REVIEW PAPER

Plant Biogeography and Vegetation Patterns of the Mediterranean Islands

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Abstract

With about 11,100 islands and islets of which ca. 250 are regularly inhabited by human, the Mediterranean Sea represents one of the regions of the world with the most islands and archipelagos. These numerous islands represent a significant component of the Mediterranean biodiversity, notably with the presence of range-restricted species and peculiar vegetation types. The aim of this review is to provide a balanced view of this highly diverse phytoecological heritage, but also taking into account the medium sized islands and the smaller ones that have not been highlighted so far. Mediterranean islands constitute both a museum for ancient lineages (paleoendemic taxa) and cradle for recent plant diversification. The complex historical biogeography (paleogeographical events of the Neogene, Messinian salinity crisis, climatic and eustatic changes of the Pleistocene, influence of glacial events) has profoundly influenced the current patterns of plant diversity. These insular landscapes were also precociously impacted by prehistoric man, possibly by Neanderthals. Among the 157 large Mediterranean islands (i.e. with a surface area exceeding 10 km^2), 49 have a surface greater than 100 km^2. The main patterns and dynamics of vegetation on the largests islands (Balearic Islands, Corsica, Sardinia, Sicily, Croatian islands, Greek islands, Crete, Cyprus) are summarized. Then, the specific ecosystem functioning (disturbance, plant-animal interactions) and vegetation structures of the small Mediterranean islands (i.e. a surface area less than 10 km^2 or 1000 ha), are highlighted by evoking successively the small rocky islands, the volcanic ones, and the sandy and flat islands. Owing to their uniqueness and fragility, Mediterranean islands urgently need some integrated and ambitious conservation planning, aiming at the long-term preservation of their outstanding biotic and cultural heritage.

Keywords Ecosystem structure · Endemism · Insularity · Mediterranean-type ecosystems · Small island

Introduction

The profound environmental heterogeneities and the complex historical biogeography explain the high diversity of landscapes and vegetation types on islands of the

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Mediterranean Basin, one of the 36 biodiversity hotspots identified around the world (Médail & Myers, 2004). With about 11,100 islands and islets (F. Médail, ined.) of which ca. 250 are regularly inhabited by human (Arnold, 2008), the Mediterranean Sea represents one of the regions of the world with the most islands and archipelagos. The numerous islands represent a significant component of the Mediterranean biodiversity, notably with the presence of range-restricted species and peculiar vegetation types (see Vogiatzakis et al., 2008; Médail, 2013, 2017; Thompson, 2020). These highly diversified insular biotas and their unicity are the result of their different geographical features inducing diverse biogeographical influences and bioclimatological characteristics (high climate variability, increasing dryness from West to East), the varied consequences of paleogeographical events, and their present wide ranges of size (from the largest island of Sicily with 25,426 km² to small islets of few dozen square meters), altitude (from 3342 m of Mt. Etna to flat islets of only few meters a.s.l.), and geology and geomorphology. The diversity of ecosystems of the Mediterranean islands is also explained by the long-lasting influence of man who acts as a major 'designer' of landscapes and vegetation dynamics through burning, cutting, grazing and ploughing (Blondel, 2008). The heritage of human activities indeed has had profound consequences on the distribution and dynamics of insular vegetation that is currently threatened by global environmental changes (Médail, 2017). But if the major vegetation structures of the large Mediterranean islands are relatively well known, they present only a partial synthesis (e.g., Greuter, 1995, 2001; Vogiatzakis et al., 2008) inasmuch as they do not take into account properly the insular biodiversity from the point of view of biogeography and environmental characteristics. The aim of this review is to provide a balanced view of this highly diverse phytoecological heritage, but also taking into account the medium sized islands and the smaller ones that have not been highlighted so far.

Historical Biogeography of Mediterranean Islands, Museum and Cradle of Plant Biodiversity

The history of the Mediterranean Basin setting is highly complex both from geologic and climatic points of view (e.g., Dercourt et al. 1993; Woodward, 2009), and this has had profound consequences on the biogeographical process explaining the current species assemblages and vegetation types. Although some pre-Mediterranean elements exist since the Paleogene, the main diversification of Mediterranean species took place during the Miocene, notably in conjunction with the collision of the African and Eurasian platforms and with movement of the Arabian plate. Recurrent episodes of species dispersal and vicariance have occurred between the eastern and western Mediterranean regions in relation to the several marine regressions/transgressions and the ongoing rise of Alpine and Atlas orogenies. These various events explain the reticulate biogeographical history of the Mediterranean Basin. Thus, the Mediterranean species pool arises from diverse biogeographical origins, and although it includes still some subtropical species, mostly derived from African and Asian lineages, the extratropical species of autochthonous and northern lineages predominate.

Concerning the Mediterranean islands, it is necessary to emphasize that the majority of them are 'continental islands' sensu lato (including continental shelf and continental fragments), i.e., they were once part of the continent before their separation and drifting (as is the case of the small continental sub-plate of Corsica-Sardinia, which separated during the Oligocene), or during various episodes of low sea level (during times of marine regression). Most of the islands have become progressively isolated from the mainland and from each other by a complex combination of tectonic and glacio-eustatic processes. The Aegean archipelago is a seminal case because its biogeographical structure corresponds well to the region's palaeogeographical evolution from the middle Miocene to the end of the Pleistocene (Kougioumoutzis et al., 2017).

But there also exists a few Mediterranean 'oceanic islands' in the geological sense, such as volcanic islands (see below) and Cyprus, which emerged from the bottom of the sea and has probably never experienced any connection with the mainland since at least the late Miocene (Poulakakis et al., 2013). Vigne (1999, 2014) also proposed to distinguish a 'true island' as an island which was '*separated from the mainland for a substantial period of time, throughout the Late Glacial and the Holocene*' (Vigne, 2014), i.e., for about 20,000 years. He estimates that this category encompasses about 20 islands or archipelagos, including the five large islands of Cyprus, Crete, Sardinia, Corsica, and Mallorca, but not Sicily, which is a special case because of its proximity to the mainland and the existence of land-connection during the marine regression of the Würm glaciation.

Influence of Neogene Paleogeographical Events

The Tyrrhenian islands present an outstanding example of the importance of ancient paleogeography to explain current patterns of plant distribution and biogeographical links. The eastern Balearic Islands (Menorca and Majorca), Corsica, Sardinia, and part of Sicily are some of the remnant areas that once belonged to the Protoligurian massif, a west-Mediterranean Hercynian formation that was fragmented in the mid-Tertiary (Oligocene-Miocene), causing, notably, the rotation and migration of the Corsica-Sardinia block between 23 Ma (= million years) and 16 Ma. The distribution of numerous Tyrrhenian endemic plants shared between these islands (e.g., *Arenaria balearica, Delphinium pictum, Helicodiceros muscivorus, Teucrium marum*) reflects this crucial paleogeographical event. Nevertheless, more recent evolutionary histories related to the climatic aridification since the Pliocene (ca. 3.2 Ma) and the onset of the Mediterranean climate also strongly influence the phylogeography of the species of the Tyrrhenian endemics, as suggested for *Thymus herba-barona* (Molins et al., 2011).

Mediterranean islands represent major refugia areas and conservatories of old, often mid-Tertiary floras, with numerous relict plants characterized by a prolonged evolutionary standstill (Médail & Diadema, 2009). The relictual nature of Mediterranean island plants is well supported by the presence of paleoendemics restricted to one or few of these islands and by the existence of some relicts of the subtropical Tertiary environments. This is the case, for example, of the Tethysian-Paleotropical fern *Woodwardia radicans* (Corsica, Sicily and Crete), of the relic tree endemic to the Cretan mountains *Zelkova abelicea* (Christe et al., 2014), of many highly isolated taxa that live only or mostly on Mediterranean islands, such as the monotypic genera of Apiaceae *Horstrissea* on Crete (Egli et al., 1990), *Naufraga* on Mallorca (Fernández-

Mazuecos et al., 2014), *Petagnaea* and *Siculosciadium* on Sicily (De Castro et al., 2009; Brullo et al., 2013) (Table 3).

Messinian Salinity Crisis

At the end of the Tertiary, the Messinian salinity crisis of the Late Miocene, represents also a major biogeographical event caused by the interruption of marine relationships due to the closure of the Mediterranean–Atlantic gateways (now the Gibraltar Strait). This episode induced a considerable evaporation and an almost complete desiccation of the Mediterranean Sea between 5.96 Ma and 5.33 Ma, with two evaporitic steps (Fig. 1) (CIESM, 2008). During these two episodes, the formation of several land bridges favoured dispersal-vicariance events and species radiations. Some opportunities existed for the migration and establishment of drought-resistant plant species and steppic communities (e.g., with *Lygeum spartum*) inasmuch as the major islands were completely joined to the continent. Therefore, the occurrence of several xerophytic or halophytic plants of North African obedience (*Asparagus horridus, Atriplex mollis, Erodium neuradifolium, Frankenia corymbosa, Lycium schweinfurthii, Periploca angustifolia,* etc.) on the offshore islands of southern Crete (Gavdhos, Gavdopoula, Chrisi, Koufonisi) (Bergmeier et al., 2001, 2011), could be a testimony of this Messinian paleogeography. Then, five million years ago, the beginning of the Pliocene was marked by the return of the sea and this resulted in the separation of some major islands (Crete and Karpathos, Corsica, Sardinia, Balearic Islands) from landmasses.

Climatic and Eustatic Changes of the Pleistocene

The onset of Mediterranean climate is relatively recent, and paleoclimatic reconstructions demonstrate that cooling and drying, with the combination of summer drought and mild winter temperatures, came about quite rapidly in Late Miocene or Early Pliocene (ca. 5–3 Ma) (e.g., Tzedakis, 2009). In the Mediterranean Basin, a gradual but deep climatic change occurred during the Pliocene (3.5–2.4 Ma), with a significant drop in temperature and a marked seasonality in
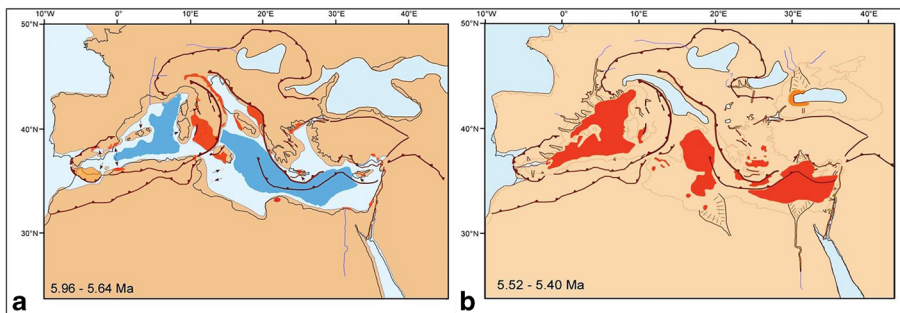
Fig. 1 Paleogeographical maps of the Mediterranean Basin during the two drying up episodes of the Messinian salinity crisis (**a**: first episode, between 5.96–5.64 Ma; **b**: second episode, between 5.52–5.40 Ma). Areas in dark orange correspond to hypersaline deep basins (after J.-P. Suc, ined., pers. comm.)

thermal and rainfall regimes; the stabilization of the summer drought arises here at ca. 2.6 Ma. Severe cooling episodes during the late Pliocene and Early-Middle Pleistocene also profoundly affected the biogeographical footprint of several Mediterranean lineages and plant assemblages (Tzedakis, 2009). The deterioration of Tertiary warm climates resulted in the extinction of several subtropical and warm-temperate species during the Plio-Pleistocene, of 45 genera of megathermic and warm-temperate ligneous species distributed in the north-western part of the Mediterranean sea (Quézel & Médail, 2003).

Other important features issue from the repeated drastic marine regressions that have occurred during the recurrent ice ages, between the end of the Pliocene and until the Last Glacial Maximum (LGM, ca. $18,000 \pm 2000$ years ago). These eustatic changes consist in more or less severe lowering of sea level, of about 100 and 150 m below current levels, allowing for the possible terrestrial migration of a more competitive cool-temperate flora onto some offshore islands. This is the case of many Aegean islands (Kougioumoutzis et al., 2017), except Rhodes, the Cyclades and the Crete-Karpathos island group, which remained completely isolated throughout the Pleistocene. These land-bridge connections explain geodispersal patterns and thus some biogeographical affinities between actually distant and isolated floras.

Although long-distance dispersal of seeds by wind, birds or marine currents almost certainly played an important role in Mediterranean islands' colonization, evidence of these processes are still rare except for common halophytes (Westberg & Kadereit, 2009). Nevertheless, an eastward, long-distance dispersal is invoked to explain the geographical disjunction of a western Mediterranean coastal sand-dune plant (*Armeria pungens*) whose Corso-Sardinian populations probably derived from ones inhabiting southwest Portugal (Piñeiro et al., 2007), and the presence of an highly isolated population of the semi-ruderal shrubs *Malva subovata* (= *Lavatera maritima*) on a small island of western Corsica (Gargalu), probably dispersed here by seabirds (Villa-Machío et al., 2018).

Insular Glacial Refugia

Phylogeography and paleocology underline that glacial refugia represent crucial areas for the long term persistence and dynamics of modern biodiversity in temperate regions such as the Mediterranean Basin (Médail & Diadema, 2009). Glacial refugia constitute territories sheltered from the strong climatic deteriorations during Ice Ages, and where species survived by avoiding the drastic consequences of severe cold and aridity during glacial events like the Last Glacial Maximum (LGM). Studies of glacial refugia reveal several interesting facts. First, there exists a clear influence of Pleistocene climatic cycles on patterns of species-richness and endemism. Second, full-glacial refugia have also had a powerful influence in shaping current patterns of genetic diversity. Finally, these refugia played an important role on vegetation dynamics during previous interglacial periods of the Pleistocene. These areas contributed to the forest recolonisation process that started approximately 13,000 years ago in the Mediterranean Basin and continued throughout the whole of the Holocene.

The major Mediterranean areas where temperate and thermophilous species survived are the three Iberian, Italian, and Balkan peninsulas, the submontane and mountain
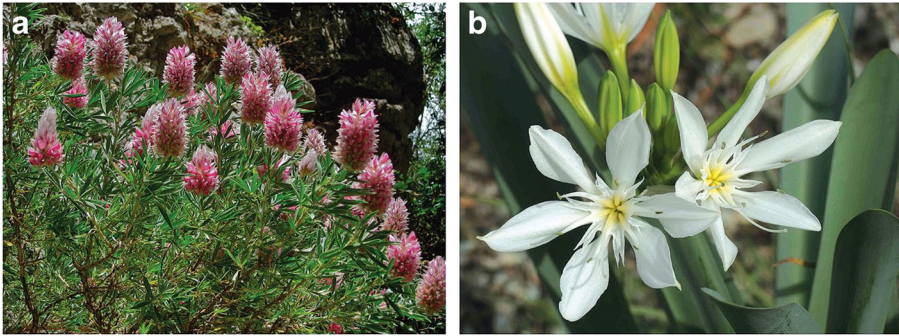
Fig. 2 As key refuge areas, Mediterranean islands contain many endemic plants. **a**: the Cretan endemic shrub *Ebenus cretica* (Fabaceae), Imbros Gorges, Crete, IV.2007; **b**: the bulb *Pancratium illyricum*, an endemic Amaryllidaceae from Corsica, Sardinia, and Tuscan archipelago; Cap Corse, V.2015 (F. Médail / IMBE)

margins of North Africa, Turkey, and Catalonia-Provence, but also the largest Mediterranean islands (Médail & Diadema, 2009) where occur numerous endemic plants that can be quite common (Fig. 2).

Recent Plant Diversification

If Mediterranean islands have served as important Tertiary and glacial refuges, their role in the local and more recent differentiation of plants is probably as important. These islands possess highly polymorphic species and vicariant endemic plants resulting from more or less recent speciation events (e.g., *Limonium, Centaurea*) (Rosselló, 2013). Isolation and environmental heterogeneity have favoured diverse evolutionary processes of gradual speciation of plants, such as genetic drift or adaptative radiation. Chromosomal rearrangements (karyotype changes, dysploidy, aneuploidy, auto- and allopolyploidy) and hybridization have also played key roles in the rapid speciation of several endemic lineages on the Mediterranean islands (Verlaque et al., 1995), even between the two narrow endemic *Centaurea* species on Tavolara island (NE Sardinia) (Pisanu et al., 2011). The analysis of karyological evolution of the endemic flora of the Balearic Islands shows that nine polyploid endemic species are probably of autochthonous origin, in contrast with the low rates of polyploid evolution reported from floras of oceanic archipelagos (Rosselló & Mercedes, 2008). On the Central Mediterranean islands, the taxa of the *Centaurea cinerea* group were assumed to be old relics but molecular dating supported recent, allopatric diversification; this homoploid speciation, whose onset dates back to less than 250,000 years ago within the Sicily group, likely followed transoceanic seed dispersal (Hilpold et al., 2011). Few well-studied examples are also found in the Aegean islands, such as the obligate chasmophytes of *Erysimum* sect. *Cheiranthus* (Snogerup, 1967) and *Nigella arvensis* complex, where the history of isolation of these multiple islands determine pronounced random plant differentiation by genetic drift following fragmentation of a former contiguous distribution area, or after long-distance dispersal. Detailed molecular studies of *Nigella* of the Aegean archipelago demonstrate that the main diversification process occurred during the Late Pleistocene (Bittkau & Comes, 2005). Therefore, if Mediterranean island floras are in part relictual, their evolutionary dynamics are probably underestimated, in particular on small islands

subject to harsh and stochastic environmental conditions. Unfortunately, we still lack studies about population genetics of contrasted micro-insular systems with respect to the type of islands (continental vs. oceanic), the duration of isolation, and to other environmental characteristics (Rosselló, 2013).

Past Vegetation Dynamics of Mediterranean Islands during the Holocene in Relation to Climatic Changes and Human Impacts

First Impacts by Man and Holocene Climatic Changes

During the Pleistocene and even more so during the Holocene, the Mediterranean islands environment were strongly affected by human uses and disturbances. So, vegetation dynamics is intimately linked to that of human societies (e.g., Ghilardi, 2016). But evidences of the earliest date of island colonisations by prehistoric man — a 'Paleolithic seafaring by Stone Age sailors' (Simmons, 2014) — are still hotly debated in the Mediterranean (Broodbank, 2006; Leppard, 2014; Runnels, 2014), because it is often difficult to assess whether human occupation was temporary along the coasts or when it became permanent (Table 1). In southern Crete (Plakias region), a lower 'Paleolithic occupation' dated to at least 130,000 years ago was suggested (Strasser et al., 2010), but this finding must be reasonably rejected inasmuch as the supposed 'prehistoric tools' more likely correspond to geofacts (J.-D. Vigne, pers. comm.). In

Table 1 Tentative chronology of first human sporadic presence and permanent settlement on the main Mediterranean islands

Island	Earliest date of sporadic human presence	Earliest date of permanent human settlement	References
Cyprus	12,200 yr (Aetokremnos)	11,200–10,600 yr (Shillourokambos)	Vigne et al. (2012)
Crete		ca. 9000 yr (Knossos)	Efstratiou et al. (2013)
Sicily[a]		16,520-15,980 yr (Riparo del Castello)	Di Maida (2020)
Malta		ca. 7000 years (7266–6846 yr) (Skorba)	Trump (2008)
Sardinia	ca. 9800 yr	ca. 7700 yr	Costa (2004) Rowley-Conwy et al. (2013)
Corsica	10,000–8000 yr (Monte Leone)	ca. 7700 yr	Costa (2004) Rowley-Conwy et al. (2013)
Mallorca and Menorca	ca. 7000 yr	4420–4220 yr	Burjachs et al. (2017); Cherry and Leppard (2018)

[a] Sicily is a special case due to its proximity with the Italian Peninsula and episodic terrestrial connections between them during the Last Glacial Maximum (cf., Vigne, 1999, 2014; Simmons, 2014). All the dates are expressed in calibrated years before present

Greece, probable Middle Paleolithic stone tools were found on the Cycladic island of Melos and on the Ionian islands of Kefalonia and Zakynthos that were insular since at least 110,000 years ago (Ferentinos et al., 2012). This could suggest a possible sea-crossing by Neanderthals (Broodbank, 2006) even if the archeologial setting is still debated (Simmons, 2014).

The first tangible testimonies of long human presence on a 'real' Mediterranean island seem to occur on Cyprus. The settlement of hunter-gatherers dates back at least around 12,500 years ago whereas the development of agriculture occurs between 11,200–10,600 years ago (Vigne et al., 2012; Zazzo et al., 2015). Thus, until now, Cyprus represents the only island where an Epipaleolithic human occupation is well attested. We have to exclude Sicily, for which an early human occupation during Upper Paleolithic was frequently indicated (e.g. Leighton, 1999), but new absolute dates suggest the current complete lack of any sites or findings until the Lateglacial and a probable late colonization of the island (Di Maida, 2020). In the western Mediterranean, the oldest sporadic settlements on islands date back to the Mesolithic (ca. 10,000 years ago) in Corsica and Sardinia, but with a gap until the Early Neolithic when these two islands were really colonised during the initial phase of neolithisation around 7700 years ago (Rowley-Conwy et al., 2013). It is noteworthy to emphasize that this Neolithic occupation also concerns smaller islands like the Tuscan archipelago (Ducci, 2000) or the Aeolian islands from which the famous obsidian was transported into several areas, for example to the central Adriatic island of Palagruža, i.e., a long journey of ca. 185 km (Castagnino Berlinghieri, 2011). This reflects the maritime abilities of these first farming migrants. Genetic analysis of the genome of human populations bordering the Mediterranean supports also the hypothesis that a maritime route and island hopping was prominent and that Neolithic migrants reached southern Europe through an Anatolian route and then, by sea, via the Dodecanese islands, Crete, and Italy (Paschou et al., 2014), in accord with archaeological findings. It seems that better dated and interdisciplinary investigations are hardly needed inasmuch as it has already been stated, '*more systematic studies have shown that the Mediterranean Sea was indeed not necessarily a barrier, but rather a corridor for pre-Neolithic seafarers*' (Simmons, 2014). Unfortunately, early human impacts on insular environments remain still elusive.

