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Sicily: the island that didn't know to be an archipelago

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Abstract

Recent geological studies demonstrated that most of Sicily was still under water during lower Pliocene, with the exception of the NE and the SE corners of the island (Peloritani Mts and Hyblaean Plateau, respectively). This geological evidence, so far not considered sufficiently by the scholars of the Sicilian flora, poses many still open questions on how and where many ancient lineages and Palaeogene relicts, currently found on the island, managed to survive. Purpose of this paper is to review the potential significance of isolation and ecological differentiation for the local floristic diversity and the evolution of narrow endemism in the Sicilian flora. In particular, the following drivers of Sicilian floristic patterns are considered: geographical segregation and age of the Sicilian terrains; climate variability and heterogeneity; geological patchiness; human influence on habitat fragmentation.

Key words: Sicily, flora, biogeography.

Introduction

Sicily is the largest Mediterranean island, with an extension of nearly 26000 km². The Sicilian territory is predominantly hilly or mountainous: one fourth of the island is at more than 700 m a.s.l.; two thirds range between 300 and 700; one sixth below 300 m a.s.l. The geographical position of Sicily, its complex geological history and the high topographic diversity make the island one of the most heterogeneous Mediterranean territories, under the geo-morphologic, edaphic and climatic viewpoint. The island is widely recognized by botanists as one of the main hot-spots of plant diversity in the Mediterranean basin (HEYWOOD 1995; MÉDAIL & QUÉZEL 1997, 1999; MYERS et al. 2000; MÉDAIL & DIADEMA 2009). Its rich flora counts approximately 3250 native species, 12.6% of which are endemites (BRULLO et al. 2012), witnessing the complex paleogeographic history and physiographic settlement of the island (NIMIS 1984, 1985). A striking feature of the Sicilian endemism is that the largest majority (9.1%, according to RAIMONDO & SPADARO 2009) are narrow endemic species, i.e., they have a distribution which is restricted to a single well-defined area within a small part of the island (BRULLO et al. 1995; BONANNO & VENEZIANO 2016).

Many Sicilian endemites exhibit what has been termed a “schizo-endemic” pattern of distribution (FAVARGER & CONTANDRIOPOULOS 1961, CONTANDRIOPOULOS 1962). The prevailing paradigm for the evolution of such endemic taxa relies on the assumption of differentiation due to the fragmentation of the range of a widespread ancestral taxon to produce endemic taxa in different parts of the original distribution (THOMPSON et al. 2005). For instance, this is the case of the Sicilian taxa ascribed to the genera *Armeria* (AGUILAR et al. 1999), *Asperula* (BRULLO et al. 2009), *Astragalus* (NIMIS 1981), *Campanula* (BRULLO 1983), *Pseudoscabiosa* (CAPUTO & COZZOLINO 1994), *Salix* (BRULLO & SPAMPINATO 1988) and *Trifolium* (BRULLO et al. 2000), among the others.

However, in the case of vascular plants, phylogeographic breaks may develop also in the absence of geographical or ecological barriers to gene flow: local genetic differentiation is

common in plants (LINHART & GRANT 1996) and local speciation associated with several different types of evolutionary processes, such as hybridization, polyploidisation, inbreeding and reticulate evolution also contribute to the evolution of endemic species throughout the Mediterranean basin (THOMPSON 2005). In this framework, Sicily makes no exception. This is the case, for instance, of many Sicilian endemites belonging to the genera *Anthemis* (GUARINO et al. 2013), *Brassica* (RAIMONDO & GERACI 2002; BRULLO et al. 2013; SCIANDRELLO et al. 2013), *Centaurea* (BANCHEVA et al., 2006, 2011), *Helichrysum* (IAMONICO et al. 2016; MAGGIO et al. 2016), *Quercus* (BRULLO et al. 1999), etc.

Moreover, in the Sicilian mosaic landscape, where environmental gradients vary strongly in space, localised floristic differentiation could represent an important driver not only for the allopatric and sympatric speciation, but also for the local genetic differentiation of plant lineages and for the overall plant species richness of the island, as well. The long-lasting human history deeply affected these natural patterns and trends, by means of induced isolation through habitat fragmentation, species migrations and the consequent set up of new species assemblages.

Purpose of this paper is to review the potential significance of isolation and ecological differentiation for the local floristic diversity and the evolution of narrow endemism in the Sicilian flora. In particular, we will focus on the following drivers of Sicilian floristic patterns and related still open questions: 1. Geographical segregation and age of the Sicilian terrains; 2. Climate variability and heterogeneity; 3. Geological patchiness; 4. Human influence on habitat fragmentation.

Taxonomic nomenclature follows the second edition of the Flora of Italy (PIGNATTI et al. 2017-2018); syntaxonomic nomenclature follows the most recent syntaxonomic list of Sicily (GUARINO et al. 2017).

1. Geographical segregation and age of the Sicilian terrains

With the exception of the NE corner of Sicily (Peloritani Mts.), which is a fragment of the Iberian Margin shifted towards SE during the Alpine orogeny (SCIANDRELLO et al. 2015), and of the SE corner of Sicily (Hyblaean Plateau), which is a fragment of the African plate isostatically raised and shifted towards NW (BRULLO et al. 2011), all the rest of the island was under water during lower Pliocene, i.e. between 5.3 and 3.6 million years ago (hereinafter abbreviated with Ma). This is true even for the highest peaks of Madonie and Nebrodi Mts., now reaching nearly 2000 m a.s.l. (CATALANO et al. 2013), as well as for the single most relevant landmark of the island, i.e. Mt. Etna (currently standing 3329 m a.s.l.), whose geological history begun just 570 thousand years ago (BRANCA et al. 2008).

