander, *Euproctus montanus* (Savi, 1838), Bisconti et al. (2013) have provided a fine example of the complex phylogeographic patterns that may exist among the populations of what has been hitherto regarded as a quite uniform insular endemic. In the case of a poorly vagile animal, an island of the size of Corsica can host indeed a lot of ancient and geographically structured variation. The most surprising result of this study is the strongly unequal distribution of recognizable lineages of *Euproctus* Gené, 1838 in the different parts of the island. The authors found five main clades, all but one restricted to northern Corsica and essentially allopatric: only in one sample did they find sympatric specimens belonging to two different lineages.

Besides the strictly scientific interest of these findings, this detailed phylogeographic analysis has important consequences in terms of conservation, because it has revealed a previously unsuspected concentration of intraspecific diversity in a restricted part of the island, contrasting with the uniform presence of one lineage only throughout most of Corsica. Critically important in terms of conservation is the fact that the four localized lineages have each been sampled in one or two localities only. Northern Corsica has been also identified as the theatre of ancient phylogeographic splittings between lineages of other organisms with limited dispersal power, such as the land snail *Solatopupa guidoni* (Caziot, 1903) (Ketmaier et al., 2010), the isopod *Helleria brevicornis* Ebner, 1868 (Gentile et al., 2010) and the rockrose *Cistus creticus* Sibth. et Sm. (Falchi et al., 2009).

Remarkable is the amount of divergence among the five *Euproctus montanus* lineages, which is

quite larger than the genetic differences found among species pairs in several lineages of European newts, for example between *Calotriton asper* (Dugès, 1852) and *C. arnoldii* Carranza et Amat, 2005 (Carranza & Amat, 2005), *Triturus marmoratus* (Latreille, 1800) and *T. pygmaeus* (Wolterstorff, 1905) (Carranza & Amat, 2005), or *T. carnifex* (Laurenti, 1768) and *T. macedonicus* (Karaman, 1922) (Arntzen et al., 2007).

The splits between these *Euproctus* lineages have been dated 2.6–5.8 Myr, in agreement with the divergence time estimated for other parallel splits involving different taxa previously studied in Corsica: these include a lizard (*Archaeolacerta bedriagae* (Camerano, 1885)) with parapatric lineages living in northern Corsica that split apart 3.7–5.9 Myr ago (Salvi et al., 2010).

Bisconti et al.'s (2013) results deserve two additional comments. The first is of methodological nature. The clear phylogeographic pattern they discovered among the populations of *Euproctus montanus* is based on comparisons of mitochondrial DNA markers, but no parallel pattern was recovered based on nuclear DNA markers. This is certainly not a reason to regard their result with suspicion, but it is a warning that the whole story has not been reconstructed yet in full. The second point, amply discussed by the authors themselves, is that the geographical isolation between the *Euproctus* clades cannot be explained in terms of either present or ancient geographical barriers; however, the palaeoclimatic history of the island may have been largely responsible for the geographic pattern of distribution of the mountain newt lineages, in the light of Suc's (1984) reconstruction, based palynologic and macroflora analyses, according to which the palaeo-environmental evolution of north-western Mediterranean was characterized during the Pliocene and Early Pleistocene by a progressive decrease in moisture, with dry summers, favouring forest clearing, becoming a regular feature approximately 3.2 Myr ago.

SPECIES IN FACULTATIVELY UNIPARENTAL ORGANISMS

Delimiting species is often very critical when taxonomic units do not coincide with close reproductive communities, that is, in the presence of hy-

bridization, but also when reproductive communities do not exist at all, that is, in the case of organisms with uniparental reproduction. Under these circumstances, it is pretty impossible to adopt uniform procedures: every case is to some extent different from the others. Particularly challenging are the plants and animals adopting a mixed reproductive strategy, that is those in which biparental and uniparental reproduction coexist. A Mediterranean example is *Rumina* Risso, 1826 (Pulmonata Subulinidae), a genus of facultatively selfing (self-fertilizing) snails. Based on morphology, three species have been traditionally recognized. A polymorphism of body colour is also long known among the populations hitherto referred to *R. decollata* (Linnaeus, 1758). A recent study by Prévot et al. (2013) has addressed the question of whether this diversity corresponds to fixed alternative phenotypes due to sustained selfing or to diverging taxonomic units. Nuclear and mitochondrial DNA sequences were compared, revealing an unexpected phylogenetic structure suggesting the presence of 7–10 species, one corresponding to *R. saharica* Pallary, 1901 and the others currently grouped under the name *R. decollata* (Linnaeus, 1758). The contribution of the facultative selfing reproductive strategy to the ongoing differentiation within this snail genus remains, however, obscure.