A severe environmental event of the Late Pleistocene and early Holocene, with probably many detrimental consequences for insular Mediterranean vegetation and landscapes, is the mass extinction of most of the endemic mammals on islands. A debate concerns the tempo and mode of this extinction and whether it resulted only from natural environmental changes, notably the global climate changes of Younger Dryas or the rapid Holocene reheating, or if it were caused mainly by humans ('overkill hypothesis'), or a combination of both. The results of Alan H. Simmons on Cyprus suggest the key role of human-induced extinctions for all the large 'mega-nano-mammals' of Mediterranean islands, and this continued during the Holocene. This could be illustrated by the disappearance of the dwarf hippos, elephants and deers on Malta, Crete, and Cyprus, or *Prolagus* on Corsica and Sardinia following the islands' colonization by humans. Thus, based upon the well-studied Cypriot site of Akrotiri, Simmons (1999) hypothesized that the accumulation of hippo and elephant bones was the result of human hunting. But new analyses on calcinated bones suggest that that the pygmy hippopotamus was already extinct, or at the brink of extinction, when

Epipaleolithic people arrived on Cyprus during the middle of the Younger Dryas and that they probably used bones as a source of fuel (Zazzo et al., 2015). On the whole, the implication of man into the extinction of large endemic mammals is now questioned when there exist precise dates of extinction such as in the Balearic Islands for the mountain goat *Myotragus balearicus* (Welker et al., 2014) or in Corsica (J.-D. Vigne, pers. comm.). But on this latter island, the extinction pattern seems different for the endemic small mammals, because there is strong evidence involving human impacts. Concerning the rodent *Prolagus sardus*, extinction is indeed recent inasmuch as the 'rabbit-rat' disappeared from the small island of Gargalu (western Corsica) less than 2500 years ago, and perhaps even during the Middle Ages in relation to deforestation, huge cultivation practices, and the arrival of new alien mammals such as the black rat, *Rattus rattus* (Vigne & Valladas, 1996).

We can imagine the strong impact that an endemic herbivorous fauna may have had on the vegetation composition and structure on small island ecosystems, and even on the largest Mediterranean islands (Caloi & Palombo, 1995), before their total extinction. This is the case of Crete, where the remarkably high number of co-occurring endemic thorny cushion subshrubs belonging to different families could not have evolved just as a sudden response to Neolithic farming (Kozlowski et al., 2014). Here grazing and browsing by deer, dwarf elephants and/or hippos, which required large and open feeding grounds, are known to have occurred long before human arrival (Caloi & Palombo, 1995). The same happened on the Balearic Islands where DNA analysis of ancient coprolites from *Myotragus balearicus*, extinct between 7700 and 6050 years ago, shows that the Balearic box (*Buxus balearica*), now locally rare, was a major component of the diet of this large mammal (Welker et al., 2014).

Since the Neolithic revolution, landscapes have been profoundly shaped by man for the past 10,000 years in the eastern Mediterranean, and for about 7500 years in the western part in relation to human colonization or acculturation (Fig. 3; Table 1) (Zeder, 2008). The ecological consequences of these first human impacts on Mediterranean biodiversity is also variously appreciated, since two contrasting theories have been
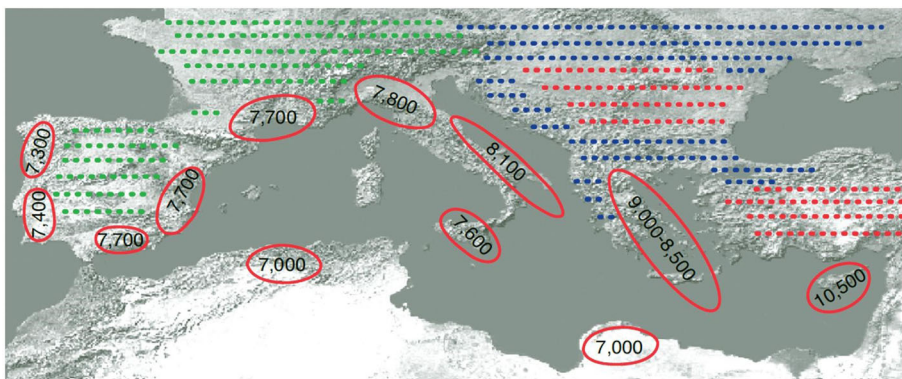
Fig. 3 Synthesis of the Neolithic expansion in the Mediterranean Basin. The location, with approximate dates (in calibrated years BP), of colonist farming enclaves is indicated by red ellipses. Red dots represent areas that are proposed to have been settled by colonist farmers; green dots indicate areas where indigenous foragers adopted elements of the Neolithic package; blue dots indicate areas of proposed integration of colonist farmers with indigenous foraging groups (Zeder, 2008)

proposed (Blondel, 2006). The first is the 'ruined landscape' or 'lost Eden' theory advocated by Thirgood (1981) and Attenborough (1987), in which it is argued that deforestation and overgrazing induced a deep degradation and desertification of Mediterranean landscapes, with the disappearance of formerly magnificent and large forests. The second theory was proposed by O. Rackham after his studies devoted to the historical ecology of the Cretan landscape (Rackham & Moody, 1996) and soon after expanded to the whole Mediterranean Europe (Grove & Rackham, 2001). This theory '*dismisses the supposedly detrimental effects of humans, arguing that the imaginary past idealized by artists and scientists does not reflect reality*' (Blondel, 2006). On the contrary, it considers that humans favoured biodiversity by shaping a variety of cultural landscapes, and that even many traditional land-use practices could act as surrogates of natural disturbances (Blondel & Aronson, 1995). According to this line of thought, savannah-like landscapes would be fairly characteristic of the Mediterranean Basin (Grove & Rackham, 2001). Of course, the 'ecological reality' is, as usual, much more complex and is positioned between these two extremes. Insular landscapes depend both on the specificities of environmental constraints and on local usages developed by diverse human societies.

Along with human impact, a second factor that has played an important role in shaping insular vegetation change is the progressive aridification of the climate during the Holocene. In Crete, some pollen assemblages suggest that driest conditions occurred from about 9375 to 8310 years ago, with a vegetation composed of open deciduous-oak forest (Bottema & Sarpaki, 2003). In central and western Mediterranean, dryness happens more recently, during the middle Holocene (ca. 4500 years ago) (Magny et al., 2012). In the Balearic Islands, aridification induces the replacement of mesophylous forests with *Corylus, Alnus,* deciduous *Quercus*, *Buxus balearicus* and perhaps *Fagus* (but long-distance dispersal of pollen cannot be excluded) by xeric-type communities with an increase of sclerophyllous species as it occurs in Sicily around 4500–4000 years ago, even if the wooded periods of these two islands are not synchronous (Pérez-Obiol & Sadori, 2007). On the whole, human actions, amplified by progressive warming and drying of the climate, have probably led to the extinction of several mesophilous species and communities and to the disruption of formerly large populations into small and isolated fragments as a consequence of habitat deterioration.

Transformation of Island Landscapes during the Antiquity

During the Antiquity, human impact on island ecosystems was undoubtedly profound and was exerted especially on two types of natural habitats, forests and wetlands-marshes, as summarized by Brun (1996) for several islands of the Central Aegean. The early destruction of forests by man for wood and the alteration of forest regeneration due to overgrazing represent a common pattern throughout the whole of the Mediterranean area (Thirgood 1981; Quézel & Médail, 2003). Alteration of forests first concerned the low plains due to increase cropland development that particularly impacted deciduous forests with various keystone species of oak. In Greece, for example, deciduous forests were largely converted to permanent crops or olive groves during the first millennium BC (Gerasimidis, 2005). This is the case of the forests of Valonia oak (*Quercus ithaburensis* subsp. *macrolepis*) on the central Aegean islands (see below) (Fig. 4). In the western Mediterranean, oak forests of *Quercus pubescens* in
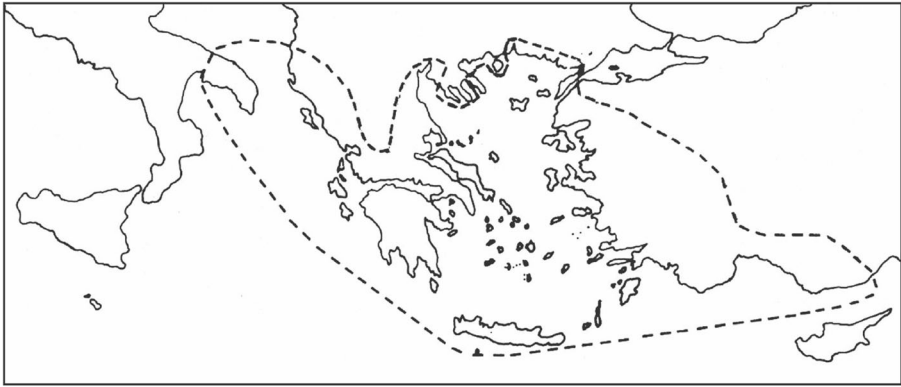
Fig. 4 Distribution range of a key north-eastern Mediterranean deciduous tree, the Vallonia oak (*Quercus ithaburensis* subsp. *macrolepis*), after Economidou (1981)

the Plaine orientale of Corsica were severely impacted by man (Gamisans, 1999), and the mixed *Quercus congesta* and cork oak (*Quercus suber*) forests of central and western Sardinia, which probably represent the remnants of formerly more extensive stands, were often turned into forest-savannahs similar to the Iberian dehesas (Quézel & Médail, 2003). Coastal marshes (Fig. 5) were still common and mentioned during the Greek Antiquity, for example on several islands of the Cyclades (Astypalaia, Leros, Rinia, Santorini, Serifos, Tinos, etc.), and the numerous places dominated by reeds are often named *Donakeus* or *Kalamos* (Brun, 1996). But these flat areas, with a deep fertile soil, were precociously drained and exploited, especially as malaria was rampant. In Aegean islands, the originality of the insular impact on wetlands probably relied on its earliness, because the favorable available lands were scarce when compared to the vast areas of the continental Greece (Brun, 1996). Without doubt this early pattern of land-use of wetlands applies to many other Mediterranean islands. Moreover, littoral wetlands were impacted from ca. 7000 years ago by a continued input of sea water in the wetlands, related to the mid-Holocene marine transgression.

Another originality within the structure of insular agriculture relies on space constraints imposed by the small proportion of low plains and the existence of often
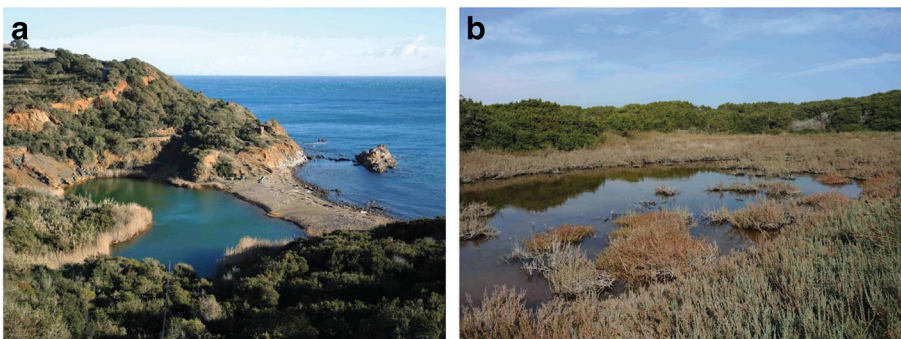
Fig. 5 Example of small coastal wetlands on two western Mediterranean islands. **a**: a freshwater pond in the eastern coast of Elba island (Tuscany), XII.2014; **b**: a semi-salty pond with *Sarcocornia fruticosa* surrounded by a shruby belt with *Juniperus phoenicea* subsp. *turbinata*, Piana island (Lavezzi, S Corsica), XI.2014 (F. Médail / IMBE)

mountainous landscapes. These topographic constraints have led the farmers, since Antiquity, to arrange the slopes in cultivation terraces to fix the soil and improve its fertility. Indeed, numerous small and medium islands were almost totally converted by this mode of land-use. This is particularly the case of the circum-Sicilian islands and the Aegean islands (Brun, 1996). On the small Greek island of Kea, the first travellers of the XVIII century in this area, notably the famous French botanist and naturalist Joseph Pitton de Tournefort, states, and rightly so, in his well documented *Relation d'un voyage du Levant fait par ordre du Roy* that '*During the Antiquity, this land was cultivated with the latest care, as appears from the walls that had been built up until the upper parts of the mountains to support the soils*' (Pitton de Tournefort, 1717). On this same island, in the nineteenth century, cultures still covered 85% of the island surface, mostly on cultivation terraces.

Although some tentatives of integrated historical ecology have been performed on large Mediterranean islands (Rackham & Moody 1996; Grove & Rackham, 2001; Rackham, 2008), attempts to do so for the smaller islands or archipelagos are indeed rare (Médail, 2021). But there are some that are related to the circum-Sicilian islands (Pasta & La Mantia, 2004), the Aegean islands taken as a whole (Brun, 1996), or more specifically like Antikythera (Bevan & Conolly, 2013). Thus, the modern view of the islands of the Aegean as barren, desolate, and windblown places can be challenged, and they were not necessarily those places of poverty and environmental disasters that earlier have been decried by the authors of the Classical and Hellenistic Antiquity (Brun, 1996). A necessary and more distanced perspective shows the strong environmental and socio-economic disparities in ancient Greece (V-II centuries BC) between large and relatively prosperous islands in the eastern part and the generally poorest smaller islands of the Cyclades.

Main Current Vegetation Patterns of the Large Mediterranean Islands

There exists exactly 157 large Mediterranean islands with a surface area exceeding than 10 km^2 (1000 ha), among which 86 (i.e., 55%) are located in Greece (Arnold, 2008). Forty-nine islands have a surface greater than 100 km^2, and of these 36 possess a surface areas greater than 200 km^2, and for the latter islands, the main vegetation studies are summarized in Table 2. Almost all Mediterranean island ecosystems are under the influence of the Mediterranean climate (Fig. 6), except for some parts of the high mountains of Corsica where there exists subalpine and alpine vegetation belts (Fig. 9a) with Euro-Siberian and even Artic-Alpine plant taxa (Gamisans, 1999, 2003). The most typical characteristics of Mediterranean ecosystems, compared to temperate or boreal biomes, are their spatial and temporal complexities inducing strong heterogeneities, in terms of physical factors (geography, geology, geomorphology, pedology, bioclimate), biological components, and species life-history traits (e.g., Médail, 2008). Paleo-geographical and historical episodes, current geographical and climatic contrasts have moulded both an unusually high biodiversity and ecological complexity, and favoured the emergence of a functional uniqueness for several ecosystems and vegetation types. High species richness and endemism due to contrasted biogeographical origins, and original functional dynamics at local and landscape

Table 2 The major 36 Mediterranean islands with a surface higher than 200 km^2 according to Arnold (2008) modified (*), and the main vegetation or phytogeographical studies (excluding pure floristic inventories) devoted to them (synthesis of F. Médail, with informations by M. Panitsa and S. Pasta)

| Island (local and English names)	Size (km^2)	Maximum altitude	Country	Main studies devoted to insular vegetation and plant biogeography
Sicilia (Sicily)	25,426.200	3342 m	Italy	Brullo et al. (1995, 2005b, 2012); La Mantia et al. (2001); Cullotta and Pasta (2004); Bazan et al. (2010); Giardina (2011); Gianguzzi et al. (2016); Guarino and Pasta (2018)
Sardegna (Sardinia)	23,821.000	1834 m	Italy	Arrigoni (1968); Camarda and Satta (1995); Bacchetta et al. (2009); Fenu et al. (2014)
Kypros (Cyprus)	9251.000	1953 m	Cyprus	Barbero and Quézel (1979); Costa et al. (1984); Géhu et al. (1984, 1990); Brullo et al. (2005a)
Corse (Corsica)	8679.800	2706 m	France	Gamisans (1976–1979, 1999, 2010); Géhu and Biondi (1994); Jeanmonod et al. (2015); Reymann et al. (2016); CBN Corse (2020)
Kriti (Crete)	8261.183	2456 m	Greece	Zohary and Orshan (1966); Barbero and Quézel (1980); Géhu et al. (1987); Zaffran (1990); Bergmeier (2002); Brullo et al. (2004); Bauer & Bergmeier et al. (2011)
Evvia (Euboea)	3661.637	1743 m	Greece	Krause et al. (1963); Trigas et al. (2008)
Mallorca	3620.858	1445 m	Spain	Bolòs and Molinier (1958); Rivas-Martínez et al. (1992b); Bolòs (1996)
Lesvos (Lesbos)	1635.998	968 m	Greece	Rauh (1949); Bazos (2005)
Rodos (Rhodes)	1401.459	1216 m	Greece	Carlström (1987); Géhu et al. (1989); Brullo et al. (2004)
Chios	842.796	1297 m	Greece	Rauh (1949)
Kefalonia (Cephalonia)	734.014	1628 m	Greece	Knapp (1965); Bolòs et al. (1996)
Menorca (Minorca)	693.587	357 m	Spain	Bolòs et al. (1970); Bolòs (1996)
Kerkyra (Corfu)	585.312	911 m	Greece	Biondi (1989)
Eivissa (Ibiza)	568.935	476 m	Spain	Rivas-Martínez et al. (1992a, 1992b); Bolòs (1996)
Djerba	526.460	55 m	Tunisia	Vanden Berghen (1977, 1978, 1979)
Samos	477.942	1434 m	Greece	Christodoulakis (1986); Christodoulakis and Georgiadis (1990)
Limnos (Lemnos)	476.288	429 m	Greece	Rauh (1949); Economidou (1981); Panitsa et al. (2003); Brullo et al. (2004)
Zakynthos (Zante)	406.619	756 m	Greece	–
Cres	*405.705	648 m	Croatia	Trinajstić (1997)
Krk	*405.218	568 m	Croatia	Trinajstić (1965)
Brač	394.570	780 m	Croatia	Domac (1965); Trinajstić (1990)
Naxos	389.434	999 m	Greece	Böhling (1994); Brullo et al. (2004)
Thasos	383.672	1207 m	Greece	Spanos et al. (2000)
Andros	383.022	995 m	Greece	Snogerup et al. (2006)
Lefkada (Lefkas)	301.106	1182 m	Greece	Hofmann (1968)
Karpathos	300.152	1215 m	Greece	Géhu et al. (1989); Höner (1991)
Hvar	299.660	628 m	Croatia	Domac (1965)

Table 2 (continued)

Island (local and English names)	Size (km²)	Maximum altitude	Country	Main studies devoted to insular vegetation and plant biogeography
Kos	287.611	843 m	Greece	Brullo et al. (2004)
Pag	284.560	349 m	Croatia	Horvatić (1934, 1963); Ljubičić et al. (2008)
Gökçeada (Imroz, Imbros)	279.240	672 m	Turkey	Seçmen and Leblebici (1978)
Kythira (Cythera)	277.746	506 m	Greece	Yannitsaros (1969)
Korčula	276.030	569 m	Croatia	Trinajstić (1973, 1995b)
Ikaria	255.320	1037 m	Greece	Christodoulakis (1996)
Malta	245.728	253 m	Malta	Lanfranco (2002); Brullo et al. (2020)
Elba	223.000	1018 m	Italy	Foggi et al. (2006); Carta et al. (2018)
Skyros	208.594	792 m	Greece	Maire (1921)

levels linked to stress effects, indeed represent key components of these ecosystems (Table 3).

The vegetation types usually considered as 'typically Mediterranean' are the evergreen and sclerophyllous shrublands and forests, dominated by sclerophyllous oaks under semi-arid (400 < P = annual rainfalls<600 mm) or sub-humid (600 < P = annual rainfalls<800 mm) bioclimates, corresponding to thermo-mediterranean and meso-mediterranean vegetation belts (Fig. 6; Table 4). Nevertheless, paleoecological data demonstrate that deciduous trees were the rivets of ecosystem dynamics during the postglacial period, notably in the northern Mediterranean, but these forests were severely impacted by man and his domesticated livestock.

For biogeographical and ecological reasons, insular conditions often determine specific patterns of vegetation types and landscapes because of the existence of
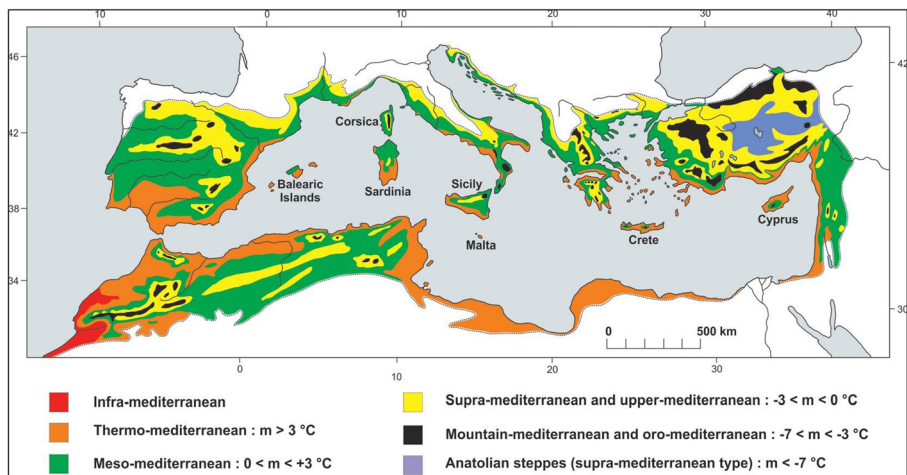
Fig. 6 Schematic organization of the vegetation belts within the Mediterranean Basin (after Quézel & Médail, 2003, modified) and situation of the main Mediterranean islands

Table 3 Specific richness of native, endemic and alien plants of the six largest Mediterranean islands or archipelago; native plant richness includes the endemic richness (Médail, 2017, updated)

Island	Area (km²)	Native plant richness	Endemic plant richness	Endemism rate	Endemic genera	Number of alien plants	% alien flora/ total flora
Sicily	25,426	3250	322	10%	*Petagnaea, Siculosciadium*	ca. 440	13.5%
Sardinia	23,821	2149	290	13.5%	*Castroviejoa, Morisia, Nananthea, Soleirolia*	508	17.4%
Cyprus	9251	1633	142	8.7%	*Lindbergella*	152	8.5%
Corsica	8679	2237	284	12.7%	*Castroviejoa, Morisia, Nananthea, Soleirolia*	466	17.2%
Crete	8261	2240	395	17.6%	*Horstrissea, Petromarula*	162	6.7%
Balearic islands	4987	1551	140	9%	On eastern islands: *Femeniasia, Naufraga, Soleirolia*	124	7.3%

endemic or range-limited plant species that characterize several ecosystems. This is the case of mountainous forests with *Pinus nigra* subsp. *laricio* on Corsica, *Cedrus libani* subsp. *brevifolia* on Cyprus, pre-forests with *Zelkova abelicea* on Crete, and a high diversity of matorrals (phryganas in the eastern Mediterranean, open and low shrublands or heathlands, dense and high matorrals). Therefore, each island possesses its own vegetation specificities even if the major physiognomical structures seem more or less similar from one island to another (Table 4). These islands are mostly covered by vegetation characteristic of the thermo-mediterranean and meso-mediterranean belts, whereas the upper vegetation levels (supra-mediterranean to oro-mediterranean) are restricted to the summits of the largest islands, notably Corsica, Sicily, Crete, and Cyprus.