So far, this geological evidence has not been sufficiently considered by the scholars of the Sicilian flora. Before the Pliocenic submersion stage some localised areas might have experienced emersion, not only during the Messinian salinity crisis (c. 5.6 to 5.3 Ma) but several times during Palaeogene and even during Mesozoic, as testified by several sedimentary successions and continental erosion surfaces on the Panormide, Trapanese, Saccense, Ibleo-Pelagian carbonatic platforms, corresponding to shallow waters basins, where slight sea level oscillations could give rise to emerged areas (CATALANO 2004).

It is likely that during upper Pliocene wider areas were emerged northwards (i.e. near Corsican-Sardinian microplate) and southwestwards (i.e. near Tunisia), and that they went underwater during the opening of the Tyrrhenian sea (ROSENBAUM & LISTER 2004). This hypothesis still needs to be utterly confirmed by geological evidence but the occurrence of Tyr-

rhennian stepping stones could explain the close floristic affinity of the NE Sicilian trachytic and crystalline siliceous substrata with the corresponding ones of Sardinia, as well as the occurrence of several W-Mediterranean and Tyrrhenian ancient lineages with remarkable disjunctions, currently found as isolated metapopulations or as schizo-endemites in parts of Sicily and/or neighbouring islets which were still submerged during the lower Palaeogene. This the case, for instance, of *Abies nebrodensis*, *Adenocarpus commutatus* and *A. bivonii*, *Ambrosina bassii*, *Bupleurum dianthifolium*, *Centaurea* gr. *cineraria*, *Centaurea* gr. *parlatoris-deusta*, *Chamaerops humilis*, *Convolvulus cneorum*, *Cytisus aeolicus*, *Eokochia saxicola*, *Genista aetnensis*, *Genista* gr. *ephedroides*, *Glandora rosmarinifolia*, *Helichrysum* gr. *panormitanum*, *Hyoseris taurina*, *Oncostema hughii*, *Pinus calabrica*, *Pinus pinaster* subsp. *escarena*, *Pseudoscabiosa limonifolia*, *Ptilostemon greuteri*, *Seseli* gr. *bocconeii*, *Silene* gr. *mollissima*, etc.

The Maghrebid-Apennine range development implied the formation of a complex chain-foredeep-foreland system. Along with the thrust drift, wide sectors of foreland (like the Hyblaean Plateau) could have emerged southeastwards already before upper Pliocene. Some of them may have sunk afterwards. Hence, many species could have colonised the collapsing emerged areas located at higher latitudes and the rising areas at lower latitudes at stepping stones or refugia. This could explain the close floristic affinity of the Hyblaean and Maltese plateaus with the carbonatic plateau of Northern Cyrenaica and with the Aegean Region (BRULLO et al. 2011), as well as the occurrence of east-Mediterranean and NE-African ancient lineages with remarkable disjunctions, currently found as isolated metapopulations or as schizo-endemites in parts of Sicily and/or neighbouring islets which were still submerged during the lower Palaeogene. This the case, for instance, of *Astragalus nebrodensis*, *A. siculus*, *A. kamarinensis*, *Berberis aetnensis*, *Bupleurum elatum*, *Calendula incana* s.l., *Crucianella rupestris*, *Carlina sicula* s.l., *Desmazeria sicula*, *Gagea trinervia*, *Helianthemum sicanorum*, *Jurinea bocconii*, *Muscari gussonei*, *Onosma canescens*, *Prangos ferulacea*, *Prunus prostrata*, *Retama raetam* subsp. *gussonei*, *Siculosciadium nebrodensis*, etc.

We intentionally included in the aforementioned list oro- to thermo-Mediterranean species, which may have reached Sicily by different times, modes and ways, even if the adaptation to the altomontane conditions, in Sicily, appears to be in most cases the result of a secondary adaptive radiation of lineages which have now become extinct in the lowlands.

The past occurrence of currently submerged stepping stones may also explain the presence of many species that spread in the Mediterranean basin during the Messinian salinity crisis and that could not have been surviving *in situ* on Sicily, given its submersion until relatively recent times. This is the case of vegetation types to which the following phytosociological units, currently well represented in Sicily, are referring: *Pegano harmalae-Salsoletea vermiculatae* (BRULLO et al. 2012), *Saginetea maritimae* (BRULLO & GIUSSO DEL GALDO 2003), *Salicornietea fruticosae* and *Juncetalia maritimi* (BRULLO & FURNARI 1976), *Rumici-Astragaletea siculi* (BRULLO et al. 2005) and the perennial steppe prairies of *Moricandio-Lygeion sparti* (BRULLO et al. 2010). All these syntaxa, related to salty substrata or to mountain debris and talus slopes, are characterized by discontinuous distribution patterns throughout the Mediterranean basin and by the abundance of relict floristic elements (GUARINO 2006, GUARINO et al. 2006).

Fairly all the coastal capes of NW Sicily experienced repeated phases of insularity, as testified by the so-called fauna of Monte Pellegrino (>1 Ma), hosting an unbalanced fauna with birds and micromammals of both Eurasian and African origin, and also the following faunistic assemblages (from 0.95 to 0.1 Ma), characterised by dwarf herbivores (hippopotamuses, elephants, red deers and aurochs), a giant otter, several big carnivores with both African (hyenas) and Eurasian (bears) origins, etc. (PALOMBO 2018). Egadi islands seem to have shared the

same destiny, as testified by their endemic element, which shows a remarkable floristic affinity with the promontories of Western Sicily (*Asperula rupestris*, *Asplenium petrarchae*, *Centaurea ucrae* and *C. umbrosa*, *Euphorbia papillaris*, *Glandora rosmarinifolia*, *Iberis semperflorens*, *Pseudoscabiosa limonifolia*, *Seseli bocconii*, *Simethis mattiazzi*, etc.).