MORPHOLOGY, DNA AND PHEROMONES

Before the advent of methods for sequencing proteins and nucleic acids, taxonomists had learned to extend comparisons beyond morphology, to include data on the presence or absence of specific molecules of modest size. Particularly attractive were sexual pheromones, because these are often a (the) key cue through which the animal assesses the identity of a potential partner. Nowadays it is possible to combine data on pheromones (or on the response to pheromones) with those obtained from morphology and standard molecular investigations, as in the recent study of Zauli et al. (2016) on the scarab beetles of the genus *Osmoderma* Lepeletier & Serville, 1828 (Coleoptera Cetoniidae). The taxonomy of these rare (and protected) insects is difficult. Traditionally, only a single species *O. eremita* (Scopoli, 1763) was recognized in our area, but other taxa were quite recently proposed,

based on slight morphological differences in agreement with a consistent geographic pattern. From a first molecular study (Audisio et al., 2009), based on the mtDNA cytochrome C oxidase I gene (COI), it resulted that at least four species should be recognized: the western *O. eremita*, the Sicilian endemic *O. cristinae* Sparacio, 1994 and two eastern species, *O. barnabita* Motschulsky, 1845 and *O. lassallei* Baraud et Tauzin, 1991; a fifth species, *O. italicum* Sparacio, 2000, occurs in S-Italy (see Audisio et al., 2007). A new study by Zauli et al. (2016) has confirmed the differentiation of *O. eremita* and *O. cristinae* at the level of species, supported now by more extensive molecular evidence (AFLP, i.e. amplified fragment length polymorphism markers, in addition to COI) and by a morphometric analysis of male genitalia. The study of pheromones, however, has failed to identify any difference between the two species: the males of both taxa produce and release (R)-(+)-c-decalactone, whose attractive power has been demonstrated in either case in the field. According to the authors, the allopatry between *O. eremita* and *O. eremita* can explain the use the same sexual pheromone by both species, due to the lack of selective pressure for the evolution of a prezygotic isolation mechanism.

DISPERSAL VS. VICARIANCE

A research on the Greek representatives of the land snail genus *Chilostoma* Fitzinger, 1833 (Gastropoda Helicidae) (Psonis et al., 2015) revealed a complex biogeographic history of these molluscs, involving both vicariance and dispersal patterns.

These snails are highly diversified and present high levels of endemism. In this study, the authors investigated the phylogenetic relationships of the lineages of the genus *Chilostoma* distributed in Greece based on partial DNA sequences of two mitochondrial DNA (16S rRNA and COI) genes. Complete sequences of one nuclear gene (ITS1) representing the major mitochondrial lineages were also analyzed. The phylogenetic trees revealed three distinct major clades, corresponding to the three subgenera *Cattania* Brusina, 1904, *Josephinella* Haas, 1936 and *Thiessea* Kobelt, 1904, which separated in the late Miocene. They started differentiating into distinct species during the Pliocene and

Pleistocene through not less than nine vicariance and seven dispersal events.

STEEP SLOPES OF PHENETIC DIVERSITY

Even in the case of species with very large distribution areas, the straits between islands or continental masses are the places where morphology changes more significantly between populations living even at a modest distance. By using a diversity of morphometrics methods, Dapporto et al. (2012) estimated this relationship between morphological differentiation and geographic proximity in terms of phenetic slope, a measure whose scores can be plotted onto a map, providing impressive and easily graspable results. Their study targeted the Western Mediterranean populations of seven butterfly species groups, including samples from Sardinia, Sicily, Corsica, the Balearic Islands and several smaller islands of the circum-Italian, circum-Sicilian and circum-Sardo-Corsican archipelagos. Geometric morphometrics was applied to the male genitalia. Here are the main results:

Lasiommata megera (Linnaeus, 1767) group - two distinct morphotypes, one (*L. paramegaera* (Hübner, [1824])) in Sardinia, Corsica, Capraia and Montecristo, the other (*L. megera*) in the remaining islands studied, Europe and North Africa. Italian populations possibly representing a third morphotype.

Pyronia cecilia (Vallantin, 1894) - two distinct morphotypes, one on most West Mediterranean islands and in Spain, the other in Italy; intermediate populations in North Africa and Sicily.