In the following sections, we present a brief and synthetic overview of the principal vegetation structures (forests, pre-forests and matorrals) for the largest islands or archipelagos (see also Table 2 and references therein).

Balearic Islands

This archipelago has remained isolated since the opening of the Gibraltar Strait (about 5.3 Ma) after the Messinian salinity crisis. Its phytogeography and vegetation structure is the testimony of the complex paleogeography of the western Mediterranean because two distinct biogeographical units are distinguishable (Contandriopoulos & Cardona, 1984). The flora and vegetation of the western or Pithyusan islands (Ibiza and Formentera) possess strong Iberian or Ibero-Maghrebian affinities whereas those of the eastern or

Table 4 Dominant vegetation structures (forests, pre-forests and matorrals) according to the vegetation belts of the six major islands or archipelagos of the Mediterranean Basin (after Barbero et al., 1995, modified and completed)

| Vegetation belts	Main bioclimatic characteristics	Balearic Islands	Corsica	Sardinia	Sicily	Crete	Cyprus
Thermo-mediterranean 0 m < altitude < 300-700 m	+3°C <m <+7°C T >17°C	- Matorrals with *Olea europaea, Pistacia lentiscus, Myrtus communis, Chamaerops humilis, Juniperus phoenicea* subsp. *turbinata* - Forests with *Pinus halepensis*	- Matorrals with *Olea europaea, Pistacia lentiscus, Myrtus communis, Juniperus phoenicea* subsp. *turbinata, Arbutus unedo, Erica arborea* - Forests with *Quercus ilex, Quercus suber*	- Matorrals with *Olea europaea, Pistacia lentiscus, Myrtus communis, Euphorbia dendroides, Juniperus phoenicea* subsp. *turbinata* - Forests with *Quercus suber, Quercus ilex, Ceratonia siliqua, Pinus halepensis, Arbutus unedo*	- Summer-deciduous matorrals with *Periploca angustifolia, Rhus* spp., *Euphorbia dendroides* - Matorrals with *Olea europaea, Chamaerops humilis, Phillyrea latifolia, Pistacia lentiscus, Juniperus phoenicea* subsp. *turbinata* and *Quercus coccifera* - Forests with *Quercus virgiliana, Quercus ilex, Quercus suber*	-Summer-deciduous matorrals with *Periploca angustifolia* and *Euphorbia dendroides* - Matorrals with *Olea europaea, Pistacia lentiscus, Ceratonia siliqua, Juniperus phoenicea* subsp. *turbinata, Arbutus andrachne* - Forests with *Pinus brutia, Cupressus sempervirens, Quercus coccifera, Quercus brachyphylla, Quercus ithaburensis* subsp. *macrolepis*	- Summer-deciduous matorrals with *Ziziphus lotus* - Matorrals with *Ceratonia siliqua, Olea europaea, Quercus coccifera, Arbutus andrachne* - Forests with *Pinus brutia, Pistacia atlantica*
Meso-mediterranean 300-700 m < altitude <1000-1200 m	0°C <m <+3°C +13°C< T <+17°C	- Forests with *Quercus ilex, Juniperus phoenicea* subsp. *turbinata*	- Forests with *Quercus ilex, Quercus suber, Pinus pinaster,* with rare *Quercus pubescens*	- Forests with *Quercus ilex* and *Quercus suber,* with rare *Quercus pubescens*	- Forests with *Quercus ilex, Quercus suber, Quercus pubescens, Fraxinus ornus, Ostrya carpinifolia*	- Forests with *Quercus coccifera* and *Acer sempervirens, Quercus brachyphylla, Juniperus phoenicea* subsp. *turbinata, Quercus ilex* (on limestone) - Forests with *Pinus brutia, Cupressus sempervirens* (on marls)	- Forests with *Quercus coccifera, Juniperus phoenicea* subsp. *turbinata, Quercus infectoria* (on limestone). - Forests with *Pinus brutia, Cupressus sempervirens* (on marls)

Table 4 (continued)

Vegetation belts	Main bioclimatic characteristics	Balearic Islands	Corsica	Sardinia	Sicily	Crete	Cyprus
Supra-mediterranean 1000-1200 m < altitude <1500-1700 m	-3°C <m <0°C +8°C< T <+13°C	- Pre-forest with *Acer opalus* subsp. *granatense* and *Buxus balearica* - Scrub vegetation with *Teucrium subspinosum*	- Forests with *Quercus ilex*, *Taxus baccata*, *Ilex aquifolium* - Forests with *Pinus nigra* subsp. *laricio* and *Erica arborea*, *Pinus pinaster* - Deciduous forests with *Quercus pubescens*, *Ostrya carpinifolia*, *Alnus cordata*, *Taxus baccata*	-Forests with *Quercus pubescens* - Spiny shrublands with *Ostrya carpinifolia*, *Alnus cordata*	- Forests with *Quercus ilex* - Forests with *Pinus nigra* subsp. *laricio* (Etna) - Deciduous forests with *Quercus pubescens*, *Quercus cerris*, *Quercus petraea*, *Celtis tournefortii*, *Fraxinus ornus*, *Acer spp.*, *Ostrya carpinifolia*, *Sorbus torminalis* and rare evergreen trees (*Ilex aquifolium*, *Taxus baccata*, *Abies nebrodensis*) - Spiny shrublands	- Forests with *Quercus coccifera* and *Acer sempervirens* (on limestone) - Forests with *Cupressus sempervirens* (on marls)	- Forests with *Quercus alnifolia* and *Acer obtusifolium* (on serpentines) - Forests with *Quercus coccifera* and *Quercus infectoria* (on limestones)
Mountain-mediterranean 1500-1700 m < altitude < 2000-2300 m	-7°C <m <-3°C +4°C<T<+8°C		- Forests with *Pinus nigra* subsp. *laricio* and some *Abies alba* and *Fagus sylvatica* stands - Spiny shrublands	- Spiny shrublands	- Forests with *Pinus nigra* subsp. *laricio* and *sempervirens* and *Genista aetnensis*, *Betula aetnensis*, *Fagus sylvatica* (Etna) - Spiny shrublands with *Astragalus nebrodensis*, *Juniperus communis* subsp. *hemisphaerica* (Madonie Mts.)	- Forests with *Cupressus sempervirens*, with *Acer sempervirens* and *Zelkova abelicea*	- Forests with *Pinus nigra* subsp. *pallasiana* and *Juniperus foetidissima*. - Forests with *Quercus alnifolia* and *Cedrus libani* subsp. *brevifolia* (on serpentines)
Oro-mediterranean altitude > 2200-2300 m	m <-7°C T <+4°		- Spiny shrublands with *Astragalus sirinicus*, *Berberis aetnensis*, *Daphne oleoides*		- Spiny shrublands with *Astragalus siculus*, *Rumex aetnensis*, *Berberis aetnensis* (Etna)	- Spiny shrublands with *Astragalus creticus*, *Astragalus angustifolius*, *Prunus prostrata*, *Berberis cretica*	

Gymnesian islands (Mallorca, Cabrera, Menorca) have clear Tyrrhenian affinities. If during all of the Quaternary period the Balearic Islands have been true islands with no land connections to other Mediterranean areas, repeated cycles of sea level changes have allowed for major changes in physiography and habitat availability, leading to several expansion and contraction events of plant populations. This pattern was confirmed by the complex and highly structured genetic diversity of the narrow endemics *Senecio rodriguezii* (Molins et al., 2009) and *Crepis triasii* (Mayol et al., 2012).

There is a 'Balearic paradox' in the late colonization of the archipelago by humans (Cherry & Leppard, 2018) (Table 1). Therefore, it seems that changes of the landscape and vegetation during the first two-thirds of the Holocene (ca. 10,000 – ca. 4300 yr BP) is mainly the consequence of the evolution of climatic conditions (Burjachs et al., 2017). The main current vegetation structures of this mostly calcareous archipelago are rather uniform and characterized by typical sclerophyllous forests and matorrals (Bolòs & Molinier, 1958; Bolòs et al., 1970; Rivas-Martínez et al., 1992a, 1992b; Bolòs, 1996) with *Quercus ilex, Olea europaea, Pistacia lentiscus, Myrtus communis*, etc., intermingled with few relictual shrubs (*Cneorum tricoccon, Rhamnus ludovici-salvatoris*). The most diverse island is Mallorca, the highest summit culminating at 1445 m a.s.l., where *Buxus balearica* forms a peculiar community with *Acer opalus* subsp. *granatense* (Bolòs, 1996). The windy and rocky coasts of the eastern islands host a remarkable plant community dominated by spiny and cushion endemics (*Launaea cervicornis, Anthyllis hystrix, Astragalus balearicus, Dorycnium pentaphyllum* subsp. *fulgurans*), locally named *socarrell*, physiognomically similar to the Eastern Mediterranean phrygana (cf. *infra*). Another *socarrell* community dominated by *Teucrium subspinosum* is also present on the windy ridges of the upper part of the Serra de Tramuntana de Mallorca, above 1100 m a.s.l. (Fig. 7). Maritime cliffs like those located on the northern coast of Ibiza island are home to numerous endemics or plants with disjunct distribution (Fig. 8). If tourism and land-use changes have profoundly altered and modified several sectors on Majorca and Ibiza, the islands of Menorca and Formentera are less impacted and traditional rural landscapes are still prevalent. The 149 small islands and islets of the Balearic archipelago, still well
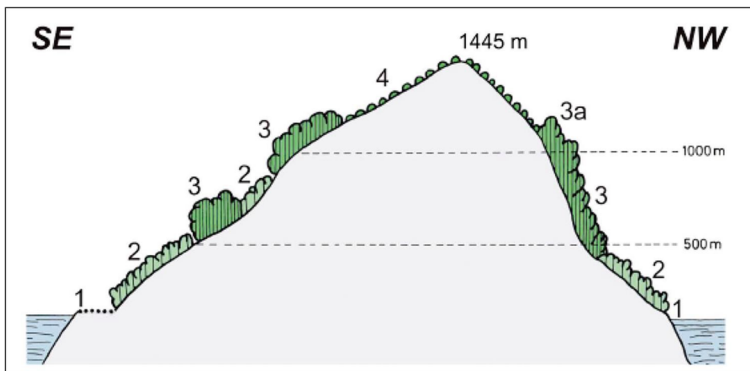
Fig. 7 Schematic SE/NW profile of the main vegetation types across the mountain Puig Major, Serra de Tramuntana de Mallorca (Balearic Islands): 1: coastal plant communities; 2: thermophilous and sclerophylous matorral with *Olea europaea* and *Ceratonia siliqua*, and forest with *Pinus halepensis*; 3: evergreen forest with *Quercus ilex, Acer opalus* subsp. *granatense* and *Buxus balearica* above 900 m; 4: dwarf and spiny scrub vegetation with *Teucrium subspinosum* on the lapiaz of the summit (after Bolòs & Molinier, 1958, modified)
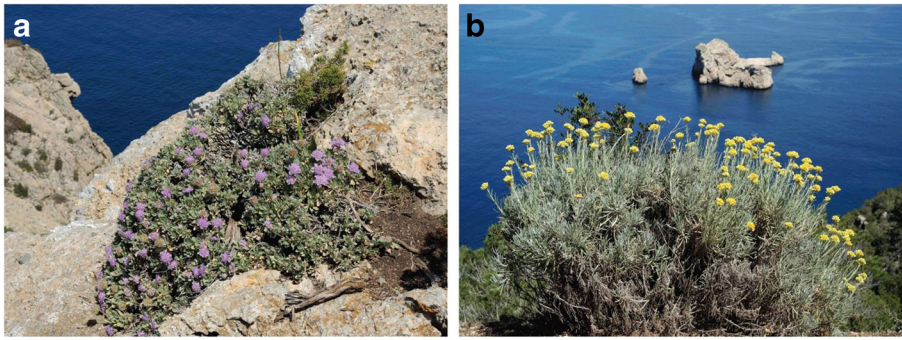
Fig. 8 Two interesting chasmophytic plants with a fragmented distribution in the Mediterranean Basin, here located on the limestone cliffs of the northern coast of Ibiza (Balearic Islands); **a**: *Lomelosia cretica* (Caprifoliaceae); **b**: *Helichrysum rupestre* (Asteraceae), and behind the islet of ses Margalides, IV.2014 (F. Médail / IMBE)

preserved from recreational activities, constitute essential refuges for coastal biodiversity (Mayol, 2020).

Corsica

This most mountainous island of the Mediterranean culminates in Monte Cinto at 2706 m, and is characterized by a high diversity of vegetation types, ranging from the restricted thermo-mediterranean belt to the alpine (Gamisans, 1999, 2010) (Fig. 6a). At low altitudes are found very specific and generally still well preserved habitats, despite growing tourist pressure. The rocky coasts harbor several peculiar vegetation types (e.g., Géhu & Biondi, 1994; Paradis, 2005) individualized by diverse endemic plants such as *Armeria soleirolii, Erodium corsicum, Limonium div. spp., Nananthea perpusilla* (see map on Fig. 36a), *Silene velutina,* etc. (see the recent *Atlas biogéographique de la flore de Corse*: Conservatoire botanique national de Corse, 2020). Temporary pools with a huge contingent of rare and restricted plants (*Isoëtes, Pilularia*), notably lcated in the southern part (Bonifacio region), constitute another remarkable habitat. From the lowlands to mid altitudes several common endemic shrubs (*Genista corsica*, *Stachys corsica*, *Stachys glutinosa, Teucrium marum, Thymus herba-barona,* etc.) form peculiar low matorral assemblages. With a forest cover of 58%, Corsica is the most wooded Mediterranean island (Fig. 9b) inasmuch as forests represents 507,000 ha of which 396,000 ha correspond to closed forests, with a recovery rate above 40% (Panaïotis et al., 2017).

Today the most common woody vegetation types are sclerophyllous forests and maquis that extend from the coast to 1200 m, because forests with broad-leaved trees were almost totaly destroyed by human impact, notably in the eastern coast (Plaine orientale). At the mountain level, the dominant tree is the Corsican pine or *laricio* (*Pinus nigra* subsp. *laricio*), which constitutes often pure and impressive stands (Fig. 10a). The upper limits of forests are currently at ca. 1600 m on northern slopes and ca. 1800 m on southern ones, but *Abies alba* can reach locally 1900 m. However, as on other Mediterranean mountains, it is likely that the treeline was lowered by human activities during past millenia. The mountain alpine vegetation above 2100 m is highly species specific (Gamisans, 1976–1979) inasmuch as it includes ca. 43% endemics of the 131 alpine taxa, with 34 strict Corsican endemics. In the alpine zone,
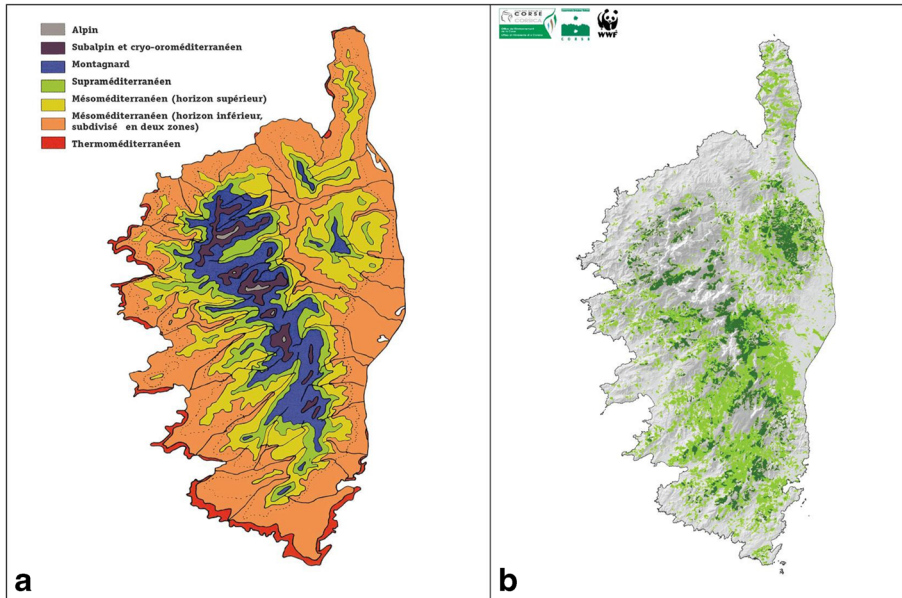
Fig. 9 **a**: Schematic distribution of the different vegetation belts occuring in Corsica (after Gamisans, 1999, modified); **b**: distribution in Corsica of ancient forests (dark green) i.e., forests occuring before 1866, and of recent forests (light green), i.e., forests appeared after 1866 (sources: Etat-major, IFN 2003–2004 and IGN, after Panaïotis et al., 2017)

north-facing slopes are covered by *Alnus viridis* subsp. *suaveolens* scrub and grass-lands, but on the south-facing slopes xerophytic dwarf-shrubs (*Astragalus greuteri, Berberis aetnensis, Genista salzmannii*) dominate the landscape. Between 1600 and 2400 m particular mire vegetation, named locally 'pozzine' (Fig. 10b), have a high conservation value with several endemic (*Bellis bernardii, Bellium nivale, Pinguicula corsica,* etc.) or noteworthy (*Carex intricata*) plants.

Sardinia

The second largest Mediterranean island is mostly dominated by lowlands inasmuch as areas up to 600 m a.s.l. represent only 13.6% of the island surface. Vegetation of
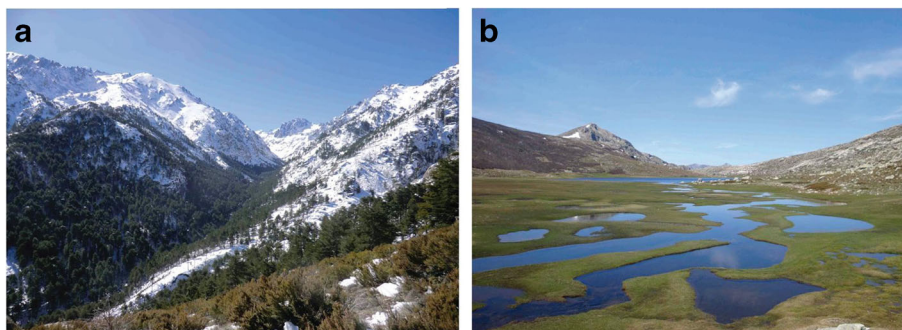

Fig. 10 The high mountains in Corsica. **a**: Laricio pine (*Pinus nigra* subsp. *laricio*) forest between Corte and the Plateau d'Alzu; **b**: *pozzines* at the Nino lake, 1743 m a.s.l. (Y. Petit / CBNC)

Sardinia is highly diversified (Camarda & Cossu, 1988) with 23 dynamic series that are currently identified (Bacchetta et al., 2009) and six main biogeographical sectors defined by cluster analysis based on the distribution of the 290 endemic plants in relation to the local geology and geomorphology (Fenu et al., 2014).

As on other large Mediterranean islands, sclerophyllous species dominate the landscape, notably with *Quercus ilex* and *Quercus suber* forests and thermophilous matorrals (Fig. 11) with *Arbutus unedo, Euphorbia dendroides, Olea europaea, Acer monspessulanum, Viburnum tinus,* etc., and with high cover of *Erica* spp. and *Cistus* spp. on acidic soils and/or under intense fire disturbance. Often associated with *Juniperus phoenicea* subsp. *turbinata*, the dwarf-palm (*Chamaerops humilis*) is commonly found on warm slopes bordering the coasts whereas this south-western Mediterranean species is curiously absent on neighbouring Corsica. At low and mid altitudes, some similarities exist with Corsica with 75 or 90 endemics (according to different authors' conceptions) shared between these two islands. On the other hand, inasmuch as there is less topographic relief on Sardinia compared to Corsica, the whole island experienced an earlier and more intense human impact, and agroecosystems are here more frequent and diverse. The prevalence of limestone rocks is another significant difference when compared to Corsica, and this induces major differences in the composition of rupiculous communities between these two islands, with several Sardinian mountains of great phytogeographical interest (Monte Albo, Monte Linas), whereas metamorphic rocks predominate on the Gennargentu massif. On the central plateau of the island (Giara di Gesturi) exists a remarkable area covered by numerous temporary ponds in basalt depressions that harbor several endemic hygrophilous plants (*Morisia monanthos, Ranunculus revelieri,* etc.). At mid altitudes and on the deep soils of the lowlands, occur deciduous trees such as downy oaks *Quercus pubescens* and other related taxa (*Q. congesta, Q. ichnusae, Q. virgiliana*), *Fraxinus ornus* and more sparsely diverse maples. Relictual populations of *Taxus baccata* and *Ilex aquifolium* occur at the timberline of the mountains, at an exceptionally low altitude of 800–900 m (Carta et al., 2014). The absence of trees above this limit is certainly due to ancient human deforestation and pasture, and the upper part of the Gennargentu massif is characterized by the presence of prostrate and spiny shrubs (e.g., *Astragalus genargenteus*) communities like in other islands' mountain tops.
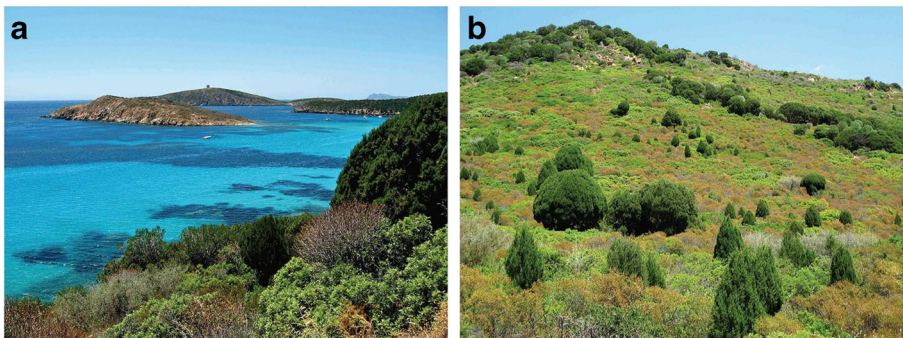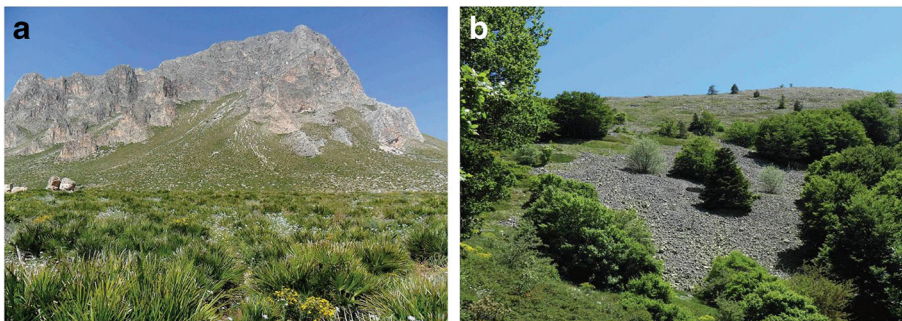

Fig. 11 Thermo-mediterranean matorrals of the south-western coast of Sardinia, VI.2009. **a**: matorral with *Euphorbia dendroides, Pistacia lentiscus, Calicotome villosa* and *Juniperus phoenicea* subsp. *turbinata*; **b**: matorral with *Juniperus phoenicea* subsp. *turbinata, Myrtus communis* and *Cistus* spp. (F. Médail / IMBE)

Sicily

Sicily, the largest and most populated Mediterranean island, is characterized by a mostly hilly inland and low and often sandy coasts on the South. Most of mountains form a nearly continuous range from West to East along its northern coasts (Madonie: 1979 m; Nebrodi: 1847 m; Peloritani: 1374 m). From a geological and paleogeographical point of view, it is one of the most complex Mediterranean territories. As Sicily was almost under water during lower Pliocene (i.e. 3.6 Ma), a pending question is to understand how the Paleogene relict flora was able to persist under these conditions (Guarino & Pasta, 2018).