Within the framework outlined, some open questions remain concerning palaeoendemics whose distribution pattern remains unexplained. A remarkable example is provided by *Urtica rupestris*, endemic to the Hyblaean canyons and similar to *Urtica morifolia* of the Canary Islands (BARTOLO et al. 1998), which has no other allied relict population in the W-Mediterranean basin. A similar case concerns *Cistus clusii*, a west Mediterranean species reaching in the Hyblaean plateau and Apulia the most eastern and disjunct outposts of its distribution range (BRULLO et al. 2011). On the other hand, it is difficult to explain how *Erica sicula*, the only representative of the section *Pentapera* in the flora of Italy, managed to reach the recently emerged cliffs of some NW coastal capes of Sicily, being its closest relatives currently scattered in Cyrenaica, Lebanon, Anatolia and Cyprus (FAGÚNDEZ & IZCO 2011).

Another unsolved enigma concerns the occurrence of *Cytisus aeolicus*, an arborescent broom endemic to Aeolian Islands with no near relatives in the whole Euro-Mediterranean. Taking into consideration its evolutionary isolation (see TROIA 2012 and references therein), it has to be considered far more ancient than the Aeolian Archipelago itself, whose volcanoes started to emerge less than one million years ago. Similarly, no one knows how *Genista aetnensis*, another ancient and taxonomically isolated species, managed to reach the much younger slopes of Mt. Etna, being the nearest wild populations in Eastern Sardinia.

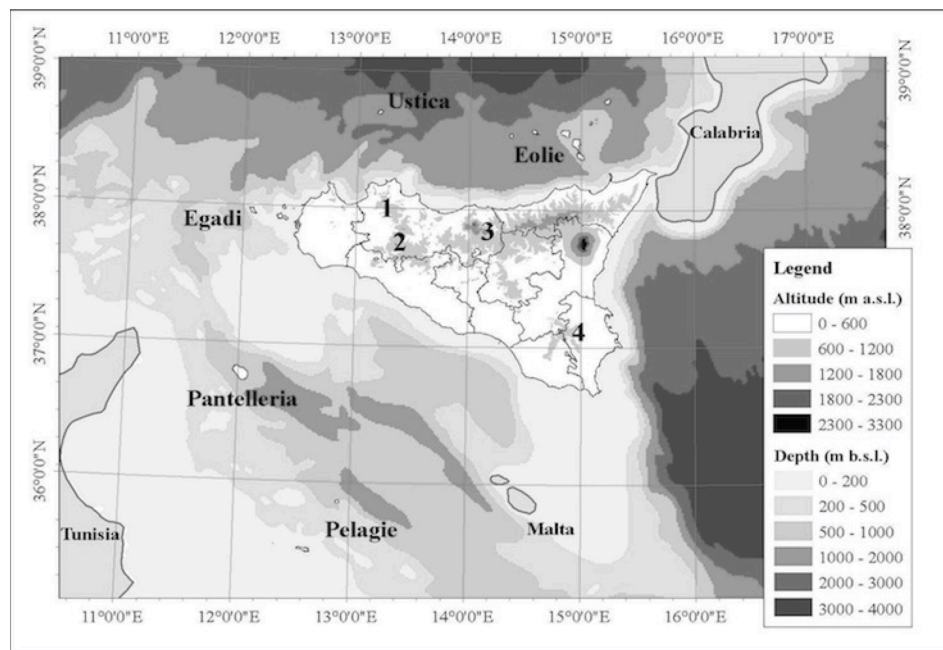


Fig. 1: Map with isobaths and name of satellite islands (after: PASTA & LA MANTIA 2013, modified)

The species belonging to the only two monotypic endemic Sicilian genera, i.e. *Petagnaea gussonei* and *Siculosciadum nebrodensis*, only occur at the boundary between Peloritani and Nebrodi Mts. the former and on Madonie Mts. the latter. Considering that their nearest rela-

tives have an Eurasian distribution in the first case and an E-Mediterranean-Iranian distribution in the second case, both of them must have colonized Sicily through Peloritani Mts. But something simply does not match very well: *Petagnaea* is a very isolated – hence probably rather ancient – genus, but unlike the other Palaeogene relicts it does not grow on steep cliffs but in a rather novel ecosystem, represented by beechwood brooklets, whilst *Siculosciadum* only grows on dolomias, a substrate which does not occur on the metamorphic massif of Peloritani Mts.

It is important to highlight that many interesting species belonging to relict genera may have evolved or have colonized Sicily quite recently and now only survive in few suitable sites: this could be the case of *Zelkova sicula* (GARFÌ et al. 2011), represented by only two

Table 1. An overview on the differential vascular plants growing in the districts corresponding to the circum-Sicilian satellite islands and archipelagos

COSYRAN DISTRICT (PANTELLERIA ISLAND)

Exclusive endemic taxa: *Genista aspalathoides* var. *gussonei*, *Helichrysum saxatile* subsp. *errerae*, *Limonium cosyrense*, *Limonium parvifolium*, *Limonium secundirameum*, *Matthiola incana* subsp. *pulchella*, *Medicago truncatula* var. *cosyrensis*, *Senecio leucanthemifolius* subsp. *cosyrensis*, *Serapias cosyrensis*, *Trifolium nigrescens* var. *dolychodon*

Exclusive non endemic taxa: *Andryala rothia* subsp. *cosyrensis*, *Antirrhinum tortuosum*, *Asplenium marinum*, *Asplenium obovatum* subsp. *lanceolatum*, *Brassica insularis*, *Carex illegitima*, *Cytisus intermedius*, *Limodorum trabutianum*, *Ophrys sphegifera*, *Pimpinella lutea* (extinct), *Pinus pinaster* subsp. *escarena*, *Schoenoplectus litoralis* subsp. *thermalis*, *Serapias cosyrensis*.