Pyronia tithonus (Linnaeus, 1767) - a highly divergent population in North Africa and a south-west to north-east cline; similarity between populations on Sardinia, Corsica and Elba with those in south-eastern France and between populations from Spain and the Balkans.

Maniola jurtina (Linnaeus, 1758) - two morphotypes, one in North Africa, Spain, Sicily, Sardinia and the surrounding islands, the other in Italy and Eastern Europe; intermediate populations in Corsica, Elba, Giglio, Pianosa, Capri, Ischia.

Coenonympha pamphilus (Linnaeus, 1758) group - two closely related species: *C. lyllus* (Esper, 1805) in North Africa, southern Spain, the Balearics, Sardinia and Sicily, *C. pamphilus* in Corsica, the Italian mainland and neighbouring islands as

well as Eastern Europe; intermediate populations in France and Catalonia.

Hipparchia semele (Linnaeus, 1758) group - the nominal species in the European mainland; vicariant species on some islands (Ponza: *H. sbordonii* Kudrna, 1984; Aeolian Islands: *H. leighebi* Kudrna, 1976). The closely related *H. aristaeus* (Bonelli, 1826) group occurs in Sardinia, Corsica and the Tuscan islands (*H. aristaeus*) and North Africa (the vicariant *H. algerica* (Oberthür, 1876)). In Sicily the two groups occur in sympatry, with *H. semele* and a taxon, *H. blachieri* (Frühstorfer 1908), of the *H. aristaeus* group. This group is represented in southern Italy by *H. neapolitana* Stauder, 1921, together with populations of the *H. semele* group and individuals with intermediate characteristics suggesting hybridization between the two lineages.

In each species (or group of strictly related, vicariant species) the morphometric analysis of the shape of genitalia reveals narrow areas of steep variation. In most cases these areas correspond to sea straits; here are examples:

P. aegeria - a steep slope around Ponza and along the Tyrrhenian Sea; minor slopes between Ischia, Capri and the mainland, at the strait of Messina and in a few mainland areas.

Lasiommata megera/paramegaera - a steep slope in the Tuscan Archipelago where the two morphotypes come into close contact without any evidence of hybridization.

Pyronia cecilia - major slopes between the Tuscan Archipelago and the Italian mainland.

Pyronia tithonus - a steep slope between the Tuscan islands and Italian mainland, between France and Italy and between Morocco and Spain but also alongside Corsica.

M. jurtina, steep slopes correspond to all sea straits between the Italian Peninsula and neighbouring islands (Elba, Giglio, Ischia, Capri, Sicily).

Summing up, this study confirms the distinctness between the insular Mediterranean populations and those of the mainland, a result to some extent surprising in a group of insects with good flying power (see also Cesaroni et al., 1994; Dapporto et al., 2009, 2011; Dapporto, 2010). As a general trend, the butterfly populations of Mediterranean islands are more similar to those of more western and southern areas. For example, those of Sardinia are very similar to those living in North Africa. To explain this trend, Dapporto et al. (2012) suggested

two hypotheses. The first of these is based on the possible passive transport by winds, which mainly blow in summer from the west, however, this might explain the similarity between the fauna of Spain and Sardinia, but not between Tunisia and Sardinia. Therefore, the authors favour an alternative hypothesis based on palaeogeography and palaeoclimatology.

QUATERNARY REFUGIA

During most of the Quaternary, the environmental conditions oscillating between peaks of cold (glacial) and temperate (interglacial) climate caused the extinction of many species and the migration of others. The complex orography of the continent put strong constraints on those migratory routes, the paths of which can be reconstructed quite accurately. During the glacial peaks, a number of species survived in southern refugia, from which they eventually moved back towards higher latitudes in the inter- or postglacial times. An excellent summary of our knowledge of these events is Hewitt (1999).

Of recent studies focussing on the reconstruction of postglacial colonization trajectories in the Mediterranean area, I will single out Fattorini & Ulrich's (2012) research on tenebrionid beetles.

According to their reconstruction, tenebrionid beetles recolonized Europe, in post-glacial times, following multiple trajectories, moving from two refugial centres, one in the Iberian peninsula, the other in the Balkan peninsula. As expected, the lineages involved in the postglacial recolonization were the more tolerant and, possibly, more mobile species, whereas many species with low dispersal capabilities that evolved in those southern refugia could not spread northwards.