Two monotypic endemic Sicilian genera, *Petagnaea gussonei* and *Siculosciadum nebrodensis*, and numerous endemic plants occur notably on rocky habitats, whereas the reliefs of western and south-eastern Sicily are more limited in area but harbour some remarkable phytogeographical elements. This is the case of *Ptilostemon greuteri*, an evergreen lauriphyllous woody Asteraceae endemic to a single locality on Trapani Mts., and of the highly relic small tree *Zelkova sicula* discovered on the Iblei Mts. (Quézel et al., 1993), whose two clonal populations live in a savannah-like patchwork of open evergreen woodland, thorny shrubland and phrygana issuing from the degradation of mesic woods dominated by summergreen, broadleaved, deciduous trees, which were probably more common some thousands of years ago (Garfi et al., 2011).

Over the course of its history, Sicily was at the crossroad of important trading routes. Indeed, human presence has impacted vegetation beginning earlier and continuing for a longer period than on the Italian peninsula, and the landscape is largely anthropogenic (Guarino & Pasta, 2018). These impacts caused the severe retraction of woodlands, which occupy at present only about 6.8% of the island's surface whereas Mediterranean and submountain grasslands occupy ca. 15.6% (Gianguzzi et al., 2016). Forests are mainly composed of oakwoods with *Quercus pubescens* and close taxa, *Q. ilex* and *Q. suber,* that represent ca. 80% of the natural woodlands. Lowlands are nearly devoid of forest vegetation, although several maquis assemblages are quite common near the coast, mostly dominated by *Olea europaea*, *Pistacia lentiscus*, *Chamaerops humilis* (Fig. 12a). True woodlands are found mainly on the slopes of the Mount Etna and on the main mountain ranges, and they include some interesting tree populations such as

Fig. 12 Vegetation of Sicily. **a**: thermo-mediterranean matorral with *Chamaerops humilis* at the piedmont of Monte Cofano, ca. 20 m a.s.l. (NW Sicily), IV.2010 (F. Longo / CNR); **b**: open stand with the endemic fir *Abies nebrodensis* and the beech *Fagus sylvatica* on screes in the Madonie mountains, VII.2014 (G. Garfi / CNR)

the highly relictual Sicilian fir *Abies nebrodensis* with only 30 natural mature individuals in the Madonie mountains (Pasta et al., 2020) (Fig. 12b), the westernmost stands of many Balkan-Anatolian species such as *Celtis tournefortii*, *Quercus cerris*, etc., or the southermost beech forest of *Fagus sylvatica* (e.g., Brullo et al., 2012). The current dynamic trend of some less disturbed areas shows a gradual replacement of the most common evergreen oaks, i.e. *Quercus ilex* and *Quercus suber,* by the semi-deciduous *Quercus pubescens*, but frequent forest fires and overgrazing have resulted in significant modifications of vegetation cover and alteration of communities' structure within the different vegetation belts, and the regular rejuvenation of woody vegetation is often strongly biased (Cullotta & Pasta, 2004).

As a typical volcanic mountain near the sea, Mount Etna shows a remarkable richness of vegetation belts along its altitudinal range (Poli, 1965; Brullo et al., 2005b), from the foothills covered with sclerophyllous evergreen vegetation, the prevalence of deciduous broadleaved woods with *Quercus congesta*, *Acer* spp., etc. above 1000 m, and then a beech forest enriched by Laricio pine, and at higher elevations by discontinuous nuclei of forest vegetation with the endemics *Betula aetnensis*, and *Genista aetnensis,* culminating in a thorny-cushion vegetation dominated by *Juniperus communis* subsp. *hemisphaerica*, *Berberis aetnensis* and the endemic *Astragalus siculus* occuring up to 2450 m.

Malta

Malta is often highlighted because of its status as an independent state, but it appears only at the thirty-fourth rank of the Mediterraean islands from the point of view of its terrestrial surface (Table 2). From a biogeographical point of view, the Maltese islands are close to Sicily and to the other islands of the strait of Sicily (Lampedusa, Linosa, Pantelleria). Malta was part of the African continental plate and relationships with North African ecosystems are confirmed by the presence of the highly relictual coniferous tree *Tetraclinis articulata* and of dry grassland with *Lygeum spartum*. The whole vegetation has been deeply modified by man since 8000 yr BP (Djamali et al., 2013; Gambin et al., 2016), and this huge impact explains the dominant man-made landscape with the occurrence of very restricted and isolated remnants of woods with *Quercus ilex,* whereas no natural patches of *Pinus halepensis* exist nowadays (Schembri, 1997). Scattered nuclei of thermophilous maquis with *Ceratonia siliqua*, *Pistacia lentiscus* and *Euphorbia dendroides,* and garrigues dominated by *Thymbra capitata*, *Erica multiflora*, *Anthyllis hermanniae*, *Teucrium fruticans,* and the endemic *Euphorbia melitensis* are the most common secondary plant assemblages issuing from various disturbances. Coastal cliffs remain the refuge of several endemic chasmophytes (Mifsud, 2013), including two controversial monotypic genera, *Palaeocyanus crassifolius* and *Cremnophyton lanfrancoi*, and the Maltese everlasting *Helichrysum melitense,* only restricted to Gozo, whereas coastal shrublands and sand dunes have less originality. A detailed survey of the vegetation types of the Maltese Islands leads to the description of more than a hundred plant communities or *associations* (Brullo et al., 2020). Besides the chasmophytic vegetation, an interesting community is that of temporary rock pools with several well-adapted plants to these drastic and fluctuating environments (*Damasonium bourgaei*, *Elatine gussonei*, *Zannichellia melitensis,* etc.).

Large Croatian Islands

With one of the most indented coastlines of the Mediterranean (Fig. 13), Croatia includes the greatest number of islands after Greece. According to Duplančić Leder et al. (2004), there are 79 islands with areas greater than 1 km², 525 islets with areas between 0.01 and 1 km², and 642 stacks whose areas are less than 0.01 km² or 1 ha, for a total of 1246 insular entities representing a whole area of 3259 km². Of these islands and islets, 60 islands have their coastal lines longer than 10 km and the 30 largest ones represent 92.2% of the total insular area of the country. On the other hand, 653 small islands and islets have coastal lines of less than 10 km, but they have well-developed soils and vegetation (Nikolić et al., 2008). The more mountainous islands possess surface areas exceeding 100 km² and the three largest islands (Cres, Krk, Brač) have areas of about 400 km² each (Table 2). Unfortunately, data about flora and vegetation are relatively scanty because only ca. 110 islands have been studied for this aspect, and often incompletely (Nikolić et al., 2008).

The outcropping rocks of these islands are mostly limestones and are subject to the Mediterranean climate with some latitudinal gradient toward the northern area (Istria), where lower temperatures and higher annual rainfall occur. Most of the islands are usually covered by a xerothermic evergreen vegetation with *Pinus halepensis, Pistacia lentiscus, Juniperus phoenicea* subsp. *turbinata* (Fig. 14b). This is true for large parts of some central Dalmatia islands such as Lastovo, Korčula, Mljet, and some areas on the islands of Brač, Hvar, Vis, and Biševo (Trinajstić, 1995a). It is on the last four islands

Fig. 13 Location of the main islands of Croatia in the Adriatic Sea (after Surić et al., 2014)
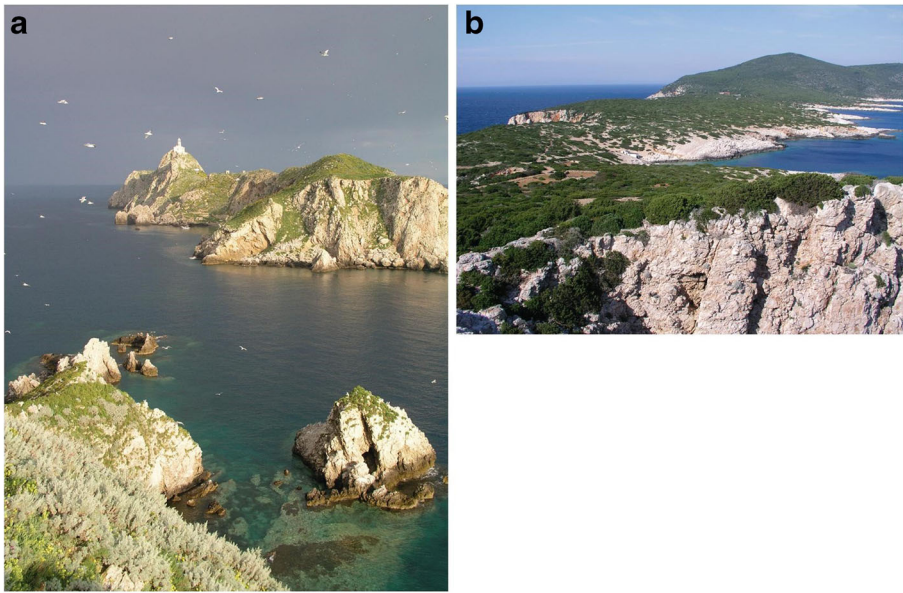
Fig. 14 Some calcareous islands of southern Croatia. **a**: Mala Palagruza island, a remote island in the middle of the Adriatic Sea; **b**: low sclerophyllous matorral covering most of the small island of Susac (377 ha, west of Lastovo island) (T. Nikolić / Univ. Zagreb)

that the west-Mediterranean garigue vegetation, with *Erica multiflora* and *Coronilla valentina,* reaches its north-easternmost distribution, as do several other shrubs on the Dalmatian islands (*Teucrium fruticans, Anthyllis barba-jovis*) (Trinajstić, 1975). On the northern and central islands, e.g., Cres, Krk, Rab, Brač, thickets (the so-called 'sibljak') with *Paliurus spina-cristi, Rhamnus intermedia, Juniperus oxycedrus* are well developed. In the warmest insular zones, from the Lošinj island (Kvarner region) in the north to the Lokrum island near Dubrovnik in the south, a thermophilous matorral with *Olea europaea* and *Myrtus communis* occurs, sometimes associated with *Quercus ilex* in more forested areas. On the northern islands, a submediterranean vegetation belt exists up to 150–350 m a.s.l., with *Quercus pubescens, Q. virgiliana, Carpinus orientalis, Ostrya carpinifolia* and *Fraxinus ornus* (Trinajstić, 1997). At higher elevations (above 400–600 m) on the largest islands, the Mediterranean-montane vegetation belt is formed by mixed forests with evergreen (*Quercus ilex*) and deciduous trees (mostly *Ostrya carpinifolia*) (Trinajstić, 1995a). But the most remarkable forest feature of this belt is the presence, on three central Dalmatian islands, of scattered Dalmatian black pine (*Pinus nigra* subsp. *dalmatica*) stands; two vegetation series are individualized, one with *Quercus ilex* on limestones of Brač and Korčula islands, and the other with *Erica manipuliflora* and *Genista sylvestris* subsp. *dalmatica growing* on the dolomites of Brač and Hvar islands (Domac, 1965; Trinajstić, 1999).

Of the 94 Important Plant Areas (IPAs) identified in Croatia (Nikolić et al., 2010), 21 include insular areas, for an estimated total of ca. 155 islands or islets (F. Médail, unpubl.). These IPAs concern a few large islands (Krk, Korčula, Vis, Lastovo) or a part of the territory of some of them (Brač, Pag, Rab, Lošinj). In the Adriatic Sea, it is worth mentioning the small archipelago of Palagruža because it is one of the most isolated in

the Mediterranean (Figs. 13 and 14a), located between the Gargano Peninsula of Italy and the Croatian island of Lastovo. These islands form an IPA including several trans-Adriatic plants (*Aurinia leucadea, Brassica incana, Limonium cancellatum*) and endemics (*Centaurea friderici* and *C. ragusina*) (Nikolić et al., 2010).

Large Greek Islands

The importance of Greek islands for Mediterranean insular biodiversity is considerable inasmuch as 27 of the 49 Mediterranean islands with surface areas greater than 100 km^2 are located in this country (Arnold, 2008), and almost three quarters (71%) of all Mediterranean islands and islets are located in Greece (F. Médail, ined). These islands are very heterogeneous from the point of view of their geology, paleogeography, and, thus, their biogeography and species assembages (Triantis & Mylonas, 2009), and although we can distinguish two main groups, the Aegean and the Ionian islands, the biogeographical subdivision is more accurate (Fig. 15).
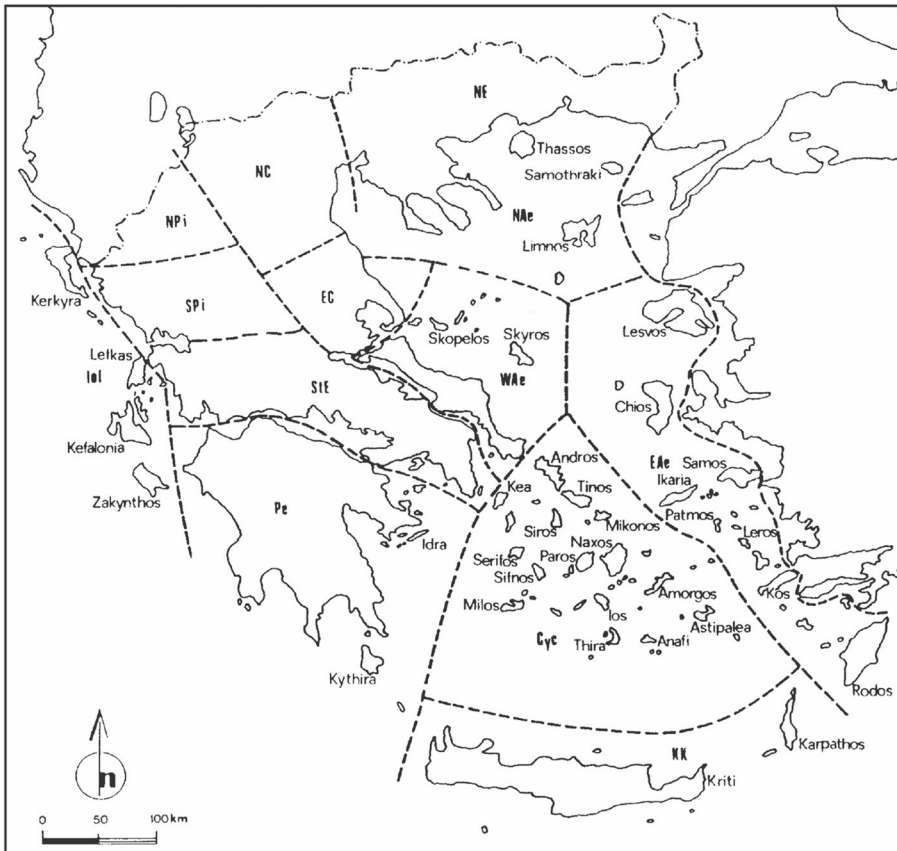
Fig. 15 Biogeographical subdivision of Greece according to *Flora Hellenica* (Strid, 1997) and the *Atlas of the Aegean Flora* (Strid, 2016), with indication of the major islands; the delimitation of the floristic regions including islands are: Ionian islands (IoI), Peloponnisos (Pe), Central Aegean (Cyclades, Cyc), Sterea Ellas (StE), West Aegean (WAe), North Aegean (NAe), East Aegean (EAe), South Aegean (Kriti and Karpathos, KK)

The Aegean islands exhibit a high geological diversity with the dominance of complex metamorphic rocks, mainly marble and shists, but also volcanic rocks, particularly for the islands of the South Aegean volcanic arc (see below), and limestone and sedimentary rocks for Crete, Karpathos and Rhodes (Higgins, 2009). These islands are characterized by high levels of plant diversity and endemism (Strid, 2016; Panitsa et al., 2018). This is explained by their complex paleogeographical history since the Miocene and the fragmentation of the continuous land mass named 'Ägäis' caused by a sea transgression and the formation of the mid-Aegean barrier (12–2 Ma) (Triantis & Mylonas, 2009), The existence in some refugia of highly relictual mid-Tertiary endemic trees (*Zelkova abelicea* on Crete; *Liquidambar orientalis* on Rodos and S. Anatolia; *Phoenix theophrasti* on Crete (Fig. 18), and some Aegean islands, Peloponnese, and S. Anatolia) adapted to a warm-humid bioclimate testify to the likelihood that the eastern migrations occurred before the breakup of the Ägäis. Then, orogenetic and eustatic changes during the Plio-Pleistocene, notably sea-level changes since the Last Glacial Maximum (21 kyr BP–Present) (Simaiakis et al., 2017), induced much of the species divergence of insular populations and taxa (Bittkau & Comes, 2005). The acute phytogeographical analysis by Rechinger (1943, 1950) led him to propose a sharp floristic separation between the Central Aegean islands (Cyclades) and the islands close to the Anatolian coasts. He suspected that paleogeography was the main factor explaining this major biogeographical borderline between Europe and Asia, a discontinuity known as '*Rechinger's line*' (Strid, 1996, 1997). The potential natural vegetation of most of the large Aegean islands is formed of thermophilous and sclerophyllous pre-forests and matorrals with *Pistacia lentiscus, Myrtus communis, Ceratonia siliqua, Arbutus unedo* or *A. andrachne, Olea europaea* (Quézel & Barbero, 1985) (Fig. 16b). *Juniperus phoenicea* subsp. *turbinata* stands are frequent in thermo-mediterranean belt of several islands such as Kalimnos, Milos, Naxos, Paros, Rodos (Brullo et al., 2004). The largest islands harbour coniferous forests located at the thermo- and meso-mediterranean levels, with only *Pinus brutia* (Thasos, Lesvos, Ikaria, Naxos) or associated with native populations of *Cupressus sempervirens* (on Chios, Samos, Kos, Rodos). Pure cypress stands occur even on Rodos on the calcareous rocky
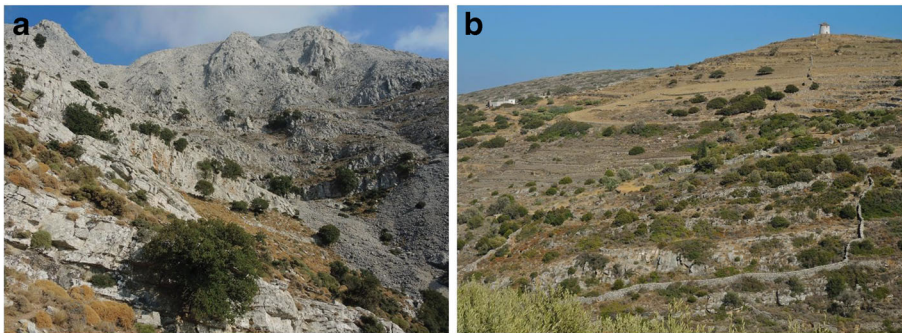
Fig. 16 Plant landscapes of two large islands of the central Cyclades (Greece), VIII.2016. **a**: vegetation of the limestone summit of the Naxos island, Mount Zaz (999 m), with the evergreen Cretan maple (*Acer sempervirens*) and a phrygana with *Sarcopoterium spinosum* and *Genista acanthoclada*; **b**: ancient agricultural landscape with abandoned terraces colonized by phrygana and evergreen matorral with *Olea europaea, Pistacia lentiscus* and *Juniperus phoenicea* subsp. *turbinata*, Paros island (F. Médail / IMBE)

slopes, between an altitude of 250–850 m and the island summit. Furthermore, the north-western Aegean islands (Euboea, Skyros, Skiathos, Skopelos, Alonissos and close islands) include stands of *Pinus halepensis*. On north-eastern Aegean islands (Limnos, Samothraki, parts of Lesvos and the Turkish island of Gökçeada), the potential natural vegetation is determined, according Quézel and Barbero (1985) by sclerophyllous oaks (*Quercus ilex, Q. coccifera/calliprinos*) that may also have occupied some areas on the more southern islands of the Aegean Sea (northern parts of Chios and Samos, central parts of Naxos (Fig. 16a), Paros and Andros), often associated with *Acer sempervirens*. Nevertheless, as mentioned above, the dynamic role of deciduous trees, notably oaks, could be underestimated as there are on several islands some relict deciduous forests. For instance, on Lesvos, deciduous forests with *Quercus ithaburensis* subsp. *macrolepis* and *Q. pubescens* occur whereas *Castanea sativa* stands are located at higher elevations on the island's peaks reaching 968 m (Biel, 2002). *Quercus ithaburensis* subsp. *macrolepis* nuclei are probably the remnants of more important forest stands, destroyed by the multi-millenary action of man as is the case on Limnos (Economidou, 1981; Panitsa et al., 2003) or Rodos.

The environmental and biogeographical components of the Ionian islands is overall simpler. They are dominated by limestone and were isolated from the mainland during the Pleistocene, or even more recently for those lying close to the coast, like Kerkyra (Corfu), which was still connected to the mainland 8000 years ago when sea level was lower (Higgins, 2009). The potential natural vegetation of the main Ionian islands (Kerkyra, Paxos, Lefkada, Ithaki, Kephalonia) is dominated by sclerophyllous oaks (*Quercus ilex, Q. coccifera*), whereas the southern island of Zakynthos is covered by a thermo-mediterranean vegetation including lentisc, carob tree, olive tree with Aleppo pine on the western coast; this community is also restricted to the driest and warmest environments on other Ionian islands (Quézel & Barbero, 1985; de Bolòs et al., 1996). On Kefalonia island, the presence of *Abies cephalonica*, also present in Euboea, represents a remarkable ecobiogeographical pattern. This endemic Greek fir forms pure stands from 900 m to 1628 m, at the peak of Mount Aenos (Politi et al., 2011), but few scattered individuals occur at lower elevations in contact with the holm-oak forest and sclerophyllous matorral.