ALGUSAN DISTRICT (LINOSA ISLAND)

Exclusive endemic taxa: *Erodium neuradifolium* var. *linosae*, *Galium murale* var. *calvescens*, *Limonium algusae*, *Valantia calva*, *Valantia muralis* var. *intricata*.

Exclusive non endemic taxa: *Astragalus warionis*, *Castellia tuberculosa*, *Lotus peregrinus*, *Ononis serrata*, *Onopordon tauricum*, *Patellifolia patellaris*, *Silene apetala*, *Spergula fallax*, *Voluntaria tubiflora*

LOPADUSAN DISTRICT (LAMPEDUSA AND LAMPIONE ISLANDS)

Exclusive endemic taxa: *Allium hemisphaericum*, *Allium lopadusanum*, *Allium pelagicum*, *Anthemis secundiramea* var. *lopadusana*, *Bellevallia pelagica*, *Chiliadenus lopadusanus*, *Cistus* × *skanbergii* (extinct in the wild), *Daucus lopadusanus*, *Daucus rupestris* (extinct), *Dianthus rupicola* subsp. *lopadusanus*, *Diploaxis scaposa*, *Filago gussonei*, *Limonium albidum*, *Limonium intermedium* (extinct in the wild), *Limonium lopadusanum* (also Linosa), *Oncostema dimartinoi*, *Suaeda pelagica*, *Thapsia pelagica*

Exclusive non endemic taxa: *Allium hirtovaginatatum*, *Caralluma europaea* subsp. *europaea*, *Cistus parviflorus*, *Diploaxis scaposa*, *Echinops spinosissimus* subsp. *spinosus*, *Hypericum aegyptiacum*, *Launaea nudicaulis* (extinct), *Marrubium alysson*, *Ophrys picta*, *Paronychia arabica* subsp. *longiseta*

AEGADIAN DISTRICT (EGADI ISLANDS)

Exclusive endemic taxa: *Allium francinae*, *Brassica macrocarpa*, *Bupleurum dianthifolium*, *Centaurea aegusae*, *Helichrysum panormitanum* subsp. *messeriae*, *Limonium aegusae*, *Limonium tenuicolum*, *Oncostema hughii*, *Prospero hierae*, *Thymus richardii* subsp. *nitidus*

Exclusive non endemic taxa: *Aristolochia navicularis*, *Daphne sericea*, *Erodium maritimum*, *Lagurus ovatus* var. *vestitus*, *Ophrys apulica*, *Ophrys scolopax*, *Thymelaea tartaronraira*

AEOLIAN DISTRICT (AEOLIAN ISLANDS)

Exclusive endemic taxa: *Anthemis aeolica*, *Bituminaria basaltica*, *Centaurea aeolica*, *Cytisus aeolicus*, *Erysimum brulloi*, *Genista tyrrhena* subsp. *tyrrhena*, *Silene hicesiae*

Exclusive non endemic taxa: *Clematis flammula*, *Eokochia saxicola*, *Helichrysum litoreum*, *Malcolmia ramosissima*, *Wahlebergia nutabunda*

clonal populations located in the Hyblaean district and only occurring along rivulets and seasonal streams. Although the genus *Zelkova* belongs to the mesothermic deciduous tree flora which gradually disappeared in the whole Europe during Pliocene and Pleistocene, the Sicilian species currently grows on basaltic lavas dating back to c. 3 to 1.7 Ma, so it may have colonized the area afterwards, perhaps exploiting the cooler phases during glaciation events.

A regional phytogeographic partitioning of Sicily based on the distribution of differential taxa (narrow endemics and exclusive species) has been published by BRULLO et al. (1995), who were able to identify as many as 15 districts. Table 1 gives an idea of the floristic originality of the districts represented by the small archipelagos around Sicily (Fig. 1). Besides local endemics, also broad ranging taxa are listed which, in the Sicilian context, only occur in a single microinsular district. These latter are grouped as “Exclusive non endemic taxa”

2. Climate variability and heterogeneity

The Mediterranean climate is not only depending on the latitude, but also on the cyclonic circulation of the oceanic air masses, whose position is ranging year by year. Annual climatic variations and major climatic changes may locally lead to the severe reduction and splitting of plant populations. Several noticeable disjunctions in the distribution ranges of plant species growing in the Sicilian dry grasslands can be attributed to these climatic changes: for example, the disjoint populations of *Heteropogon contortus*, *Artemisia alba*, *Sesleria nitida* subsp. *sicula*, *Koeleria splendens*, *Helictotrichon convolutum*, have probably reached the island during the dry interglacial periods of the Pleistocene. Similarly, during the coldest phases of Pleistocene, many taxa reached the mountains of northern Sicily, exploited their most suitable microhabitats as refugial areas, and eventually begun to differentiate on site. This is the case of *Allium ursinum*, *Aquilegia vulgaris* subsp. *sicula*, *Betula aetnensis*, *Circaea lutetiana*, *Epilobium angustifolium*, *Fagus sylvatica*, *Lonicera xylosteum*, *Populus tremula*, *Ribes uva-crispa*, *Sanicula europaea*, and many other species typical to the Sicilian beechwoods (BRULLO et al. 2012). So, the Pleistocene glaciations affected the Sicilian flora in at least two ways: (I) they triggered floristic richness and heterogeneity in the mountain stands (but not on the top of the highest ones, where periglacialism occurred repeatedly), whilst (II) sea level lowering promoted not only the migration of Balkan species such as *Carpinus orientalis*, *Cercis siliquastrum*, *Fritillaria messanensis*, *Nectaroscordum siculum*, *Ostrya carpinifolia*, *Paliurus spina-christi*, (PEZZETTA 2011) through S Italy thanks to the regression of the Adriatic Sea but also some floristic exchanges between Sicily and northern Africa through the Sicilian Strait (LAMBECK et al. 2014), like in the case of *Pinus pinaster* subsp. *escarena* in Pantelleria and *Calendula incana* subsp. *maritima* along the western shores of the main island (even if, for this species, an human introduction to Sicily cannot be excluded, see PASTA et al. 2017).