These results are broadly in accordance with the long established patterns of recolonization from a number of glacial refugia in southern Europe (e.g., Taberlet et al., 1998; Dapporto et al., 2009, 2011; Dapporto, 2010), but also revealed that the whole biogeographic history of Europe throughout the Holocene and late Pleistocene cannot be reduced to that. Fattorini & Ulrich (2012) interpret the high levels of endemism of tenebrionids in Spain and Sardinia as witnessing that the faunas of these regions originated during the Tertiary period and have remained substantially isolated since then. This in-

dicates a complex history involving geographical isolation and past and current conditions. In other terms, besides the effects of the last Pleistocene glaciation that largely erased the effects of previous palaeogeographic and palaeoecological events, some pre-Pleistocene patterns are still evident in the distribution of European tenebrionids. This is suggested for example by phylogenetic reconstructions of the Mediterranean species of *Tentyria* Latreille, 1802 (Palmer & Cambefort, 2000) and *Blaps* Fabricius, 1775 (Condamine et al., 2011), indicating an ancient colonization of southern European areas from North Africa across the Gibraltar Strait.

BIOVIVERSITY ACROSS THE STRAIT

If the Mediterranean basin as a whole is long acknowledged as a hotspot of biological diversity, less attention is generally paid to the local concentration of biodiversity in smaller, sometimes very strictly localized areas. In a very informative review paper, Rodríguez-Sánchez et al. (2008) focussed on the floristic diversity of two shores of the Strait of Gibraltar, itself a pivotal area between two larger biodiversity hotspots as the southern part of the Iberian Peninsula and NW Africa. This small region hosts a relict flora with a high percentage of endemic species, and the dominance of vegetation types other than the usual Mediterranean-type sclerophyllous forests and shrublands.

The authors show that plant endemism in the area of the Strait of Gibraltar is associated with poor soils and mild Mediterranean climate, whereas relictiness is primarily associated with riparian and humid habitats, probably stable to some degree since the Late Tertiary.

The phylogeographic studies performed thus far on a number of animals have shown that the degree of isolation correlated to the presence of the Strait of Gibraltar is very different from case to case. Although narrow, this strait separates distinguishable lineages in a nearly sedentary bird such as the great bustard *Otis tarda* Linnaeus, 1758 (Broderick et al., 2003). However, other animals with low dispersal power have been apparently able to cross the Strait during the last 60 000 years, in some cases at least with the help of humans; there are examples among mammals (the white-toothed shrews of the genus *Crocidura*

Wagler, 1832; Cosson et al., 2005) and snakes (the false smooth snakes of the genus *Macroprotodon* Guichenot, 1850; Carranza et al., 2004) and even in the salamanders of the genus *Pleurodeles* Michahelles, 1830 (Veith et al., 2004). A different story is told by the lizard *Psammodromus algirus* (Linnaeus, 1758), which crossed the Strait around 2 million years ago, despite its poor attitude to long-distance dispersal (Carranza et al., 2006). Unable to cross the Strait were other vertebrates, currently represented by different, vicariant species on the European and African shores: for example, the spadefoot toads are represented by *Pelobates cultripes* (Cuvier, 1829) in Iberian Peninsula, by *P. varaldii* Pasteur et Bons, 1959 in northern Africa (García-Paris et al., 2003). By vicariant taxa are also represented, on the European vs. African side of the Strait, the painted frogs of the genus *Discoglossus* Otth, 1837 (Fromhage et al., 2004) and the freshwater fishes of the genus *Barbus* Cuvier et Cloquet, 1816 (Zardoya & Doadrio, 1999).

CLIMATIC NICHE EVOLUTION THROUGH SPECIATION

Ahmadzadeh et al. (2016) used the large ocellated lizards of the genus *Timon* Tschudi, 1836 to study the evolution of ecological niches through comparative phyoclimatic analysis and to determine the possible role of climatic niche evolution during the speciation process.

The authors established first a phylogeny of this taxon, based on three mitochondrial and two nuclear genes, and provided an age estimate for all lineage splittings leading to the six living species.

The large ocellated lizards are estimated to have diverged from the sister genus *Lacerta* Linnaeus, 1758 ca. 18.6 Myr ago. Within *Timon*, two main clades diverged 14.5 Myr ago and today have widely disjunct distributions. The eastern clade includes the two oriental species *T. princeps* (Blanford, 1874) and *T. kurdistanicus* Suchow, 1936, which split apart 7.9 Myr ago. The western clade consists of the European subclade with the species *T. lepidus* (Daudin, 1802) and *T. nevadensis* (Buchholz, 1963), and the African subclade with the species *T. pater* (Lataste, 1880) and *T. tangitanus* (Boulenger, 1889). These two subclades are estim-

ated to have split apart 7.4 Myr ago, while species divergence inside the European and African subclades has been dated 5.7 Myr and 6.0 Myr respectively.