On the whole, most of these large Greek islands are covered by various types of scrub plant communities, especially thorny phrygana that extend from sea shores to the hill tops and are continuously grazed by sheep, goats, horses or donkeys. These open dwarf scrub communities are mainly composed of cushion-shaped, dense, spiny, low (rarely exceeding 60 cm in height), and slow-growing shrubs and they occur on dry rocky places, particularly on limestone. The dominant subshrubs of the phrygana are *Anthyllis hermanniae, Micromeria juliana, Sarcopoterium spinosum*, *Satureja thymbra, Thymbra capitata,* with *Euphorbia acanthothamnos* and *Centaurea spinosa* occurring near the coasts (Strid, 1997). Of course, depending on the biogeographical location of the island, the plant composition of phrygana may vary. For instance, Rodos hosts both a coastal phrygana with the south-eastern Aegean endemic *Carlina tragacanthifolia*, and an inland phrygana with *Glandora hispidula*, an eastern Mediterraean plant restricted to a few locations in Europe. Other taller evergreen scrub communities (matorrals named 'maquis' or 'garigues') are composed of shrubs commonly found around the Mediterranean but with some eastern elements (*Genista acanthoclada, Erica manipuliflora, Hypericum empetrifolium,* etc.).

The chasmophytic vegetation is also highly diverse and it is impossible to go into details because each insular biogeographical sector has its own endemic plant communities, especially on limestone rocks and cliffs (Dimopoulos et al., 1997). Aegean cliffs constitute biologically closed communities (i.e. 'habitat islands') that serve as refugia for obligate chasmophytes, whose richness in 120 islands and islets is estimated at 286 species and subspecies (Kontopanou & Panitsa, 2020). The majority are Greek or Aegean endemics, like some noteworthy chasmophytes of the impressive maritime cliffs of Amorgos as Tournefort had already pointed out at the very beginning of the eighteenth century (Pitton de Tournefort, 1717) (Fig. 17).

Crete

This long-isolated continental island gradually separated from continental land masses starting about ca. 11 Ma and became fully isolated around 5.3 million years. As it was almost entirely spared by Quaternary glaciations, Crete forms a major refuge area in the Mediterranean (Médail & Diadema, 2009) (Fig. 18). The high phytogeographical interest of Crete is related to its endemism including 183 single island endemics (Kougioumoutzis et al., 2020a) and the presence of diverse floristic elements from the Balkans, Anatolia, and to a lesser extent North Africa (Greuter 1975). Spatial pylogenetics reveal the existence of several endemism centers and Crete's bioregionalization is strongly explained by the spatial configuration of the 'paleo-islands', roughly the Cretan mountain massifs, existing during the Pliocene-Pleistocene (Kougioumoutzis et al., 2020a). Hotspots of Cretan endemic plants are mostly located above 1500 m a.s.l. (with the western massif of Lefka Ori hosting the most single island endemics), and they correspond to climatic refugia, i.e. areas with higher climatic stability (Kougioumoutzis et al., 2020b). Crete has experienced an
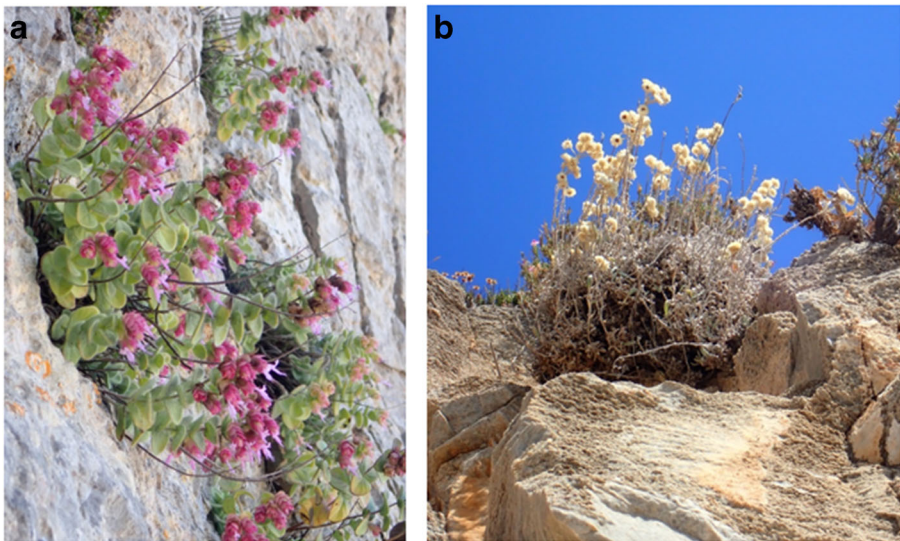
Fig. 17 Two narrow endemic plants of the central Cyclades (Greece) present on the calcareous cliffs of Amorgos island, VIII.2020. **a**: *Origanum calcaratum* (Lamiaceae), NW of Stavros; **b**: *Helichrysum amorginum* (Asteraceae), near the monastery of Chozoviotissa (F. Médail / IMBE)
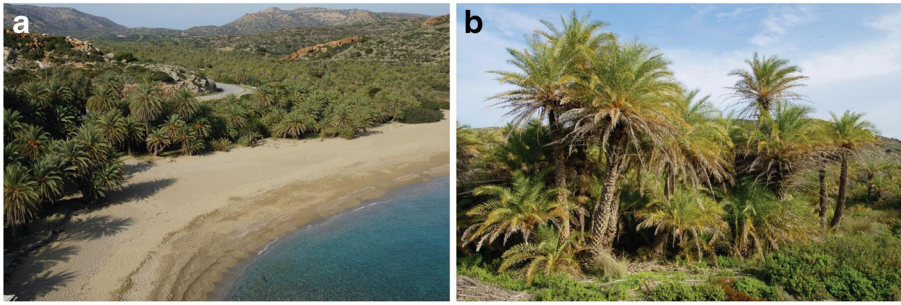
Fig. 18 The native palm-grove of the tertiary relict *Phoenix theophrasti* (Arecaeae) in its *locus classicus* of the Vai beach, eastern Crete, I.2011 (F. Médail / IMBE)

important post-isolation mountain uplift, and the study of elevational patterns of vascular plant species richness and endemism suggest an upward colonization and diversification mainly by the 'tolerant' lowland plant species (Trigas et al., 2013).

Scrub communities dominate the Cretan landscape, with several types of matorrals including *Cistus* spp., *Olea europaea, Pistacia lentiscus, Arbutus unedo, Erica arborea* and *Quercus coccifera*, and phrygana with floristic compositions similar to those of the Aegean islands but with some specificities such as the presence of the endemic *Verbascum spinosum* in south-western Crete. Woodlands at low and mid altitudes are mainly composed of sclerophyllous trees (*Ceratonia siliqua, Phillyrea latifolia, Quercus ilex, Quercus coccifera*) with *Pinus brutia* forests, whereas deciduous oaks (*Quercus pubescens, Q. ithaburensis* subsp. *macrolepis*) occur only nowadays as relic stands at the thermo-and meso-mediterranean levels of vegetation (Barbero & Quézel, 1980; Brullo et al., 2004; Bauer & Bergmeier, 2011).

Crete is characterized by four main mountain ranges: Psiloritis (2456 m) in the central part, Lefka Ori in western part (2452 m), and the Dikti Mts. (2148 m) and Thripti Mts. (1476 m) in the eastern part of the island. The vegetation of the mountains (above 1400 m a.s.l.) was well studied and is highly specific with ca. 35% of endemic plants (see the synthesis of Zaffran, 1990 and Bergmeier, 2002). In montane areas, *Acer sempervirens* and *Cupressus sempervirens* are the dominant trees (Fig. 19) along with *Quercus coccifera*. One of the most interesting tree is *Zelkova abelicea* (locally named 'ambelitsiá' or 'anégnoro'), a relict elm-like tree that is present but sparsely distributed on all four mountain ranges at elevations between 850 and 1800 m a.s.l. (Kozlowski et al., 2014). Otherwise, treeless mountain areas are dominated by tragacanth plant communities with cushion-shaped and spiny dwarf shrubs (*Berberis cretica, Acantholimon androsaceum, Astragalus cretica, A. angustifolia,* etc.) and harbour a high number of endemic plant communities, with a greater similarity between Mts. Psiloriti and Dikti than to Levka Ori (Bergmeier, 2002). The clayey doline bottom of karst depressions is a very particular mountain habitat with a distinct vegetation induced by afflux of water and colluvial soil (Fig. 23). These dolines are characterized by several very rare plants and endemics such as the monotypic genus *Horstrissea dolinicola* (Apiaceae), the creeping dwarf shrubs *Hypericum kelleri* and *Polygonum idaeum* (Egli, 1991).

As on other large islands, the early colonization of Crete by man, about 9000 years ago, profoundly altered the natural balance, and landscapes still bear the marks of
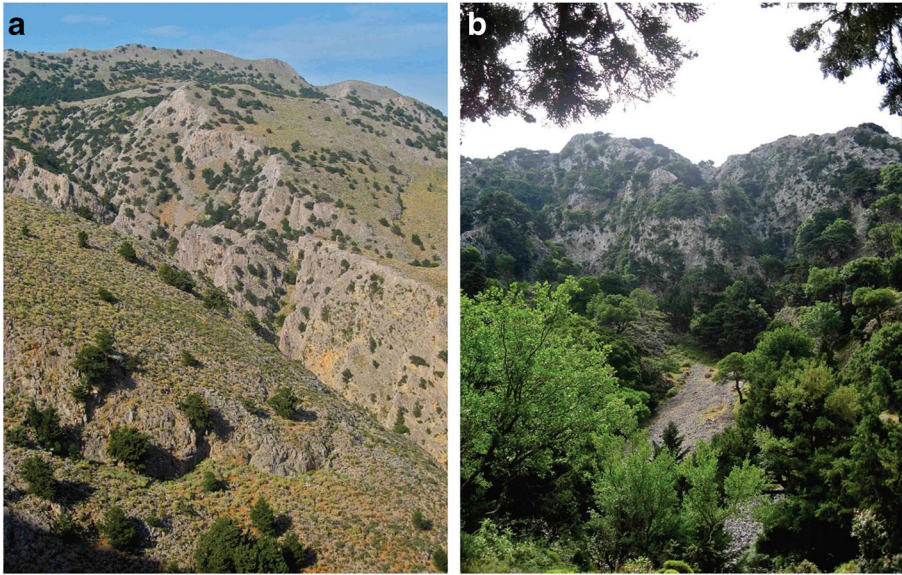
Fig. 19 Vegetation of the Cretan mountain in the Lefka Ori, IV.2007. **a**: southern slope with scattered *Cupressus sempervirens* near Chora Sfakion; **b**: open forest with *Acer sempervirens* and *Cupressus sempervirens* on screes, Imbros gorges (F. Médail / IMBE)

thousands of years of intensive exploitation (Rackham & Moody, 1996). Even if forest patches are rare, Crete is not very extensively exploited nowadays by agriculture, but the number of livestock has impressively increased due to European Union support of local husbandry (Bauer & Bergmeier, 2011). Land-abandonment has lead to an increase of pinewoods whereas woods with Cypress (*Cupressus sempervirens*) have roughly doubled during the last hundred years. At present, the most threatened habitats are sandy beaches and dunes, wetlands, and traditionally cultivated olive groves and fields with a rich flora of annual weeds.

Cyprus

The third largest Mediterranean island includes two mountain ranges, which formed originally separate islands, the Troodos Massif (1952 m), with basic and ultrabasic rocks, and the Pentadaktylos range (1024 m), composed primarily by limestone. The dominant natural woody vegetation are pine forests (Barbero & Quézel, 1979), with the Calabrian pine (*Pinus brutia*) extending from sea level to about 1400 m, whereas the Pallas pine (*Pinus nigra* subsp. *pallasiana*) occupies a restricted area of 6000 ha on the Troodos massif between 1200 and 1900 m with some sparse woods of *Juniperus foetidissima*. The Troodos also harbours unique forests of the endemic trees *Cedrus libani* subsp. *brevifolia* and *Quercus alnifolia* (Fig. 20), and about 95 endemic plants, most of them adapted to serpentine soils (Tsintides et al., 2007). The clearings among these orophilous forests are colonized by dwarf-shrub vegetation typical of the highest Mediterranean mountains including four main plant associations defined by several strict endemic taxa (e.g., *Alyssum cypricum*, *Dianthus troodi*, *Hypericum stenobotrys*,

Fig. 20 The unique forest with the Cypriot cedar (*Cedrus libani* subsp. *brevifolia*) (**a**) and the Golden oak (*Quercus alnifolia*) (**b**) on the ultramafic substrate of the Troodos massif (highest altitude: 1952 m a.s.l.) in the center of Cyprus, VI.2017 (F. Médail / IMBE)

Nepeta troodi, Onosma troodi) (Brullo et al., 2005a). Native cypress stands occur mainly on Pentadaktylos Mt., on limestone and marls.

Due in large part to the destruction of forests by human activities, thermophilous matorrals cover a large part of the island, with notably the Cyprus Broom (*Genista fassellata*), and evergreen shrubs (*Cistus* spp., *Lithodora hispidula*, *Pistacia lentiscus, Phlomis* spp., etc.), but also with several dwarf shrubs characteristic of phrygana (*Asperula cypria*, *Noaea mucronata, Sarcopoterium spinosum,* etc.) on dry and eroded substrates, and on repeatedly burned or overgrazed areas. Cultivations cover ca. 45% of the island, mainly on lowland plains with a large development of agro-ecosystems dominated by the carob tree (*Ceratonia siliqua*). Some remnant stands or patchy individuals of the deciduous oak *Quercus ithaburensis* subsp. *veneris* are probably the relics of larger forests in the past that occured between sea level and ca.1400 m a.sl.

The flora and vegetation of Cyprus are, indeed, characterized by a strong biogeographical specificity explained by the long isolation of this oceanic island, probably only briefly connected with the mainland during the Messinian (ca. 5 Ma) (Poulakakis et al., 2013), and the geological peculiarities of the Troodos massif. Nevertheless, this island has clear biogeographical affinities with Anatolia and Lebanon, whereas several plants belonging to the African-Arabian element (*Lycium schweinfurthii, Prosopis farcta, Pteranthus dichotomus, Tetraena alba*), thus testifying to the arid conditions occurring in the lowlands, and perhaps past connections due to the sea having dried up during the Messinian salinity crisis.

Main Current Vegetation Dynamics on Large and Medium Islands

Dynamics of landscape and vegetation on Mediterranean islands represents a complex process depending both on environmental constraints and on local socio-economic tendencies. Mediterranean climate induces severe and contrasted stresses to species and communities. Stresses depend on the unpredictable nature of climatic patterns, and organisms often have to cope with drastic temporal variation in climate and resource availability. However, during the last century, the magnitude of climate change did not significantly impact the structure and function of Mediterranean ecosystems. Currently, the situation is changing rapidly so that severe impacts on island ecosystems and biodiversity are expected (Vogiatzakis et al., 2008; Médail, 2017), in particular on

the oro- and alti-mediterranean belts and on spatially-restricted summit areas of mountain ranges, as in the Lefka Ori massif on Crete (Kazakis et al., 2007). On the other hand, some recent studies that focused on the response of single species (e.g., Fazan et al., 2017, about *Zelkova abelicea*) or on entire plant communities (e.g., Henne et al., 2015) underline that we may have underestimated the ecological amplitude and tolerance of many so-called 'temperate' species that thrive on Mediterranean mountains but could tolerate drier and warmer climates.

But most of the ups and downs in Mediterranean ecosystems are closely linked to human population pressures that have changed many times through the long common history of ecological systems and human societies. Therefore, the dynamics of human populations will still be the determining factor in the future of the Mediterranean biodiversity (Blondel & Médail, 2009). The major islands are usually characterized by a slight increase of permanent human population, whereas the medium islands — except some hotspots of tourism such as Corfu and Djerba — are subject to a clear demographic decline. But even for large islands, disparities are strong between a very densely populated island like Malta (1330 people/km^2) and a less-populated island as Corsica (36 people/km^2). Furthermore, since the 1960s, tourism on islands has greatly increased, with a paroxysm on some Balearic Islands (Mallorca and Ibiza) where a peak was reached in 2000–2001 with 11 millions of tourists. This huge human pressure induces a strong urban development, which is concentrated along the coasts, thereby threatening or even destroying several fragile ecosystems such as sand-dunes and wetlands, and to a lesser extent coastal rocky habitats. For example, on the Greek island of Skiathos (N. Sporades), tourism development since the 1970s has resulted in an 80% reduction of these coastal ecosystems (Economidou, 1995).

Beginning in the nineteenth century and a constant acceleration throughout the last century, major land-use changes on large and medium islands can be explained by the widespread collapse of the 'traditional Mediterranean tryptic' named *ager-saltus-sylva* (agriculture, pastoralism, forestry), which has moulded insular landscapes during several centuries, and even millennia. Until the mid-twentieth century, natural resources served as the crucial resource for island populations, for their food, livestock, nutraceutical and healing compounds, and various other usages (e.g., for fiber, weaving, resin). These needs were huge when one considers, for example, that during only one year (1867) more than 7000 t of wood and coal were consumed on Palma de Mallorca for domestic and artisanal uses (Mayol, 1995). Caused by the end of nearly autarchic economies on islands, changes in agricultural and livestock farming extending inland have induced in many cases a reduction of pressures on natural resources and therefore a global increase of matorral and forest areas, and the abandonment of cultivated terraces that were formerly the rivet of agricultural landscapes on steep and mountainous islands (e.g., Cerabolini et al., 1996, for Elba; Petanidou et al., 2008, for Nisyros: see Fig. 21).

Nevertheless, as local specificities are exacerbated on islands, any generalization of these environmental trends is hazardous. For example, the issue of the ongoing struggle between progressive succession mechanisms and increased grazing pressure after land abandonment is still uncertain on many Mediterranean islands (e.g., Rühl & Pasta, 2008; Tzanopoulos & Vogiatzakis, 2011; Schaich et al., 2015). In some cases, the vanishing of traditional agricultural activities and landscapes (Figs. 22 and 23) has led to severe soil erosion or the rapid extinction of many ruderal endemics and several
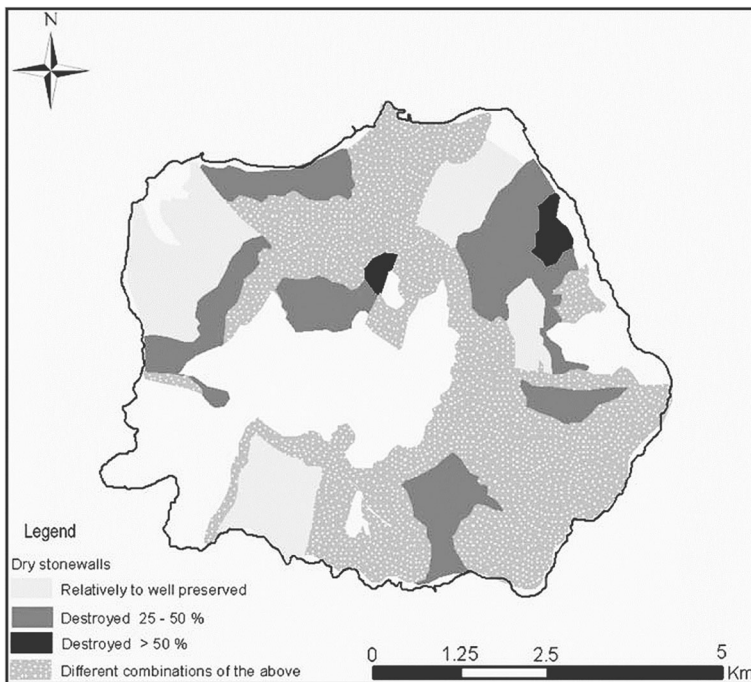
Fig. 21 Distribution of terraces (year 2000) on the small cone-shaped volcanic island of Nisyros (41 km², max. elevation = 598 m) in the SE Aegean, illustrating the current collapse of their supporting dry stonewalls. White areas are not terraced (Petanidou et al., 2008)

interesting archaeophytes (La Mantia et al., 2011). Throughout the Aegean archipelago, collapse of cultivation practices on terraces after the beginning of the twentieth century has induced profound landscape changes, and the near disappearance of traditional crops since the 1960s: lentils on Samos and Lesvos, wheat on Chios, beans on the Cyclades (Boillot, 1995), and on most of them, the islands' unique terraced landscapes have vanished (Fig. 21). In the western part of Crete, between 1945 and 1990, human immigration from arid mountains has lead to the decline of agricultural land surfaces by almost 40%, and this has favoured the recover of forest ecosystems dominated by the

Fig. 22 Traditional agroecosystems on medium islands. **a**: cereal fields with almond and carob orchard, Ibiza, IV.2014; **b**: terracing on Zebbug, N. Gozo (Malta archipelago), III.2011 (F. Médail / IMBE)
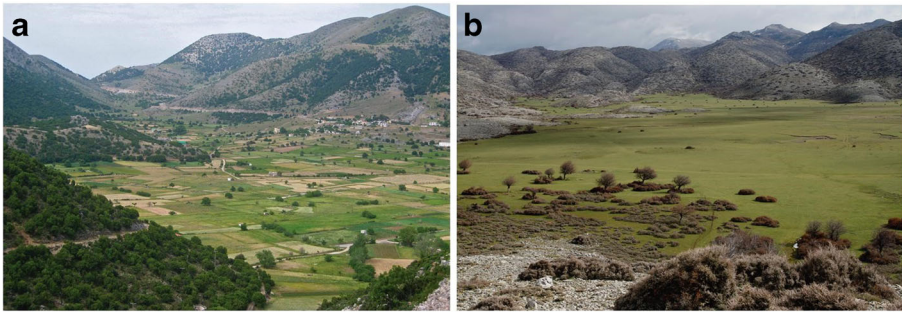
Fig. 23 Open landscapes of the Cretan mountains. **a**: cultivated *polje* in the Lefka Ori, IV.2007; **b**: Nida plateau in the Psiloritis, gradually colonized by deciduous trees and *Berberis cretica*, I.2011 (F. Médail / IMBE)

coniferous *Cupressus sempervirens* and *Pinus brutia* or by deciduous trees and *Berberis cretica* on the mountain dolines or plateaus (Fig. 23b).