Millennial climatic trends are associated, as well, to remarkable year-to-year fluctuations of rainfalls and temperatures, that are affecting Mediterranean climates more than any other climatic type worldwide (DONLEY et al. 1979, HOFRICHTER et al. 2001). These fluctuation could explain the general evolutionary tendency of many Mediterranean plants towards theophytism (MOSSA et al. 2004), rewardless species-specific pollination strategies (DAFNI 1987), and high investment in seed productivity (WELLS 1969). Obligate seeders have greater numbers of sexually produced generations, resulting in greater genetic recombination, which in turn contributes to more rapid speciation. This could explain why the Mediterranean region has such an high diversity of plant and insect species (MÉDAIL & QUÉZEL 1997). We know that insects are quite precise in their flower-visiting habits and in the Mediterranean dry grasslands several examples of co-evolution between flowers and insects are known, especially

among representatives of the families *Fabaceae*, *Lamiaceae* and *Orchidaceae*. The Sicilian flora makes no exception to these general trends and the remarkable climatic heterogeneity of Sicily, ranging from semi-arid to humid ombrotypes and from thermo- to cryo-oromediterranean thermotypes (BRULLO et al. 1996, BAZAN et al. 2006), favoured over time the floristic enrichment and differentiation of the island.

A regional assessment of the distribution of vegetation types per bioclimatic units has been recently published by BAZAN et al. (2015). However, the evolutionary consequences of such a remarkable climate variability and heterogeneity are acting at local scale within each single vegetation patch: relatively short generation time and intense gene flows may easily segregate new forms or varieties, particularly among annual plants, which can efficiently occupy new peculiar niches, that given to the patchiness and heterogeneity of the Sicilian landscape are very common. Most of this intraspecific variability is still poorly investigated in the Sicilian flora, but noticeable examples of local speciation as the ending result of micro-evolutionary processes that promote population differentiation are provided, for instance, by the species complex of *Silene* sect. *coloratae* (BRULLO et al. 2012, 2014 a-b, 2015). Random gene fixation and subsequent divergence may be a common feature, so far poorly investigated, in the population biology of many Sicilian annuals and, more in general, of insect-pollinated herbaceous species, particularly when climate change affects population size and isolation, in ecologically marginal or geographically peripheral populations.

3. Geological patchiness

The geographical position of Sicily, its complex orogeny and high topographic diversity make the island one of the most heterogeneous Mediterranean territories (CATALANO et al. 2013). The main points of the geomorphological evolution of Sicily are the following (Fig. 2):

- 1) Strong conflict between tectonic uplifting (which creates relief) and subsidence processes (which destroy it);
- 2) Relief is created in the south and destroyed in the north, where it collapses towards the Tyrrhenian Sea;
- 3) An ever-changing relief in central Sicily, where soft rocks crop out;
- 4) An increasingly old terrain, as you move from south (newly emerged areas) to north (heavily eroded areas);
- 5) Conservation of the oldest terrains in mountain districts of the north, where more “erosion-resistant” rocks crop out;

The single most relevant landmark of the island is Mt. Etna, the biggest volcano in the Mediterranean region. It dominates the Eastern side of Sicily, with multiple layers of erupted materials that cover an area of 1190 km², with a basal circumference of 140 km.

Apart from Etna, the main elevations of Sicily (ranging from 1400 to 1979 m) are aligned along the so-called Sicilian Apennine, ranging along the NE-coast from the Strait of Messina up to the valley of the Torto River. Three sectors can be recognized, from east to west: Peloritani-, Nebrodi- and Madonie Mountains. Peloritani are constituted by the oldest outcrops of Sicily: a complex of different metamorphic rocks (gneiss, schistose and phylladic alternations) partially covered by sedimentary sandstones and limestones. Nebrodi are mostly consisting of quartz sandstones, clayey and siltose depositions belonging to the Numidian Flysch. Madonie are formed by carbonatic, dolomitic and quartzitic outcrops, frequently interrupted by outcroppings of salty clays and layers of halite. Carbonatic and dolomitic rocks are forming, as well, the reliefs in the western part of Sicily, overlapping a basal complex constituted by carbonate sands and clays.

The central and southern parts of Sicily are characterized by the hilly complex of ‘normal’ and ‘chaotic’ sediments dating back to upper Messinian (5.96-5.33 Ma) and belonging to the Messinian evaporitic series (the so-called ‘Gessoso-Solfifera’ Formation), mixed with whitish marls of the late Pliocene and by yellowish Plio-Pleistocenic calcareous sandstones.