The phylogenetic analysis suggests that the divergence between the eastern and western groups of *Timon* was determined by multiple vicariance events. As remarked by the authors, the same biogeographical patterns involving divergence and vicariance between a western and an eastern Mediterranean lineages has been found in other genera of reptiles and amphibians: among the reptiles, in the amphisbaenian genus *Blanus* Wagler, 1830 (the western *B. cinereus* (Bedriaga, 1884), *B. mettetali* Bons, 1963, *B. mariae* Albert et Fernández, 2009 and *B. tingitanus* Busack, 1988 vs. the eastern *B. strauchi* (Bedriaga, 1884)) (Vasconcelos et al., 2006; Albert et al., 2007; Sindaco et al., 2014); among the amphibians, in *Pelobates* Wagler, 1830 (the western *P. cultripes* (Cuvier, 1829) and *P. varaldii* Pasteur et Bons, 1959 vs. the eastern *P. syriacus* Boettger, 1889) (Tarkhishvili & Gokhelaishvili, 1999; Crotini et al., 2010) and *Pelodytes* Bonaparte, 1838 (the western *P. punctatus* (Daudin, 1802) and *P. ibericus* Sánchez-Herráiz, Barbadillo-Escrivá, Machordom and Sanchíz, 2000 vs. the eastern *P. caucasicus* Boulenger, 1896) (Van de Vliet et al., 2012).

In the following steps of their study, Ahmadzadeh et al. (2016) used multivariate statistics on species distribution models to characterize all species in terms of their ecological niches. The authors used the latter term in the sense of the so-called Grinnellian niche (cf. Grinnell, 1917), defined by Soberón (2007) as a “subset [...] of scenopoetic variable space [average temperature, precipitation, solar radiation, terrain aspect, etc.] corresponding to geographic areas defined by actual or potential properties of [a] species”, rather than as Eltonian niche (cf. Elton, 1927; MacArthur, 1968), measured instead in terms of biotic interactions and resource-consumer dynamics (bionomic variables).

Niche divergence among species was quantified by Ahmadzadeh et al. (2016) by computing multivariate niche overlaps via two-dimensional and n-dimensional approaches. A generally low niche divergence emerged among the members of the eastern group, contrasting with the remarkable climatic divergence observed within the western group. The results suggest an important role of tem-

perature seasonality in a Mediterranean and Atlantic climate context and a substantial degree of niche conservatism in terms of microhabitats as described by vegetation cover.

POPULATION CHANGES DURING THE LAST CENTURY

Against the background of studies such as the example of *Euproctus montanus* discussed above, revealing a phylogeographic structure essentially frozen for a few million years, it is sensible to close with an example of the unexpectedly rapid pace at which the geographical distribution of different haplotypes can change in vagile organisms as are the hawkmoths (Sphingidae). The study of Mende & Hundsdoerfer (2013) on *Hyles euphorbiae* (Linnaeus, 1758) is also an excellent example of the precious information we can obtain from molecular studies of museum specimens.

Six distinct mitochondrial lineages are recognized in the Mediterranean region for this group of large moths. The mitochondrial lineage found throughout most of Europe (*H. euphorbiae*) is also present on Malta, but is replaced by a different lineage (informally known as '*H. italica*') in Southern Italy and Sicily. By analyzing DNA sequences obtained from museum specimens collected at different times between 1884 and 1986, Mende and Hundsdoerfer (2013) provided a reconstruction of the evolution throughout the Twentieth Century of the mitochondrial demographic structure of the *Hyles euphorbiae* complex in Italy and Malta.

At the beginning of the XX century, the European (*H. euphorbiae*) lineage coexisted with the southern ('*H. italica*') one both in Southern Italy and in Sicily. The frequency of the latter lineage, however, went on increasing; if ca. 120 years ago it was slightly more abundant there than the *H. euphorbiae* lineage, its frequency increased till eventual fixation in recent years. The current areal disjunction between *H. euphorbiae* and '*H. italica*' is thus a very recent pattern, tentatively explained by the authors as due to genetic drift following anthropogenic habitat loss and fragmentation, perhaps in combination with an impact from recent climate warming that may have favoured the spreading of '*H. italica*' populations.

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