The same process has occurred on the Balearic Islands where drastic changes have occurred (Marull et al., 2015) (Fig. 24). Forests covered by Aleppo pine multiplied their surface by more than five on Mallorca during the last century, and between 1971 and 1999 pinewoods increased from 55,000 ha to 115,000 ha in the Balearic Islands (Gil et al., 2003). In the same way, holm-oak forests also increased from 5000 ha to more than 10,000 ha on Mallorca, and from 900 ha to 2600 ha on Menorca since 1860 (Mayol, 1995).

In contrast, the high shrublands and natural forests of eastern Sardinia have diminished by 35% between 1955 and 1996, whereas pastures, burned low shrublands and afforestations are progressing. Landscape dynamics are more contrasted on Corsica. Since the beginning of the twentieth century, land-abandonment has induced a global increase of shrublands and forested areas. The afforestation rate reached only 17.6% in 1866 (i.e., 153,775 ha) against 58% currently (i.e., 507,000 ha), i.e., an increase of 3.3 times in the surface area of Corsican forests over a period of 150 years (Panaïotis et al., 2017). But this increase may be locally counterbalanced by frequent illegal fires often linked to pastoral practices. Corsican rural area still occupies 80% of the territory and sectors of traditional summer transhumance herds span more 130,000 ha throughout the mountainous ridge (source: PNRC). Grazing is a well known obstacle to forest expansion and regeneration, and a key driving force of ecosystem dynamics as it has been practiced on Mediterranean islands for millennia, shaping both the landscape and biodiversity pattern. This long history of grazing is exacerbated on most of the Greek islands, with large flocks of sheep and goat usually free to graze. But uncontrolled practices can lead to overgrazing and even to desertification, i.e., land degradation under arid and semi-arid climates (e.g., Arianoutsou-Faraggiraki, 1985; Papanastasis et al., 2002). Nevertheless, we must be cautious with the apparent past 'desertification' of the Mediterranean environments on larger islands. As demonstrated by the assessment of natural environment in Cyprus between 1878 and 1960 (Harris, 2012), the 'classic degradation thesis of deforestation' is in fact a simplified story of presumed desertification in order to justify the environmental policies of colonial authorities or centralized governments.
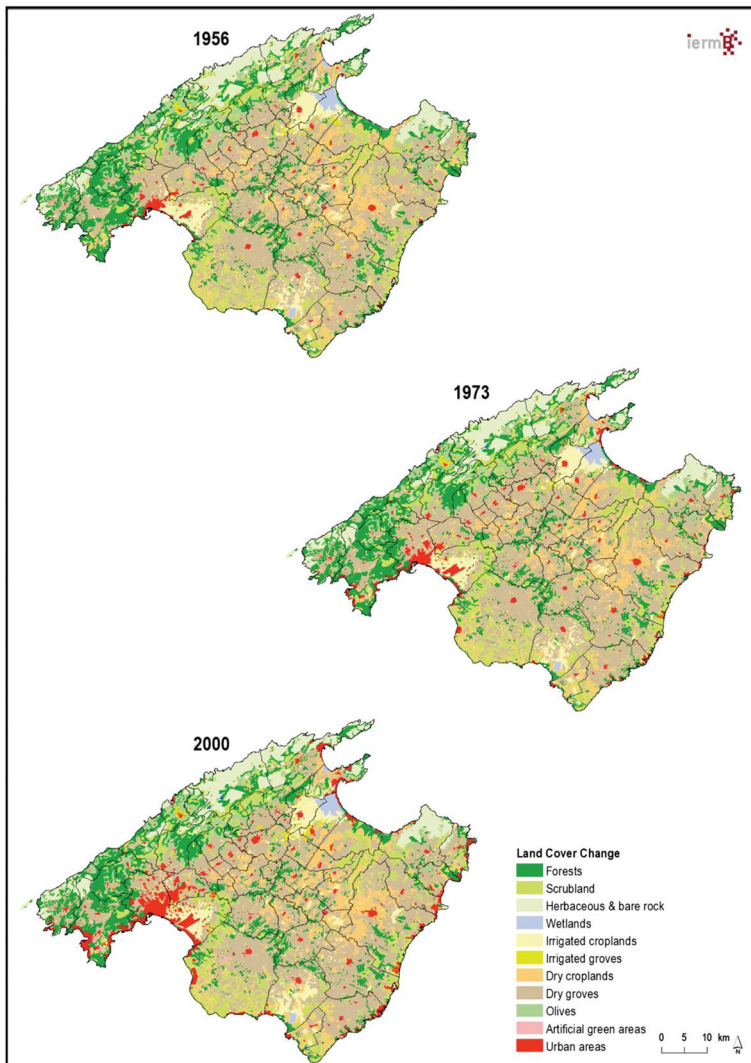
Fig. 24 Main land-cover changes in the island of Mallorca (Balearic Islands) in 1956, 1973, 2000 (Marull et al., 2015)

Like grazing, forest fire is a major driving force for Mediterranean ecosystem dynamics since the emergence of the Mediterranean climate, 3.6 Ma ago. Indeed, several studies suggest that paleo-fires contributed to the control of shrubland dominance during the mid-Holocene (ca. 8000–7000 years ago) under dry conditions, as it is the case with *Pistacia* matorrals on Sicily (Calò et al., 2012) and Malta (Djamali et al., 2013), and for the dense *Erica scoparia* and *E. arborea* stands in north-eastern Sardinia (Beffa et al., 2016). Fires can slow down the expansion of forest cover explained by the general collapse of traditional human practices on islands, in particular on persisting terraces that promote fast vegetation recovery. Thus, ancient or mature woodlands are scarcely represented because of recurrent fires, and matorrals, or sometimes xerophytic

grasslands, still dominate the insular landscape as is the case on the Tyrrhenian island of Ponza (Stanisci et al., 2005) or for the thermo- to the supra-mediterranean vegetation belts in Sicily (Cullotta & Pasta, 2004). In Greece, the situation has been particularly worrisome for the last few decades because of the increase in frequent and intense wildfires. On Thasos island, for example, a series of wildfires since 1984 caused the reduction of forest cover from 61.6% to almost 20% (Ranis et al., 2015). Furthermore, there often exists a spatial congruence between between the most fire-affected micro-regions and the main areas of cattle-rearings, as in Corsica (Fig. 25). On this fire-prone island, 28,000 fires occurred between 1973 and 2004 (i.e., ≈ 1000 fires /year) and a third of the total surface of Corsica was burned in 30 years. In the future, the probable increase of drought, as anticipated under global change conditions, could induce a higher fire activity on on most, if not all, of the Mediterranean islands, with its corollary effects of land degradation and erosion.

Thus, despite a generalized abandon of cultivation, ancient woodlands are often scarcely represented on Mediterranean islands because of frequent fires and uncontrolled grazing, which strongly control the speed, the direction and the patchiness of local dynamic processes. Hence matorrals and phrygana still dominate most of the insular landscape, notably under arid conditions.
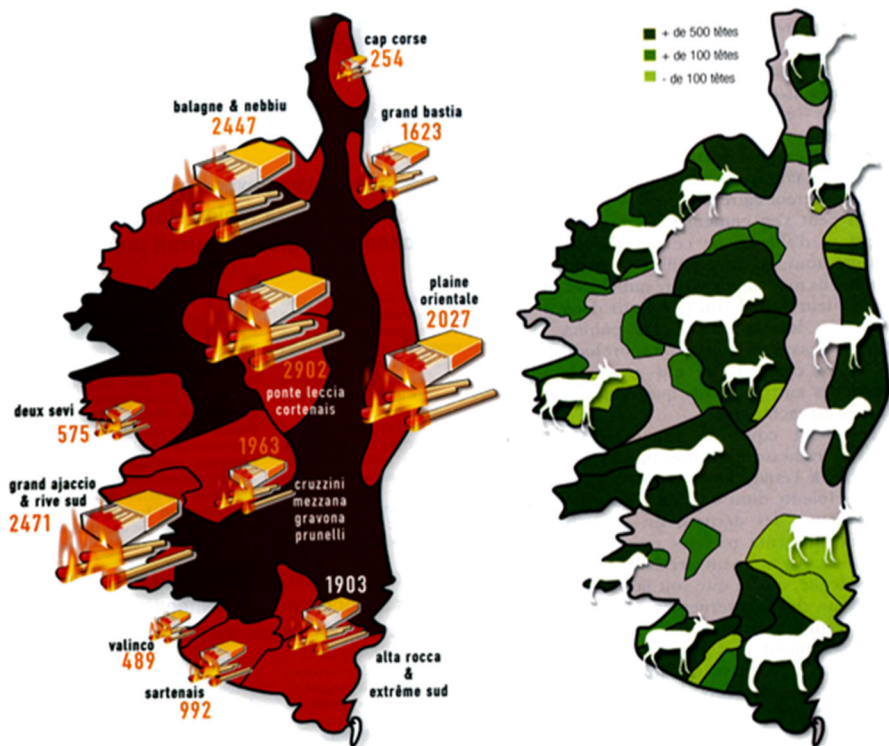

Fig. 25 Spatial congruence between the micro-regions of Corsica severely threatened by fire hatching (for each sector, the figure corresponds to the number of fires during the period 1973–2004), and the main cattle-rearings. After *Corsica Magazine*, sept. 2005 and Prométhée Database (www.promethee.com)

Islands of the world have proven to be especially sensitive to biological invasions in both frequency and the degree of impact when compared to continents. Invasions often modify population dynamics, community structure, the composition and functioning of ecosystems, and may accelerate the extinction of indigenous plants. Mediterranean islands and islets are also in places seriously threatened by aggressive alien plants, notably along coasts, in lowlands, and along rivers (Hulme et al., 2007). Compared to their surface area, small islands are probably the most threatened by plant invasions (e.g. Pretto et al., 2012). Recent studies carried out on several large Mediterranean islands demonstrate that the impacts depended on both the identity of the invasive plant and of the invaded island, suggesting that the impact of invaders is context-specific (Traveset et al., 2008). The most invaded large islands are Corsica and Sardinia with a percentage of alien plants slightly higher than 17% (466 and 508 alien taxa respectively, according to Puddu et al., 2016), but the percentage of invasive plants is almost twice as high in Corsica (21.2%) as in Sardinia (12.6%). The other major islands are characterized by a lower number of alien taxa, comprised between 6.7 to 9.5% (Table 3). Some of the most invasive plants are the trees *Acacia* spp., *Ailanthus altissima* (e.g., distribution in Sicily: Fig. 26), the shrub *Nicotiana glauca*, the perennial herbs *Cortaderia selloana* and *Oxalis pes-caprae*, the succulent plants *Carpobrotus* spp. and *Opuntia* ssp., and the liana *Senecio angulatus*.

Of course, all of these main exogenous factors affecting ecosystem and landscape dynamics must be considered in interaction to better estimate the ecological consequences of these changes, including the more recent drivers such as climate warming and aridification, and sea level rise (Médail, 2017).
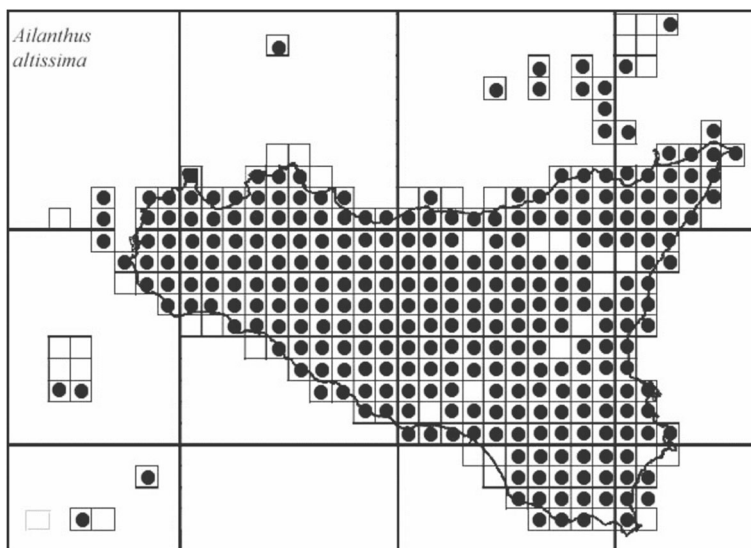
Fig. 26 Distribution of the invasive Tree of Heaven (*Ailanthus altissima*) in Sicily following the UTM grid of 10 × 10 km; data point out the impressive expansion (from 0 to 1300 m a.s.l.) since its introduction at the beginning of the XIX century and its diffusion in the field during the 1860s (Badalamenti et al., 2012)

Specific Dynamics and Vegetation Patterns of Small Mediterranean Islands

The small islands (1–100 ha) and islets (less than 1 ha) — according to the classification of Arrigoni and Bocchieri (1996) — represent in fact the most common insular realm of the Mediterranean Basin with several thousands of units. Nevertheless, their vegetation patterns and dynamics (i.e., plant succession and turnover) were less investigated compared to the large Mediterranean islands (but see Snogerup & Snogerup, 1987; Höner, 1991, Vidal et al., 2000; Panitsa et al., 2006; Dimopoulos et al., 2011, etc.), and a meta-analysis of vegetation types and functional biogeography according to geographical, environmental, and land-uses patterns is still lacking.

Here, we consider a 'small island' as an island with a surface area less than 10 km² (1000 ha), a commonly accepted definition by the *Mediterranean Small Islands Initiative* ([PIM Initiative]: Renou, 2012; *www.initiative-pim.org*). In this context, the 'Greek archipelago' is the most important of the Mediterranean archipelagos with approximately 7580 islands and islets in the Aegean Sea, and more than 90% of them are smaller than 10 km² (Triantis & Mylonas, 2009). In the Ionian Sea, the number is more reduced, with ca. 300 Greek islands and islets. Croatia, the second country with the most islands contains 653 small islands and islets with coastal lines shorter than 10 km, but with developed soil and vegetation (Nikolić et al., 2008).

Environmental Characteristics as Main Drivers of Vegetation of Small Islands

Due to lower elevation and to poor soil development, local environmental specificities — notably the topography and the nature of substrate — have a major influence on vegetation patterns of small islands and islets. Most of these Mediterranean small entities are formed by calcareous or siliceous rocks with a more or less hilly landscape. Nevertheless, there also exist several volcanic islands and, in North Africa, several archipelagos of flat islands composed of sandy substrates in arid and semi-arid bioclimates. These geological features give rise to a wide spectrum of plant assemblages that often show original structures and composition, which are briefly discussed below.

Small Rocky Islands

Most of the small islands and islets of the Mediterranean have a rocky geomorphology (Figs. 27 and 28). Here we discuss the siliceous (i.e., base-poor) or limestone (i.e., base-rich) apart from the volcanic ones. For example, the Croatian part of the Adriatic coasts is predominantly rocky and steep with 84% of shorelines included in the coastal karst (Lovrić, 1993). Because of the geological structure of the Croatian coast, the sandy shores are indeed a very rare type of habitat. Due to the large number of such islands (several thousands), it is impossible to present the various types of vegetation. However, there are some common structural traits of local plant communities, and habitat diversity is a key factor explaining local species richness patterns.

The coastal vegetation zone is characterized by only a few halophytes that are able to produce low cover (Fig. 28a), mostly *Crithmum maritimum* (Apiaceae) and one or several apomictic taxa of the genus *Limonium* (Plumbaginaceae) for which many narrow endemics
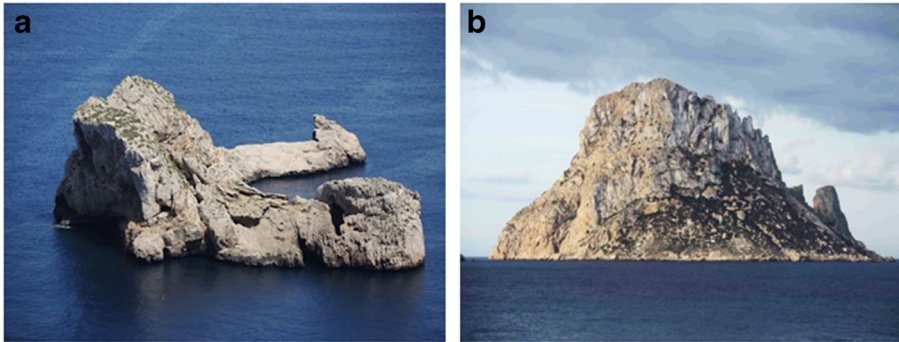
Fig. 27 Example of small rocky islands around Ibiza (Balearic Islands), IV.2014. **a**: Ses Margalides (1 ha), NW Ibiza, which houses the unique natural population of the endemic shrub *Euphorbia margalidiana*; **b**: Es Vedrà island (640 ha), an impressive peak emerging from the sea, SE Ibiza (see Fig.30) (F. Médail / IMBE)

are described from these small islands. The spatial importance of this vegetation belt depends on the island's topography and geomorphology. If it is usually restricted to a more or less narrow belt, on islets, the whole surface of this zone, which is exposed to the sea wind, is inhabited by true halophytes. On maritime cliffs exposed to prevailing winds, salt spray can reach an altitude of one hundred meters or more, which may explain the presence of halophytes in clearings of the coastal matorrals. In the vegetation belt located slightly inland, or in areas more protected from prevailing winds, occur a mosaic of xerophytic and salt-resistant matorrals with low evergreen shrubs (*Anthyllis, Armeria, Astragalus, Euphorbia, Genista, Teucrium, Thymelaea,* etc.), and open ground with herbs (*Dactylis, Brachypodium, Bromus,* etc.) in between them. These dwarf littoral phrygana formations occur mainly in the Eastern Mediterranean but some similar types exist also in the Western Basin on limestone islands (e.g., with *Astragalus tragacantha* on Marseilles' islands (Fig. 28b), *Astragalus balearicus* on Mallorca and Minorca, or *Centaurea horrida* in NW and NE Sardinia). All of these coastal vegetations frequently suffer from recurring impacts of marine birds that alter their structure and composition and promote the expansion of halo-nitrophilous plant communities (see below). Then, various types of thermophilous matorrals, often dominated by the lentisc (*Pistacia lentiscus*) and the tree spurge (*Euphorbia dendroides*), are, in general
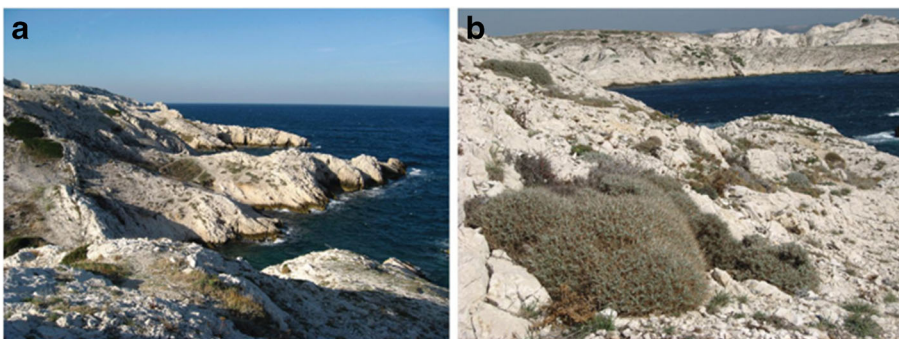
Fig. 28 Open coastal vegetation on the windy calcareous archipelago of the Frioul, near Marseille (SE France). **a**: western coast of Pomègues island with few halophytes (*Crithmum maritimum, Limonium pseudominutum, Daucus carota*); **b**: coastal phrygana with *Astragalus tragacantha* on Ratonneau island, X.2009 (F. Médail / IMBE)

located, on these small islands, but their own floristic composition depends on the biogeographical situation and environmental characteristics. Finally, small rocky islands below several hundred of hectares are often too small to house well-developed and species-rich forest communities and wetlands, but there is no rule. In fact, some densely wooded small islands exist along the N. Mediterranean coasts, in particular in Provence; this is the case of most of the islands of the Port-Cros National Park (Médail et al., 2013) (Fig. 29), and even of some islands under 50 ha area: Saint-Honorat island near Cannes and Île Verte near Marseille (Médail & Vidal, 1998).

The 'biogeographical signature' of each island is exacerbated on rupicolous habitats that often harbor interesting endemics or plants with disjunct distributions. An emblematic case is that of small islands with a very tormented topography and high elevation/surface rate. Some of them have become true 'landscape icons' and this high geomorphological heterogeneity induces a great diversity of natural habitats and species, with some narrow endemics. Therefore, they represent local biodiversity hotspots of great interest, as is the case for Es Vedrà (surface: 640 ha; altitude: 384 m) in SE Ibiza (Figs. 27b and 30), Tavolara in NE Sardinia (surface: 589 ha; altitude: 565 m), Panarea in the Aeolian archipelago (surface: 335 ha; altitude: 420 m), Zembra in N. Tunisia (surface: 389 ha; altitude: 435 m), or Antimilos (surface: 795 ha; altitude: 671 m) in the western Cyclades.

These contrasted topographies induced highly diverse microclimatic niches and sharp ecological differences between southern and northern exposed cliffs. The establishment of ecological indicator values of Ellenberg for southern Aegean plants shows that those located on sunny slopes of offshore islets are characterized by a specific functional type related to situations of most intensive insolation (Böhling et al., 2002). On the other hand, on north-facing cliffs often subjected to long-lasting or even continuous shade conditions, mesophilous plants such as the chasmophytic ferns *Asplenium marinum* or *Asplenium sagittatum* occur on some western Mediterranean islands, and especially diverse paleoendemic lineages that have found refuge here after the aridification episodes of the Quaternary. This is the case of long-lived perennial endemics such as *Crepis triasii* (Asteraceae), located on mesic slopes of limestone cliffs in the eastern Balearic Islands (Mayol et al., 2012), or of the woody relics of Sicily such as *Bupleurum dianthifolium* and *Pseudoscabiosa limonifolia* on the cliffs of Marettimo (Egadi) (Fig. 31).