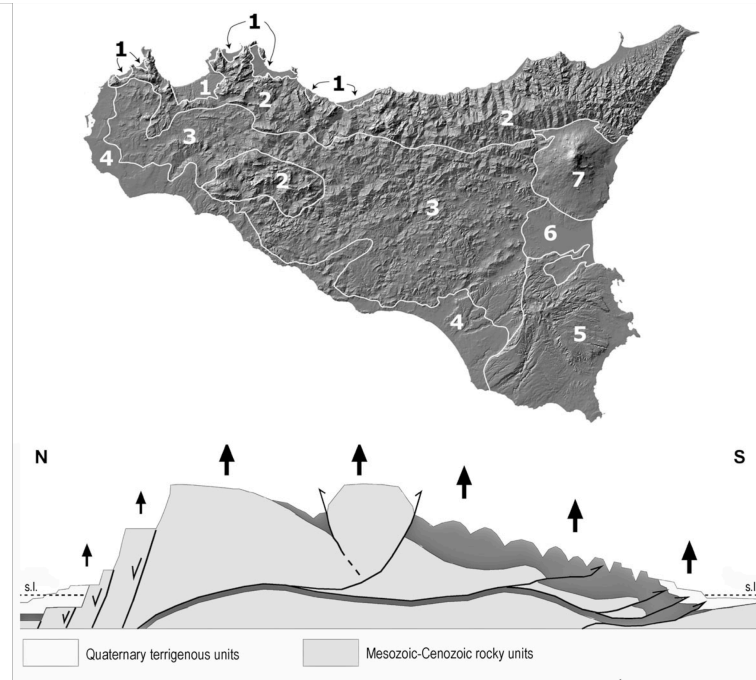


Fig. 2: Geomorphologic and geodynamic schemes of Sicily (after CATALANO et al. 2013, modified): (1) flat areas set on Quaternary tectonic depressions, dominated by coastal morphogenesis; (2) mountains dominated by river incision and selective erosion, in response to the regional uplift, marked by a general congruence between topography and structure; (3) hilly areas of the foreland dominated by river incision and selective erosion, in response to the regional uplift, characterized by processes of inversion of the relief; (4) gradually uplifting areas, dominated by the interaction between coastal morphogenesis and Quaternary uplifting; (5) flat areas of foreland dominated by smoothing processes; (6) alluvial plains; (7) Etna volcanic buildup.

The south-Eastern corner of Sicily is formed by the carbonate platform named ‘Hyblaean Plateau’, a succession of horizontal layers of mesozoic limestones frequently interrupted by a radial system of deep canyons departing from the highest elevation (Mt. Lauro, 970 m a.s.l.) formed by alkaline basaltic flows and calcareous tuff that covered the northern portion of the plateau during the Pliocene. The Hyblaean and the Etnean districts are divided by the largest alluvial plain of Sicily, the so-called ‘Piana di Catania’, created by the sediments of the main Sicilian river: the Simeto, catching water from the southern side of Mt. Soro (i.e. the highest peak of Nebrodi Mts.) and all along the western slopes of Mt. Etna. The plain of Catania is the most important agricultural area in the region, consisting of 108,097 ha of arable land and 102,350 ha of permanent crops.

Simeto is the only river of Sicily whose flow is reaching the average of 18 m³/sec., followed by the Alcantara- (8.8 m³/sec.) and the Platani River (6.9 m³/sec.). Most of the Sicilian rivers are modest (less than 1 m³/sec.), with a pronounced seasonal gap during the summer months,

due to the lack of rainfall, the short persistence of snow and the relatively small extension of the catchment basins.

Numerous peculiar habitats and microhabitats contribute to regional landscape discontinuity, hence to species-richness. This is the case of the naturally dynamic and disturbed riverbeds and screes, of the wide karstic areas of the inner island, of the humid areas such as rock pools, temporary and permanent ponds, saltmarshes and coastal lagoons. Other portions of Sicilian territory are characterised by extremely hostile soils issuing from the pedogenesis on gypsum, dolomia or salty clays or characterized by impressive seasonal changes in terms of water flow (e.g. braided streams flowing towards N and NE Sicilian coastlines), soil humidity (e.g. badlands), etc.

Because of the few or null frosty days, and because of the relatively scarce rainfall, the weathering of rocks is relatively slow in Sicily and the soils reflect with unusual fidelity the chemical composition of the mother rocks (FIEROTTI 1988). Different soil chemistry and texture are selecting remarkably different species assemblages, as it happens, for instance, in the three orders belonging to the class *Tuberarietea guttatae*: *Tuberarietalia guttatae* on acidic soils, *Stipo-Trachynietalia distachyae* on alkaline to neutral soils and *Malcolmietalia* on sandy soils.

Local speciation due to habitat heterogeneity may be common in plants due to random genetic drift and the selection of novel variants if they happen to have an adaptive advantage in novel ecological conditions, or if they happen to attract with higher frequency a pollinator different from that of the ancestors (LEVIN 1993). This two-fold process may be particularly important in peripheral populations due to their small size, potential isolation, inbreeding, wider numerical fluctuations in the population than in the barycentre of the range. Genes with no major impact on fitness in large populations may confer a selective advantage in the novel conditions experienced by smaller, isolated populations (LEVIN 1970). In Sicily, the abundance of micro-species of *Ophrys*, *Allium*, *Centaurea*, *Helichrysum*, *Brassica* may be the result of local differentiation driven by niche heterogeneity and/or diversification of pollinators in small sized populations.

4. Human influence on habitat fragmentation

Over the centuries, Sicily has attracted many human cultures and civilizations, leaving behind a unique blend of natural and cultural heritages all over the island. The Sicilian lands have been a time Phoenician-Carthaginian or Greek, Roman, Byzantine, Arab, Norman, Swabian, French and Spanish, just to name the origin of some of the most influential settlers of the island. Human presence in Sicily knows no pauses since 14-13 millennia (MANNINO et al. 2012), and not only species but entire plant assemblages were probably erased - or at least intensively shaped - by the early onset of agro-silvo-pastoral practices, especially during the past three millennia (TINNER et al. 2016, and references therein).

Through the centuries, rural communities have managed their environment and farmed the land in their own natural way, creating a rich diversity of landscapes, choral representation of historical identity of the territory and cultural human heritage (Fig. 3).

Until the recent past, agro-silvo-pastoral practices induced the prevalent imprint on the Sicilian landscapes. Traditional small-scale farming contributed to the development of highly complex socio-ecological systems, which are only partially known and investigated. The vegetation of the island shows almost everywhere the traces of a long-lasting exploitation of the land.