Another interesting biogeographical pattern is that small offshore islands can determine extreme limits for the geographical distribution of plants that are more characteristic of an adjacent biogeographical area. This stepping-stone or land-bridge

Fig. 29 The islands of Port-Cros (**a**) and Porquerolles (**b**), in the Port-Cros National Park (SE France), are densely covered by forests with holm-oak and Aleppo pine, and a high maquis with *Arbutus unedo* and *Erica arborea*, VI.2012 (F. Médail / IMBE)
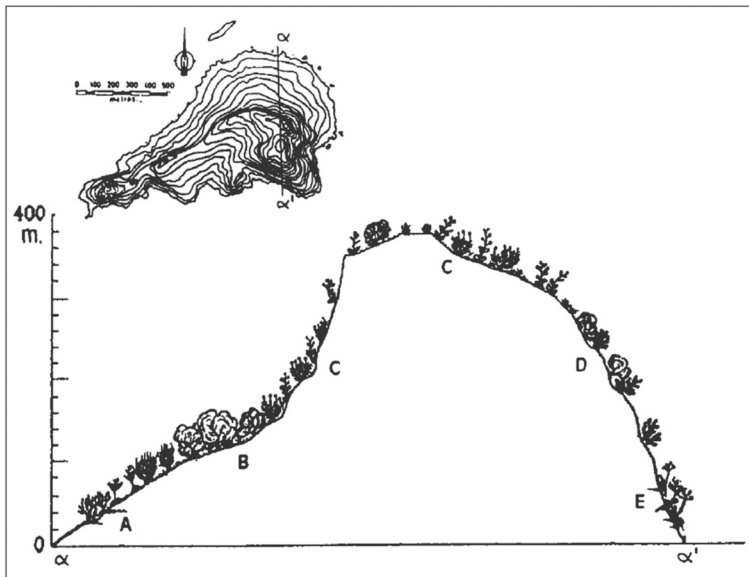
Fig. 30 Schematic distribution of the dominant vegetation on Es Vedrà island, a high elevated (384 m) but medium size (640 ha) island of SE Ibiza (Balearic Islands) (see Fig. 27b) (Tebar et al., 1989). A: halonitrophilous matorral with *Suaeda vera*; B: typical Pityusic matorral with *Pistacia lentiscus* and *Cneorum tricoccon* on the N slope; C: endemic dwarf-shrub community with *Thymus richardii* subsp. *ebusitanus* and *Hippocrepis grosii* on the basal slope of maritime cliffs; E: halophilous vegetation with *Limonium caprariense*

phenomenon can be depicted in several Mediterranean insular areas. This pattern is well illustrated by the northernmost distribution of several N. African plants confined in Greece, or even in Europe, to the small offshore islands of S. Crete that includes several Saharo-Arabian elements such as *Atriplex mollis* (Bergmeier et al., 2011) that is absent from the nearby Crete (see the paragraph related to the Messinian salinity crisis). In the Adriatic Sea, the Tremiti archipelago, off the Italian coast of Gargano Peninsula, includes a few taxa of the trans-Adriatic plants element as the western limit of distribution, notably the local endemics *Limonium diomedeum* and *Asperula staliana* subsp. *diomedea*. This latter represents the south-westernmost element of a trans-Adriatic lineage of vicarious taxa belonging to the *Asperula* ser. *Palaeomediterraneae*, encompassing several disjunct and relic taxa, one of which (*A. naufraga*) reaches the Ionian island of Zakinthos, while the others are located on a few western Mediterranean islands (*A. crassifolia* on Capri and Li Galli islands near Naples; *A. deficiens* on the NE Sardinian island of Tavolara; *A. paui* s.s. on the western Balearics) (Korica et al., 1992). In the western Mediterranean Basin, the N. Tunisian island of Zembra harbors the south-westernmost populations of some plants located mainly on the Italian Peninsula and Sicily (*Erodium maritimum, Iberis semperflorens*) or in the Tyrrhenian (*Asplenium balearicum, Galium minutulum*), and that are otherwise absent from the close (ca. 10 km) continental coast (Médail et al., 2020). The same occurs on many circum-Sicilian satellites islands such as Marettimo, Strombolicchio, and Lampione, which harbour many local endemics or the only known populations of many plants that are otherwise absent on adjacent islets and on the whole Sicilian territory (e.g., Lo Cascio & Pasta, 2012, 2020; Pasta & La Mantia, 2013). Finally, this biogeographical pattern is
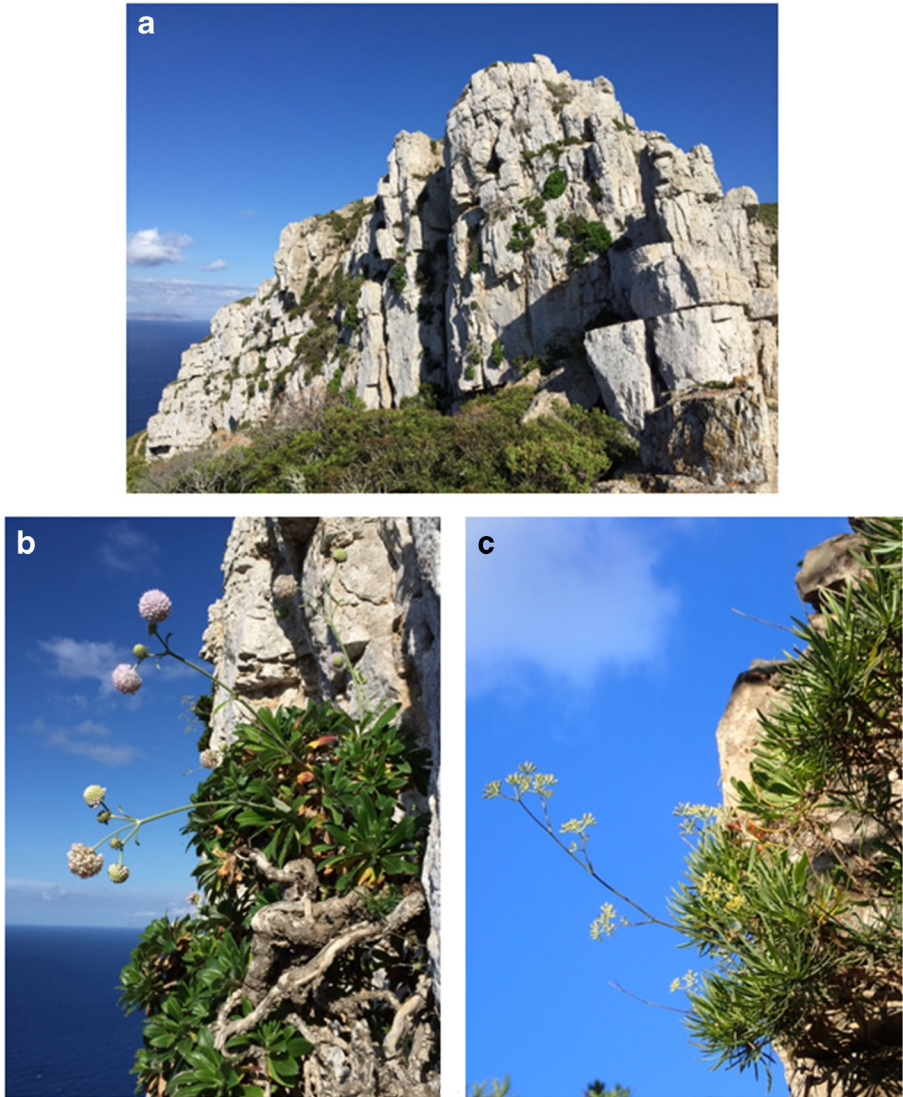
Fig. 31 Endemic vegetation on the mesic limestone cliffs of Marettimo island (Egadi, W Sicily) (**a**), including the western Sicilian endemic *Pseudoscabiosa limonifolia* (Caprifoliaceae) (**b**), and the single island endemic *Bupleurum dianthifolium* (Apiaceae) (**c**), VI.2018 (F. Médail / IMBE)

also found in S. France, on the Hyères archipelago (Fig. 29), a remnant of the Tertiary Protoligurian massif sheltering several Tyrrhenian endemics (*Delphinium pictum, Ptilostemon casabonae, Teucrium marum,* etc.), which are totally absent along the close mainland of the siliceous Provence, even though environmental conditions are similar (Médail et al., 2013). If the functional explanation for this pattern deserves to be accounted for, it is possible that various magnitudes of insular biotic interactions, notably the level of interspecific competition could explain it.

Small Volcanic Islands

Relatively few volcanic archipelagos and islands exist in the Mediterranean Sea, but these 'oceanic entities' are very interesting from both an ecological (primary succession patterns) and island biogeographical points of view. Indeed, because they were never connected to continental landmasses, these insular communities were only moulded by more or less long-distance dispersal of species, through wind, birds, or sea currents. This allows us to evaluate the process of primary natural colonization by plants and community assembly rule from a zero-base-line.

In the Eastern Mediterranean, the South Aegean volcanic arc, dating from the Pliocene to the Present, constitutes the most important volcanic structure of the Mediterranean area, extending along a North-West/South-East belt between the Saronic Gulf (Aegina island) and the island of Nisyros. It forms a belt of volcanic centres, in particular the well-known Santorini island group (S. Cyclades), which is still shaped by active volcanism. The Santorini archipelago is a prominent example of seaborn emergent islands (Fig. 32), where the age of the lava was found to be the most important structuring factor for primary succession of vegetation (Dimopoulos et al., 2011). Inside the seawater-filled caldera of Thira, the 2200–year old island Palea Kameni is currently covered by a mosaic of evergreen sclerophyllous community dominated by *Pistacia lentiscus,* which represents the final stage of succession, whereas the younger Nea Kameni island emerged between 1570 and 1950 A.D. harbours only an open-canopy pioneer community rich in grasses and legumes (Raus, 1988). On this younger island, the mechanism of community assembly are complex and stochastic processes prevail (Karadimou et al., 2015). The distribution of ashes and the physical-chemical properties of the soil constitute here the second driver of vegetation patterns, but the arid environment imposes a strong stress limiting the rapid development of plant cover and the establishment of woody communities (Dimopoulos et al., 2011). Some other islands of the Aegean volcanic arc, characterized by greater topographic and geological heterogeneities, show higher diversity of woody vegetation of scrubs and phrygana with dominant *Erica manipuliflora, Cistus creticus* or *Anthyllis hermanniae* and even a


Fig. 32 View of some islands of the Santorini archipelago (Aegean Sea, Greece) in the caldera of Thira: the large and younger Nea Kameni with predominant bare lava, then behind the older island Palea Kameni and the islet of Aspronisi, VIII.2020 (F. Médail / IMBE)

Pinus brutia forest on the small island of Gyali in the SE Aegean Sea (Brofas et al., 2001), or with a restricted stand of the indigenous palm *Phoenix theophrasti* on Anafi island, a local plant biodiversity hotspot in the southern Cyclades (Kougioumoutzis et al., 2012).

In the Adriatic Sea, only two volcanic small islands occur, located in Central Dalmatia (Croatia) and belonging to the Vis archipelago: the islands of Brusnik and Jabuka, which is an impressive peak of 22 ha emerging from the sea to 97 m. They include a few Illyrian-Adriatic endemic plants such as *Centaurea ragusina* on Brusnik, *C. friderici* subsp. *jabukensis* and *C. crithmifolia* on Jaburka, and *Limonium vestitum* on the both (Bogdanović & Mitić, 2003; Nikolić et al., 2010).

In the Central Mediterranean, the islands of the Eolie (Aeolian) archipelago near the coasts of northeastern Sicily, exhibit a great variety of natural landscape and plant communities where sclerophyllous matorrals predominate but with some biotic originalities (e.g., Lojacono Pojero, 1878; Ferro et al., 1992). The slopes of the craters of Stromboli (Fig. 33a) and Vulcano islands are characterized by peculiar plant communities, with open pre-forests individualized by two arborescent endemic Fabaceae (respectively *Cytisus aeolicus* and *Genista tyrrhena*), and the scattered clumps of *Centaurea aeolica*. Already cited by the Greek botanist Theophrastus in the fourth century BCE, *Cytisus aeolicus* is a strikking example of extreme persistence for a tree under permanent volcanic activity (Fig. 33b); the metapopulation of Stromboli is surprisingly healthy and very dynamic despite recurrent eruptions (Zaia et al., 2020).

Cliff vegetation is noteworthy in particular on the northern slopes of Panarea and Alicudi islands with a community including many endemics such as *Dianthus rupicola* subsp. *aeolicus*, *Hyoseris taurina*, *Lomelosia cretica*, *Silene hicesiae*, *Iberis semperflorens* and *Seseli bocconei* (the latter two only on Panarea), *Brassica incana* and *Erysimum brulloi* (these two only on Alicudi) (S. Pasta, pers. comm.). These rupicolous communities have clear affinities with those occurring on some northern Tunisian islands (Zembra). The vegetation of Aeolian islands has also phytogeographic links with the central Tyrrhenian volcanic islands (Ponziane archipelago), which represent the northern limit of some southern-central Mediterranean plant communities, notably the matorral with *Genista tyrrhena* and *Erica multiflora* (Stanisci et al., 2005). The flora of the satellite islets of the Aeolian archipelago includes
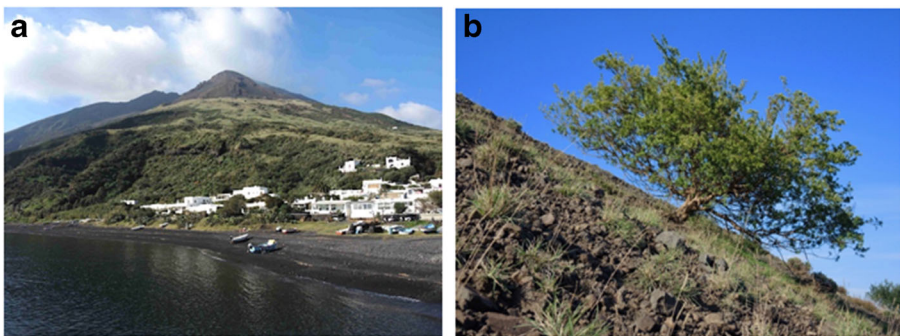
Fig. 33 The vulcanic island of Stromboli in the Aeolian archipelago (NE Sicily), XI.2015. **a**: NE slope of the volcano (924 m a.s.l.); **b**: the endemic tree *Cytisus aeolicus* (Fabaceae) on the basaltic screes of the volcano (F. Médail / IMBE)

several interesting plants not recorded on the largest islands like *Eokochia saxicola* or *Parapholis marginata* (Lo Cascio & Pasta, 2020).

In the Gulf of Napoli (Naples) and its surroundings, there occurs two small volcanic archipelagos, the Ponziane and Flegree islands. The Ponziane islands includes the main islands of Ponza and Palmarola, which are covered by different thermophilous matorrals: (i) an original macchia with the endemic Fabaceae, *Genista tyrrhena* subsp. *pontiana*, and *Erica multiflora*, (ii) an evergreen sclerophylous macchia dominated by *Arbutus unedo, Erica arborea* and a few *Quercus ilex*, and (iii) a high matorral with the dwarf-palm which is still sparse but expanding on the western slopes of Palmarola (F. Médail, pers. obs.). Scattered and isolated stands of deciduous trees (*Quercus virgiliana* and *Sorbus domestica*) located on the northern slopes and on the colluvial sites of Ponza are probably the remnants of the woodland that once covered the whole island (Stanisci et al., 2005). Among the Flegree islands (Ischia, Procida, Vivara), Ischia is the largest one and is covered by pines, downy oaks and chestnut groves. It hosts some interesting macrothermic plants such as *Woodwardia radicans* and *Cyperus polystachyos,* whereas the monotypic genus *Eokochia saxicola,* a very rare islet specialist endemic of some maritime cliffs of Central Mediterranean, has disappeared in its *locus classicus* of Scogli di S. Anna near the main island of Ischia (Ricciardi et al., 2004). But this halophilous dwarf shrub still occurs on Capri and on the islet of Strombolicchio, close to Stromboli island, and it has been quite recently found on the coast of Campania (Strumia et al., 2015).

Finaly, few small volcanic archipelagos occur in the westernmost part of the Mediterranean Basin, in Spain, Morocco and NW Algeria. Along the Spanish coasts, the vegetation of the small Columbretes archipelago is remarkable by the presence of an halo-nitrophilous plant community with the Ibero-Levantine-Balearic endemic shrub *Medicago citrina* associated with *Malva arborea* (Carretero & Boira, 1991). Along the coasts of Almeria (Andalusia), some volcanic islets include a few 'islet specialists' of considerable biogeographical interest such as *Malva durieui* (= *Lavatera mauritanica*) and *Fumaria munbyi,* which is also present on the volcanic islands of Columbretes, and of NW Algeria (Habibas and Rechgoun) (Pavon et al., 2016). All these small semi-arid islands, mostly located in the Alboran Sea, show strong biogeographical affinities despite a remoteness up to 500 km (Véla, 2013). Between Andalusia and Morocco, the flat, small Alborán island (7 ha) constitutes the remnant of a volcanic structure dating from the Miocene. Its isolation and age explain the low richness but the specificity of the flora and vegetation with some endemics (*Anacyclus alboranensis, Diplotaxis siettiana, Senecio alboranicus*) forming several types of halo-nitrophilous grass-lands (Mota et al., 2006). Four miles off the Mediterranean coast of northern Moroccan, the Chafarinas or Djafaren archipelago is formed of three volcanic small islands (from 12 to 22 ha) within a semiarid bioclimate (320 mm mean annual rainfall). The vegetation is sparse because of regular disturbance by seagull popu-lations, and it is dominated by chenopod shrubs (*Salsola oppositifolia*, *Suaeda vera, Atriplex halimus*) (García et al., 2002). Along the NW Algerian coast, the Habibas archipelago and Rechgoun islands exhibit also some specificity in vegetation, notably a chasmophytic community with three narrow endemics (*Brassica spinescens, Spergularia pycnorrhiza, Sonchus tenerrimus* subsp. *amicus*) on rocky escarpments (Maire & Wilczek, 1936; Véla, 2013).

Small Sandy and Flat Islands

Relatively few small sandy islands and islets exist within the Mediterranean Sea, and they are mainly located along the south-eastern coast of Tunisia, notably in the Gabès Gulf (Médail et al., 2020), with a few additional islets along the western coast of Sicily (Stagnone archipelago) and the Tripolitania coast of Libya.

These main Tunisian archipelagos are: (i) the Kerkennah Islands, located about eighteen kilometers from the coastal town of Sfax and including two main islands (Gharbi, 48 km^2 and Chergui 99 km^2), and thirteen small satellite islands or islets for a surface area of around 4,5 km^2 (Médail et al., 2015) (Figs. 34 and 35); (ii) the Kneiss archipelago, consisting of one main island (El Bessila, 440 ha) and four vegetated islets, situated near the coast south of Maharès (Médail et al., 2016); and (iii) the Djerba archipelago, which includes the eponymous island, the largest one of Tunisia (526 km^2), situated at 1,5–2 km from the coast and surrounded by nine satellite islands or islets sheltering vegetation (Médail et al., 2021). Annual rainfall measures between 200 and 300 mm so that these islands are clearly under an upper arid bioclimate *sensu* Emberger's classification.

These archipelagos are very flat since the maximum altitude is only 51 m a.s.l. for Djerba and 13 m for the Kerkennah, and whose lowlands, with elevations of less than 2.5 m, represents more than 50% of the islands' areas (Etienne, 2014). The bedrock consists of Mio-Pliocene gypsiferous clays and, on some islands, above this layer lies a calcareous crust dated from the lower Pleistocene. The lithological context explains the high vulnerability to erosion and this fragility induces a rapid retreat of the coastline and a continuous extension of the *sebkhas* (low, sandy and salty areas under the influence of the sea) at the expense of steppic areas and palm groves. The topographic contour of these islands was shaken up by deep eustatic changes, especially subsidence, up to two meters over the last two thousand years (e.g., Oueslati, 1995). Land salinization induces a significant progression of halophilous plant communities and species, and seriously threatens the steppic and xerophilous vegetation (Médail, 2017). On the Kerkennah islands, this land salinization has indeed induced a sharp increase in the area covered by *sebkhas* (+ 20% for thirty years) (Etienne et al., 2012; Etienne, 2014).
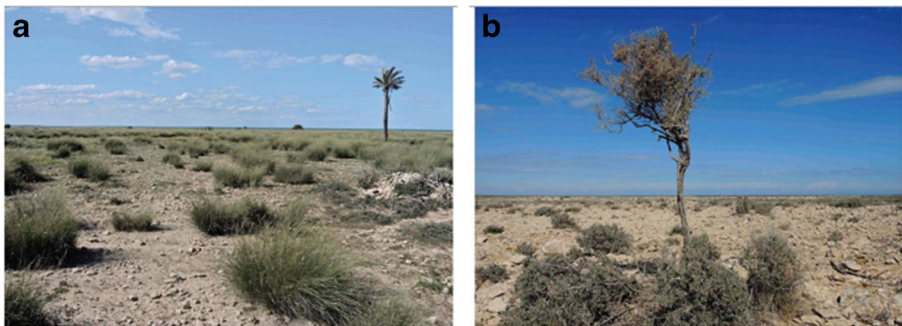
Fig. 34 The flat satellite islands of the Kerkennah archipelago (E Tunisia). **a**: open steppe with *Lygeum spartum* (Poaceae), III.2014; **b**: rocky steppe with remnants of the endemic shrub *Salsola tunetana* (Amaranthaceae), a remarkable specimen 1.5 m high, Roumadiya island, X.2015 (F. Médail / IMBE)
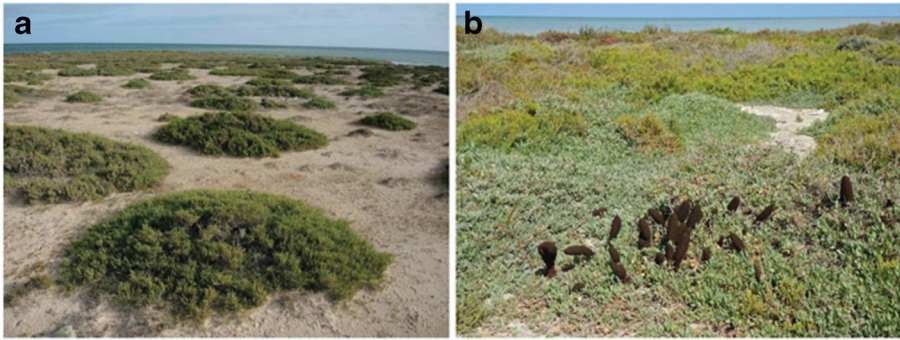
Fig. 35 Typical vegetation of the flat and sandy islands of the eastern Tunisian coast, on the Kerkennah archipelago, III.2014. **a**: halophilous shruby vegetation on sebkhras with *Arthrocnemum macrostachyum* and *Sarcocornia fruticosa* (Amaranthaceae), Gremdi island; **b**: halophilous and nitrophilous vegetation with *Halimione portulacoides* parasitized by the 'Maltese fungus' *Cynomorium coccineum*, a vascular parasitic plant of the Cynomoriaceae family, Keblia island (F. Médail / IMBE)

The dominant vegetation is composed of low halophilous or salt-resistant shrubs, mainly several Amaranthaceae species (genera *Anabasis, Arthrocnemum, Atriplex, Halimione, Halocnemum, Salsola, Sarcocornia, Suaeda,* etc.) (Médail et al., 2015, 2016) (Fig. 35). These monotonous and species-poor plant communities are characteristic of *sansouires* and *sebkhas*. They occupy the vast expanses of salty clay soils and marshy areas, and they cover the total surface of most of the islets below a few hectares. In mosaic with the previous vegetation type, some salty steppes with few annual plants (*Limonium avei, Frankenia pulverulenta, Salicornia europaea, Sphenopus divaricatus,* etc.) occupy the sandy and clay soils. The short coastal stretchs are covered by a sandy layer supporting several psammophilous communities, notably on Djerba, which contains the 'common' perennial vegetation linked to the coastal dunes, enriched on fixed sands by several plants belonging to the southern Mediterranean element, such as *Silene succulenta, Helichrysum conglobatum, Echiochilon fruticosum, Launaea fragilis, Tetraena alba* (Vanden Berghen, 1977–1979). Then, from a few feet above sea level, more xerophilous steppic and rocky grasslands occur (Fig. 34), with some dominant grasses (*Lygeum spartum, Stipa capensis*) or unpalatable plants such as *Charybdis maritima* aggr.