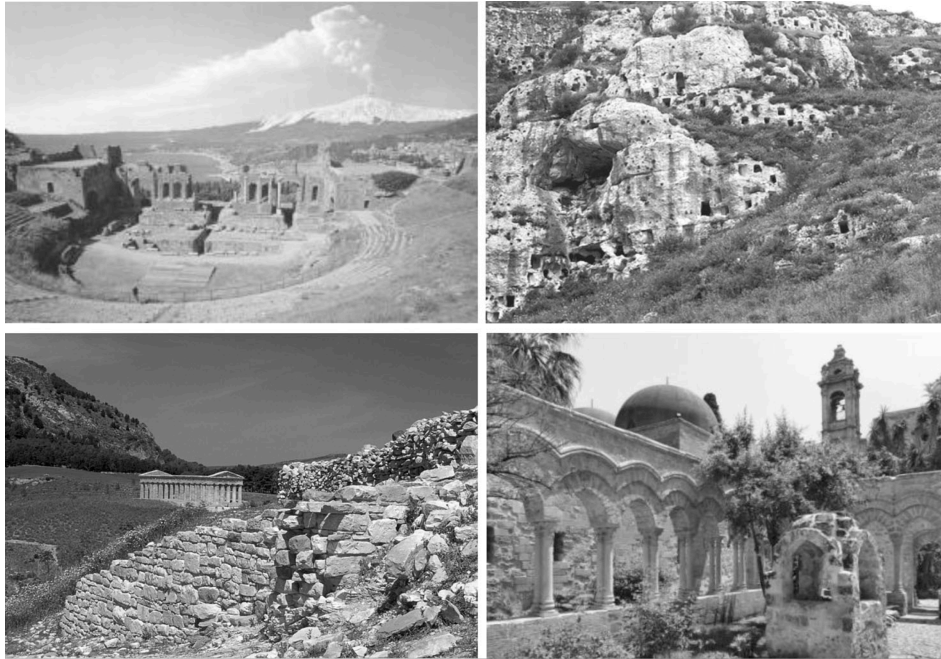


Fig. 3: examples of Sicilian UNESCO world heritage: the Greek theatre of Taormina, built in the third century BC with Mt. Etna in the background (above, left); the rocky Necropolis of Pantalica, containing over five thousand tombs carved from the 13th to the 7th century BC and vestiges of Byzantine early medieval settlements (above, right); the temple of Segesta, built in the 420's BC and left unfinished because of the Carthaginian conquest of the city (bottom, left); Cloister and Arab cistern of San Giovanni degli Eremiti, founded as a church in the 6th century AC, converted into a mosque after the Islamic conquest of Sicily and returned to the Christians by Roger II, after the establishment of the Norman domination in Palermo (bottom, right). (Photos Guarino)

The remarkable landscape diversity of Sicily had a direct influence not only on the number of species, speciation processes and genetic variability in the natural vegetation, but also on the human cultural diversification and stratification, which is one of the main features of the island. In the last ten thousand years, since the beginning of agriculture and commercial trading, the human activity increased the natural patchiness of the Sicilian landscapes up to the exasperation. Many alien plants reached the island from their original milieus and, in some cases, they gave rise to new polyploid populations, sometimes hybridogene, which occasionally (see, for instance, *Poa annua* and *Veronica persica*) achieved a worldwide success (BRULLO & GUARINO 2007).

Even if the effects of the human interaction with the native flora, in terms of species migration and habitat fragmentation, are rather evident and relatively well known, also in this case there are some still unsolved open questions: for instance, it is hard to explain why some species, which in the Eastern Mediterranean are clearly favoured and spread by transhumance and pastoralism, in Sicily remained shelved on the Hyblaean Plateau, without having spread to the carbonatic substrates of the rest of the island. This is the case of *Phlomis fruticosa*, *Ferulago nodosa*, *Salvia triloba*, *Sarcopoterium spinosum* which are very common in the Hyblaean district but absent from the rest of the island, if we except some small and localised occurrences of *Phlomis fruticosa* near Palermo (GIANGUZZI et al. 1995) and in the Peloritani Mts. (SCIANDRELLO et al. 2013).

At present times, the Sicilian flora counts approximately 400 fully naturalized xenophytes, half of which are archaeophytes. The only well preserved patches of natural vegetation are limited to the most inaccessible places (cliffs, screes, rocky ledges, very steep slopes and windy ridges, plus the Etnean heights). In total, they cover a surface of about 7300 ha, i.e. 0.29% of the island (BAZAN et al. 2009). With reference to the phytosociological classification of the Sicilian vegetation (GUARINO et al. 2017), the best preserved natural plant communities of the island are those belonging to the following syntaxa: *Rumici-Astragaletea siculi* (orophilous chamaephytic vegetation), *Dripidetea spinosae* (hemicryptophytic and chamaephytic vegetation of screes, talus slopes and riverbeds) *Saxifragion australis* (chasmophytic vegetation on alkaline rocks of the top of mountain ranges), *Dianthion rupicolae* (chasmophytic vegetation on alkaline rocks up to 800 m a.s.l.) and, in part, *Crithmo-Staticetea* (halo-chasmophytic vegetation of rocky coasts).

The Sicilian woodlands can be also included in the relatively well preserved natural vegetation, although most of them are (or have been until recent) disturbed by husbandry, periodical coppicing and frequent arsons. In total, Sicilian woods are covering approx. 72000 ha, i.e. 2.9% of the island (BAZAN et al. *l.c.*). The rest of the island is mostly colonized by secondary and anthropogenic vegetation. The secondary vegetation includes chestnut and hazelnut groves and reforestations (mainly *Pinus* spp. and *Eucalyptus* spp.), scrublands (*Pistacio-Rhamnetalia alaterni*, *Prunetalia spinosae* and *Pyro spinosae-Rubetalia ulmifolii*), garrigues (*Cisto-Micromerietea julianae*, *Cisto-Lavanduletea stoechadis*), perennial semi-natural grasslands (*Molinio-Arrhenatheretea*, *Lygeo spartii-Stipetea tenacissimae*), covering in total 23.12% of the island.

The synanthropic vegetation (*Artemisietea vulgaris*, *Papaveretea rhoeadis*, *Chenopodietea*, etc., reviewed in BRULLO et al. 2007) is widely distributed on 1,245,000 ha, i.e. nearly 50% of the island, wherever an extensive agriculture is (or have been until recent) performed. Most of the Sicilian territory is occupied by hard-wheat fields, but other forms of dry-land farming, like olive groves and plantations of almond, pistachio, ash-tree, carob tree, still characterize a relevant part of the Sicilian rural landscape (Fig. 4).

As a consequence of agricultural intensification and urban sprawl, several traditional man-made landscapes and habitats, such as dry stone terraces and fallows (RÜHL & PASTA 2008, LA MANTIA et al. 2011) or salt pans (TROIA 2006) are fading, with impressive consequences on the overall plant species richness. Currently, those traditional landscapes and many others suffer abandonment or, worse, the imposition of new transformations to which we refer with numerous neologisms: coastalization, urban sprawl, gentrification, etc. (GUARINO et al. 2014.). Nowadays intensive agriculture covers around 25% of the island. Citrus groves, orchards, greenhouses and vineyard are included here. The impact of intensive agriculture is progressively increasing, dealing with the popularity of the Sicilian wines and early fruits.

Mechanized agricultural practices, chemical fertilizers and pesticides are drastically selecting the weedy plants, penalizing the Mediterranean plants and enhancing the chances of non-native weeds, which also take advantage of nutrient- and water input. Modern technology, like everywhere in the world, underpin the modern trend ‘from local to global’. It is hard to believe that ubiquitous plants, like *Ailanthus altissima*, *Oxalis pes-caprae* or *Pennisetum setaceum*, colonized Sicily such a short time ago. They belong to a process of ‘banalisation’ of the landscape that is one of the newest forms of global impact.

On the other hand, approximately 1/4 of the whole Sicilian flora (about 750 taxa) has got a remarkable biogeographical and systematic interest (BRULLO et al. 1995; RAIMONDO et al. 2011). Many of these elements are currently threatened with human activities. Most natural



Fig. 4: examples of traditional rural landscapes of Sicily: preparation of a charcoal kiln in coppice, Etna, 1967, courtesy of Salvatore Cavallaro (above, left); the wheat harvest at Milena, 1927, courtesy of Charlotte Day Gower (above, right); parceled Hyblaean agricultural landscape, Donnafugata, 2002 (bottom, left); terraced olive grove, Ragusa, 2017 (bottom, right). (Photos Guarino)

communities have been degraded or permanently altered throughout Sicily and surrounding islets. The natural vegetation is threatened by continuing conversion to agriculture, pasturelands and urban areas. Land abandonment, frequent fires, logging of remaining native woodlands, exotic species, intensive grazing and browsing are also common threats, as well as the touristic exploitation of the coastal districts. As Sicily has been a central crossroad of human activity for thousands of years, it offers a major perspective on all the problems and challenges of accommodating humans and nature in the much trampled Mediterranean basin.

Conclusions

The vascular flora of Sicily and surrounding islets is currently estimated in around 3250 native taxa and approximately 400 xenophytes (GIARDINA et al. 2007): floristically, the Sicilian territory turns out to be one of the richest in the Mediterranean. The high species-richness is primarily related to the high topographic and climatic heterogeneity of the island. Moreover, for its geographical position, Sicily can be defined the crossroad of the Mediterranean flora, as many species are reaching here the northern (*Reaumuria vermiculata*, *Rhus tripartita*, *Ziziphus lotus*, etc.), southern (*Allium ursinum*, *Fagus sylvatica*, *Ferulago campestris*, etc.), eastern (*Ambrosina bassii*, *Chamaerops humilis*, *Cistus crispus*, etc.), and western (*Fritillaria messanensis*, *Salvia fruticosa*, etc.) limit of their distribution range. These occurrences testify ancient biogeographical connections with the Eurasian and African mainlands (starting from the Messinian), as well as the plant migrations driven by the Plio-Pleistocene climate swings.

At the same time, the insularity and the geographical segregation of refuge areas (coastal capes, high mountain districts, N-facing mid altitudes of the Tyrrhenian mountain ranges) pro-

moted the survival of many biogeographical relics (not only the previously mentioned palaeo-endemics but also species linked to warm-humid conditions such as the ferns like *Pteris cretica*, *Woodwardia radicans*, etc.), and the differentiation of a rich endemic flora, among which the genera *Allium*, *Anthemis*, *Astragalus*, *Brassica*, *Centaurea*, *Erysimum*, *Limonium* and *Viola* display remarkable examples of schizo-endemism resulted from the splitting of ancient distribution ranges, combined with the efficient occupation of particular ecological niches.

The most fascinating premise of such a remarkable plant diversity is that most of Sicily was still under water during lower Pliocene (i.e. until 3.6 Ma), leaving many open questions, reviewed in this paper, on how and where the many ancient lineages and Palaeogene relicts currently growing on the island managed to survive. On that purpose, we hope that in the near future the extensive use of genetic molecular tools and procedures will allow to better assess the timing of the colonisation and differentiation-evolution processes giving birth to many enigmatic endemics of Sicily, in order to disentangle the effects of remote and recent events.

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