The matorrals are rare and fragmented by human activities. There exist some halo-nitrophilous thickets with *Limoniastrum monopetalum, Atriplex halimus* and *Nitraria retusa* and, henceforth, a more restricted and threatened xerophilous matorral with *Lycium schweinfurthii, Thymelaea hirsuta, Periploca angustifolia, Rhus tripartita* and the Fabaceae *Retama raetam,* which is present only on Djerba and on the two main Kerkennah islands. These shrubs are very rare or absent on the small satellite islands. The spiny summer-deciduous shrub *Ziziphus lotus* — the putative famous *lôtos* of Lotophagous island (Djerba) haunted in Homer's Odyssey — has probably disappeared from this island during the first half of the twentieth century because of human impact. Due to the scarcity of paleoecological data, it is difficult to estimate what may have been the probable natural vegetation of these islands during the Post-Glacial period. Nevertheless, the presence of ancient woody remnants of juniper (*Juniperus phoenicea* subsp. *turbinata*) and *Pistacia lentiscus* from a site of Djerba dated to 4200–4300 years

ago (Damblon & Vanden Berghen, 1993), and the presence of several bio-indicator plants suggest the former existence of a denser sclerophyllous matorral or open pre-steppic forest, with the possible occurrence of the Aleppo Pine and native Olive tree on these Tunisian islands (Médail et al., 2015).

Despite their relative uniformity, these islands contain rare and interesting plants from a biogeographical point of view and they play a leading role in the conservation of the flora of the Eastern Tunisian coast (Médail et al., 2020).

Specificity in Ecosystem Functioning of Small Islands

Small Island Effect and Islet Specialists

A small island effect' is often perceptible for islets of less than a few hectares (1–5 ha) and with an elevation of less than 50 m a.s.l., because elevation also represents a crucial factor influencing the diversity of vegetation types. These factors explain why an important set of plant species and some vegetation types (e.g., permanent or temporary rivers, wetlands) cannot occur on islands below a critical size. Indeed, there exists, in general, a positive correlation between island surface and the number of habitat types (Médail & Vidal, 1998).

Some striking differences in vegetation composition and structure occur between these offshore islets despite, in general: (i) the rather short time of separation, which generally occurred ca. 15,000 years ago, during the last marine transgression following the Last Glacial Maximum episode; (ii) the reduced distances between them and the main islands and/or the continent; and (iii) the apparent similarity of present abiotic conditions. Indeed, one of the most fascinating and intriguing pattern is related to the biological uniqueness of each small island. Some close islands show different plant species assemblages, suggesting the existence of specific and local environmental pressures or history, selective plant dispersal through some narrow arms of sea, as well as random colonization–establishment–extinction processes ('stochastic events'). For example, the distribution of ca. 60 plants species (notably *Campanula, Dianthus, Erysimum, Helichrysum*) restricted to mostly maritime cliffs (chasmophyte plants) of the Aegean show marked differences between islands, even less than 10–20 km apart (e.g., Snogerup, 1967). Despite repeated land-connections linked to sea-levels changes during geological times, small distances between these islands have served as an effective barrier to plant dispersal, allowing for the isolation and speciation of various insular populations.

Small islands often harbour some 'islet specialists', i.e., plants that grow exclusively or are very abundant on the most exposed and isolated islets but that are not on the mainland or on the closest larger island despite the presence of similar suitable habitats (Höner & Greuter, 1988; Bergmeier & Dimopoulos, 2003; Georgiou et al., 2006). These plants are often adapted to some disturbance and stress (ruderal and stress-tolerant strategies *sensu* Grime) and are salt-tolerant, but not strictly halophilous. There also often exists a 'life-form imbalance', with the overrepresentation of annuals (therophytes) or shrubs (chamephytes and nanophanerophytes). Some islet specialists possess a large pan-Mediterranean distribution (*Allium commutatum, Hymenolobus procumbens, Malva arborea*), others constitute narrow endemics: e.g., *Euphorbia margalidiana* on an unique Balearic islet of Ibiza (Fig. 27a), *Nananthea perpusilla* (Fig. 36a) and *Silene velutina* on some satellite islets around Corsica and Sardinia, or
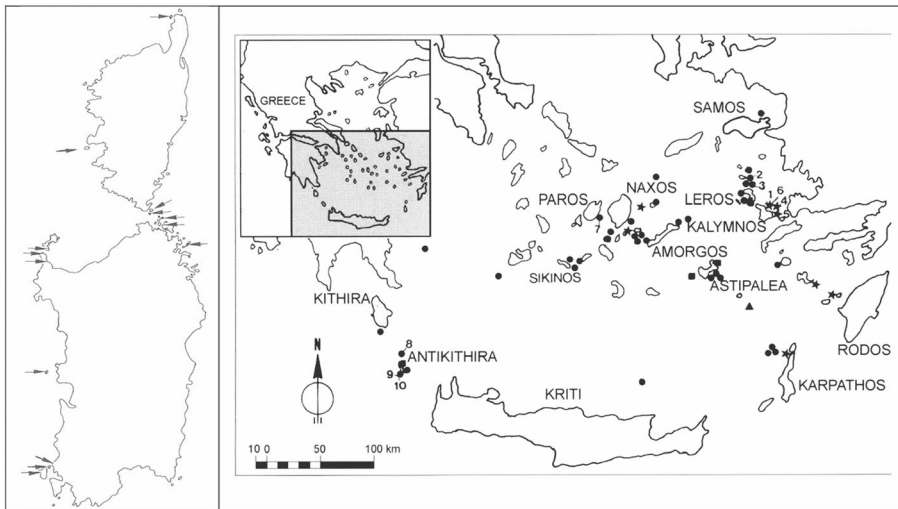
Fig. 36 Distribution range of two islet specialists of the Asteraceae family; **a**: *Nananthea perpusilla* on the small satellite islands of Corsica and Sardinia (R. Verlaque, ined.); **b**: *Anthemis scopulorum* (● var. *scopulorum*, ★ = var. *discoidea*, ▲ = var. *conica* and ■ = var. *ofidousa*) on Aegean small islands and islets (Georgiou et al., 2006)

Anthemis scopulorum (Fig. 36b), *Atriplex recurva* and *Silene holzmannii* on some small Aegean islands. Islet specialists often possess a good ability for dispersal by sea drift over distances of hundreds of kilometres inasmuch as floating diaspores can withstand up to a month in the sea water. Their distribution and abundance can be explained by their optimal specialisation to the highly harsh and unusual environmental conditions of these small islands. Islets specialists could characterize highly specific plant communities, such those with *Bellium* spp. on Greek and Sicilian channel islets, or the palaeoendemic *Nananthea perpusilla,* which forms pioneer and temporary humid grasslands restricted in the shade of granitic rocks (Paradis, 2005).

Disturbances on Small Islands

Compared to the continent and larger islands, small insular communities and ecosystems are more sensitive to exogenous disturbances and to environmental stochasticty, which often promotes rapid and contrasted dynamics. This is particularly the case of medium and small islands (1–100 ha) and islets (less than 1 ha) that are subject to harsh environmental conditions (continuous salt-spray and strong winds) but also suffer greater disturbance (storms, nesting seagulls, grazing). A detailed analysis of the drivers explaining the composition of alien and endemic plants for fourty small islands of Sardinia show the complexity of the processes involved and of the factors related to three climatic, geographic and landscape, and anthropogenic domains (Fois et al., 2020).

Small islands often house large seabird colonies that exert specific disturbance with a high pressure on ecosystems by modifying patterns and dynamics of plant communities (Fig. 37). Seabirds are responsible for the energy inflow from sea to terrestrial ecosystems through guano, fish scraps, various items of rubbish and their decomposing
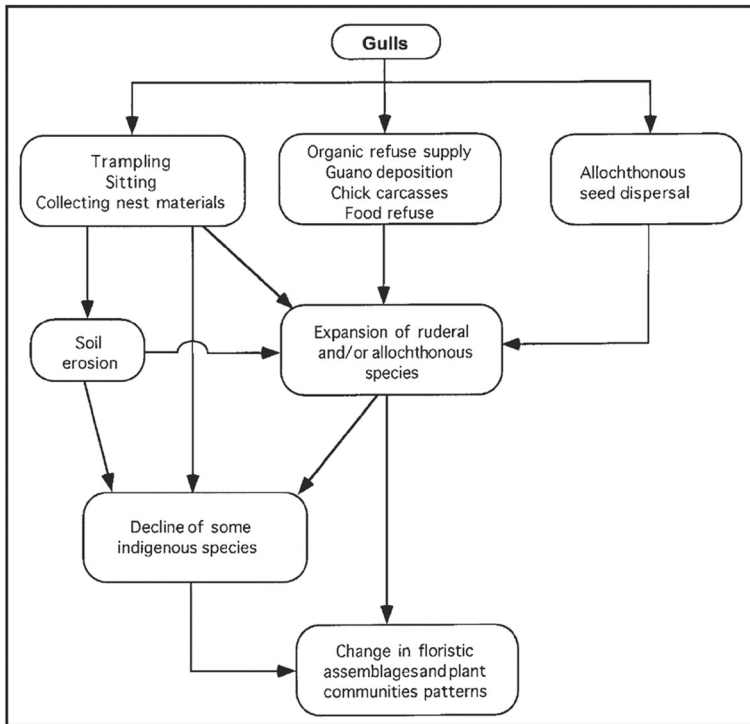
Fig. 37 Diagram of impact by the yellow-legged gull on the flora and vegetation of some south-eastern France islands (Vidal et al., 1998)

carcasses. The impact of seabirds, notably gulls (Fig. 38a), on Mediterranean oligotrophic vegetation is, therefore, often severe because of physical (trampling, pulling-up, soil erosion, burrowing) and chemical (soil manuring induced by guano rich in phosphorous and nitrogen compounds, salt deposition) disturbances (Vidal et al., 1998, 2000; García et al., 2002; Baumberger et al., 2011). Seagulls influence may lead to severe imbalances for insular ecosystems since they could induce: (i) drastic soil changes with excessive contents of extractable P, K and Mg and soluble salts; (ii) changes in the leaf nutrient status of the dominant plants; (iii) alteration of the cover, abundance, composition and/or turnover of plants; (iv) modification of species interaction. These strong ecological pressures favour the most resistant (ruderal) plant species and vegetation types at the expense of more oligotrophic and stress-tolerant species. This is the reason why numerous Mediterranean small islands, specially the flat ones, are covered by roughly similar vegetation types of open and ruderal scrublands composed by halo-nitrophilous shrubs (Fig. 38b), notably Amaranthaceae (e.g., *Arthrocnemum, Atriplex, Halimione, Sarcocornia, Salsola, Suaeda*), with perennial (e.g., *Daucus, Malva*) or annual (e.g., *Amaranthus, Mesembryanthemum, Parietaria, Senecio, Portulacca*) herbs. Besides wind, birds also act as important natural vectors for the dispersal of seeds from the mainland or other islands. Thus, passive introductions of new plants — with numerous alien and invasive plants — on islets are indeed frequently observed near nesting colonies of seagulls. These biotic changes, and notably the shift of demographic strategies of plants *sensu* Grime (2001), from stress-
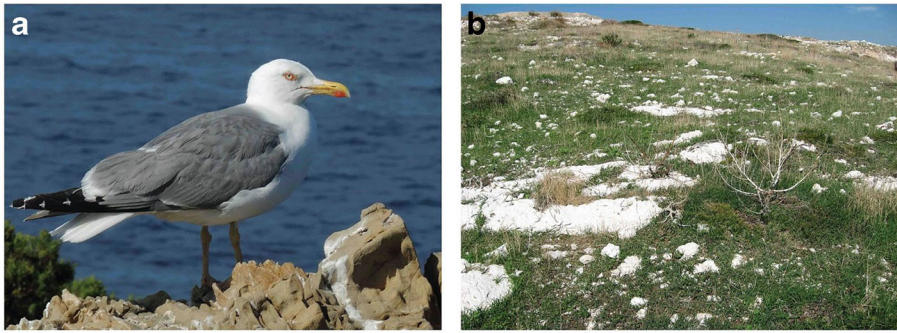
Fig. 38 High densities of the yellow-legged gull (*Larus michahellis*) (**a**) induce severe vegetation changes on the Mediterranean small islands, as in Ratonneau island near Marseille where ruderal species increase (*Lobularia, Hordeum, Urtica, Fumaria, Heliotropium, Portulaca*, etc.) and halo-tolerant plant like *Malva arborea* disappeared (**b**), X.2009 (F. Médail / IMBE)

tolerant species to ruderal ones can induce a significant increase of the primary productivity of the vegetation and a deep reorganization of these over-simplified trophic networks with an overrepresentation of some invertebrate groups. These later could be moreover favoured by high energy inputs from the sea and a reduced level of predation by top-down predators (Polis & Hurd, 1996).

Several studies have examined these complex seagull influences on small Mediterranean islands. For instance, on the Chafarinas islands (near the Moroccan coast), seagulls clearly influence the abundance of different halophilous shrubs: the relative cover of *Salsola* is reduced 30–fold in habitats that have been severely disturbed by birds whereas *Suaeda* has the highest abundance here; this induces a substantial niche segregation along the gradient of seabird influence (García et al., 2002). In the Marseille archipelago (south-eastern France), the effects of an increasingly large yellow-legged gull (*Larus michahellis*, Fig. 38a) colony on the island flora and vegetation were studied through the analysis of floristic changes (*species turnover*) that have occurred in the past forty years (Vidal et al., 2000; Baumberger et al., 2011). Generally, plant turnover appears to be positively linked to gull nesting density, and it is inversely correlated to island area because small islets appear to be more affected than larger islands (but see Panitsa et al. (2008) that did not detect any effect of gulls on richness or structure of plant communities for some E. Aegean islets). Plants with the highest turnover rate were primarily ruderal, annual, wind-dispersed species, with a wide geographic distribution.

Disturbance by seabirds favours the massive establishment of non-native species that has led to the local extinction of some endangered plants on islets characterized by important species turnover. Another worrying issue is that a decrease in gull nest density does not necessarily induce a return to previous vegetation composition patterns. This suggests the deep inertial nature of the changes in island vegetation in the face of strong disturbances such as a drastic expansion of seabird colonies.

Another major disturbance on Mediterranean small islands and islets is grazing by goats, sheeps, cows, pigs, and donkeys, and even camels on some N. African islands. Even if this current use, which had been in effect for thousands years, were abandoned in some regions, micro-insular pasture is still practised in the Aegean (Bergmeier & Dimopoulos, 2003) and eastern Tunisian islands (Médail et al., 2015, 2016). Shepherds

use these islets for free-roaming livestock, and thus practicing a true 'insular transhumance' widely performed on numerous Aegean islands since Antiquity (Brun, 1996). They carry goats and/or sheep on small boats — or even by swimming for some cows that had to reach the Lavezzi archipelago in southern Corsica! — and then there was animals that became isolated in these natural folds without food or water being provided by the shepherds. To our knowledge, this practice is documented in Balearic Islands, Provence, Corsica, Sardinia, Tunisia, and Greece; whereas, it was abandoned some 40–50 years ago in Sicily. Insular toponyms attest to these practices of transhumance and grazing with diverse names for islands, such as Tragia ('goat island') near Samos in the E. Aegean Sea, or the ancient name of Favignana Island in W Sicily (*Aigousa* = populated by goats), or Capri, Capraia, and Caprera in the Tyrrhenian Sea, and along the coasts of Sardinia, the Asinara island that is linked to the past presence of donkeys. Of course, recurrent grazing on these reduced and fragile ecosystems causes strong perturbation to the local biodiversity, and the vegetation is often deeply modified with the local disappearance of the palatable plants, or their extreme range retraction in inaccessible places. An interesting finding is also the existence of a negative interaction between goats and gulls in the Skyros archipelago, i.e., during the grazing years, nests were less numerous and restricted to remote rocks (Pafilis et al., 2003). This additional interaction pattern could modify the magnitude of vegetation dynamics. Therefore, in the past the dramatic consequences of the grazing effect on Mediterranean islets likely contributed to the homogenisation of the composition and structure of micro-insular vegetation.

Special Plant-Animals Interactions on Small Islands

Because of the intrinsic characteristics of small island ecosystems (Médail, 2013) (Table 5), peculiar types of plant-animal interactions exist (Traveset & Navarro, 2018) that could also influence the structure and dynamics of plant communities. One of the most striking example is the plant-lizard mutualism deeply studied in the Balearic archipelago. Here, endemic lizards (*Podarcis lilfordi* and *P. pityusensis*) acted as probably the only seed dispersers of the native shrub species *Cneorum tricoccon* (Rutaceae) (Riera et al., 2002) and of the endangered endemic shrub

Table 5 Main patterns determining the ecological and functional importance of small islands (Médail, 2013, modified)

Structure of island communities / continent	Functioning
Communities with original taxonomic composition (numerous endemic taxa)	Simplified and specific functional processes (flux, biotic interactions)
Poor communities with few redundant species	Impacts exacerbated by exogenous disturbances
Higher abundance of rare, endemic and relictuals species, often at their range limit	Inflation density: relaxation of competition processes / expansion of ecological niches
Isolated populations, founded by few individuals	Processes of genetic differentiation (genetic drift, founding effects) and local adaptation
Communities subject to drastic ecological stress, affected by important stochasticity	Huge spatio-temporal fluctuations of plant richness and composition

Daphne rodriguezii on Minorca (Traveset & Riera, 2005). But introduction of carnivorous mammals onto the Balearic Islands has caused a dramatic disruption of mutualism between *Daphne rodriguezii* and *Podarcis lilfordi*. Seed dispersal by lizards is the critical stage that limits population expansion and seedling recruitment, thus drastically reducing *Daphne* populations, except in the Colom islet where lizards still persist (Rodríguez-Pérez & Traveset, 2010). Disperser loss has also had a negative impact on the genetic diversity of this *Daphne,* which possess higher relatedness among individuals for Menorcan populations (Calviño-Cancela et al., 2012), and this could induces putative changes in ecosystem functioning. On some small islands and islets, lizards may also play a key role for the pollination of several common Mediterranean plants, notably if these lacertids occur with a high density as is the case of the pollination of *Anthyllis cytisoides, Crithmum maritimum, Daucus carota, Euphorbia dendroides* on the island Sa Dragonera near Mallorca (Balearic Islands). With respect to the latter, a very rare case of double mutualism has been discovered between the lizard *Podarcis lilfordi* and the gymnosperm *Ephedra fragilis*: lizards qualitatively contributed to the reproductive success of the shrub, (i) as their transport large amounts of pollen from male to female cones, (ii) as small seeds coming from lizard-pollinated cones germinated at higher rates than those pollinated by wind or insects, and (iii) act as their main seed dispersers; in return, the lizard obtains energy resources thanks to its consumption of pollination droplets of the ephedra that constitutes its principal food source in summer (Fuster & Traveset, 2019).

Conclusion

The complicated historical biogeography of Mediterranean islands has induced the persistence of unique and relictual floras, but also the repeated local extinctions and re-colonisations of several specialized plants in relation to physiography, disturbance, and biotic interactions. The fragmentation of an originally widespread distribution or the coalescence of previously distinct territories explain some biogeographical relationships between islands, but insular plant biodiversity is also moulded by long-distance species dispersal and by a centuries-long history of diverse forms of human impact through different land-uses.

Whereas a general outline of both the plant assemblages and the main biogeographical patterns is now quite well known for the major Mediterranean islands, serious gaps in knowledge still deserve to be examined in the future. We need targeted meta-analyses of existing data to better understand the magnitude of insular biodiversity compared with that of the mainland.

First, only rough, preliminary or incomplete data on flora and vegetation patterns are still available for many archipelagos, and for many islands no data are available at all. Thus we need accurate floristic surveys and robust estimation of landscape trends in order to properly compare the biotic originality and dynamics of these insular ecosystems, notably in relation to global change. Several studies highlight the disproportionate risks that the Mediterranean island ecosystems could suffer because of climat change's impacts, and conservation-prioritisation planning is essential to preserve the evolutionary and functional heritage of these unique floras (Médail, 2017; Kougioumoutzis et al., 2020b).

Second, we need to fill gaps related to the nature and timing of the biogeographical mechanisms at the origin of present distribution patterns of plant species in general and of endemic ones in particular; the same is true as concerns the functioning and evolution of insular ecosystems, in particular those of tiny islets. The functional biogeography (Violle et al., 2014) of insular biota represents without doubt an interesting topic that still needs further research in the near future.

Third, we need more multidisciplinary collaboration among prehistorians, archeologists, paleoecologists, historians, socio-economists, pedologists, current ecologists and biogeographers to disentangle the complex interactions between past human societies and insular environments. Obviously, the links between current ecological and socio-economic trends deserve to be better studied, within a holistic perspective (Vogiatzakis et al., 2008; Médail, 2017).

These lacks are particularly worrisome inasmuch as they are essential in order to develop sound policies and practices for the optimal conservation of these unique and fragile insular floras and plant communities (Delanoë et al., 1996; Médail, 2013). The smallest islands must not be neglected, as they often represent isolated territories where micro-speciation processes occur and current refuge-areas with respect to the disproportionate human impacts destroying the coasts of adjacent mainlands. Owing to their uniqueness and fragility, Mediterranean islands urgently need some integrated and ambitious conservation planning, aiming at the long-term preservation of their outstanding biotic and cultural heritage.

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