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The specific vulnerability of plant biodiversity and vegetation on Mediterranean islands in the face of global change

Frédéric Médail¹

Abstract The numerous Mediterranean islands (>10,000) are very important from a biodiversity point of view, both in term of plant species (numerous endemics, presence of ‘climate relicts’) and of ecosystems’ assemblage. These patterns can be explained by complex interactions between a highly heterogeneous historical biogeography and ecological processes related to diverse island conditions. Furthermore, most of the ups and downs of this biodiversity were closely linked with human pressures which have changed many times through the long socio-ecological history of these island landscapes since the Neolithic period. At present, insular plant biodiversity and rural landscapes are threatened by diverse global environmental changes related to urbanization, habitat fragmentation, unsustainable tourism and other practices (e.g. overgrazing, forest fires), and by other more recent drivers such as climate warming and aridification, sea-level rise and biological invasions. Some of these impacts will be exacerbated on islands because of no (or highly limited) adjacent areas of expansion, notably on the smallest ones (i.e. size < ca. 1000 ha). With regards to the biome crisis facing the Mediterranean basin and induced by human activities, islands constitute key ecological systems and ‘current

refugia’ to ensure the long-term preservation of coastal plant biodiversity. They also represent fascinating ecological systems to disentangle the role of environmental versus human pressures on spatially simplified communities of the Mediterranean coastal areas. Future detailed studies of these ‘natural island microcosms’ could greatly improve our knowledge of the functional and evolutionary processes induced by rapid environmental changes in this region.

Keywords Coastal ecosystems · Human impacts · Insular biogeography · Land use changes · Mediterranean region · Sea-level rise

Introduction

The complex historical biogeography and the profound environmental heterogeneity explain the high diversity of landscapes and vegetation types on islands of the Mediterranean basin, one of the 35 terrestrial biodiversity hot spots of the world (Médail and Myers 2004). The associated high levels of biodiversity and ecological complexity have favoured the emergence of functional uniqueness for several ecosystems and plant communities that occur nowhere else. With about 10,000 islands and islets (ca. 250 regularly inhabited by humans), the Mediterranean Sea represents one of the regions of the world with the most islands and archipelagos. Its islands contain a significant component of Mediterranean biodiversity, notably a number of range-restricted species and peculiar vegetation types (e.g. Vogiatzakis et al. 2008; Médail 2013, 2017). Past geographical and climatic changes, combined with current environmental heterogeneities, have moulded unusually high levels of biodiversity and biogeographical complexity. The diversity of ecosystems

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of Mediterranean islands is also linked to the long-lasting influence of humans as ‘designers’ of landscapes, who have shaped vegetation dynamics through burning, cutting, grazing and ploughing (Blondel 2008). More recently, the biodiversity and functioning of these ecosystems were threatened by global environmental change, notably ecological footprint due to human expansion, climatic and sea-level changes, and biological invasions.

The diversity of Mediterranean islands

Mediterranean islands are a kaleidoscope of environmental and biotic conditions (Médail 2017). This is due to the wide range of sizes (from the largest island of Sicily covering 25,700 km² to small islets a few dozen square metres in size), in altitude (from Mt. Etna, 3342 m a.s.l. to flat islets only one metre a.s.l.) and in remoteness, all of which represent key parameters in island biogeography. There are a total of 157 large islands exceeding 10 km² (1000 ha) in size, of which 86 (55%) are located in Greece (Médail 2017). Forty nine islands cover more than 100 km², of which 36 cover more than 200 km². Small islands with a surface area less than 10 km² are the most common, and there are several thousands of such islands. Most islands belong to the Greek archipelago with ca. 7600 islands and islets in the Aegean Sea, more than 90% of which cover less than 10 km² (Triantis and Mylonas 2009), and ca. 300 islands and islets in the Ionian Sea. Croatia is the second country in terms of the number of islands ($n = 1246$), whose 79 islands of more than 1 km² and 653 small islands and islets have vascular vegetation (Nikolić et al. 2008).

Nearly all Mediterranean island ecosystems are under the influence of the Mediterranean climate (Fig. 1), except some parts of the high mountains of Corsica that contain subalpine and alpine vegetation belts with euro-siberian and even arctic-alpine plants (Gamisans 1999). The insular vegetation types usually considered as ‘typically Mediterranean’ are the evergreen and sclerophyllous shrublands and forests under semi-arid ($400 < P =$ annual rainfall < 600 mm) or sub-humid ($600 < P =$ annual rainfall < 800 mm) bioclimates, corresponding to thermo-mediterranean and meso-mediterranean vegetation belts (Table suppl.); Fig. 1). If deciduous trees were the cornerstones of ecosystem dynamics during the post-glacial period, notably in the northern Mediterranean, these forests were severely impacted by humans and their livestock (Quézel and Médail 2003; Médail 2008). This is the case of the forests of Valonia oak (*Quercus ithaburensis* subsp. *macrolepis*) in the central Aegean islands, of the Downy oak forest (*Quercus pubescens*) in western Corsica or of the mixed *Quercus congesta* and cork oak (*Quercus suber*) forests in Sardinia (Médail 2017).

The existence of endemic or range-limited plant species can determine specific patterns of insular vegetation types and landscapes. On large islands, plant endemism ranges from 8 to 17%, whereas the total number of taxa is greater than expected, usually between 1600 and 2800 species and subspecies (Table 2). In mountain ranges of islands, the level of endemism is higher: above 1700 m a.s.l. endemics represent 35–40% of the vascular flora in Corsica and in Crete. Each island has its own specificities of vegetation even if major physiognomic structures may appear similar from one island to another. They are mostly covered by typical vegetations of the thermo-mediterranean and meso-mediterranean belts, whereas the upper vegetation levels are restricted to the summits of the largest islands, notably Corsica, Sicily, Crete and Cyprus.

Biogeography of Mediterranean islands, museum and cradle of plant diversity

The history of the Mediterranean basin setting is highly complex both from a geologic and a climatic point of view (e.g. Woodward 2009; Fig. 2). Tectonic events and the Messinian salinity crisis—which induced an almost complete desiccation of the Mediterranean Sea between 5.96 million years (Ma) and 5.33 Ma (CIESM 2008) (Fig. 2c)—have strongly influenced the palaeogeography of the region, and thus the biogeographical history. If some pre-Mediterranean plant taxa exist since the Eocene (ca. 40 Ma: Fig. 2a), the main diversification of the Mediterranean species took place during (1) the Miocene (Fig. 2b), notably in conjunction with the collision of the African and Eurasian plates with the Arabian plate and (2) the Pliocene with the onset of the Mediterranean climate (Fig. 2d). Recurrent episodes of species dispersal and vicariance have occurred between the eastern and western Mediterranean regions in relation to the several marine regressions or transgressions and the ongoing rise of Alpine and Atlas orogenesis (e.g. Mansion et al. 2008).

The majority of Mediterranean islands are ‘continental islands’ *sensu lato* (including continental shelf and continental fragments according to Whittaker and Fernández-Palacios 2007), *i.e.* they were once part of the continent before their separation and drifting (such as the small continental sub-plate of Corsica-Sardinia which separated during the Oligocene), or during various episodes of low sea level (marine regression). Most of them have become progressively isolated from the mainland and each other by a complex combination of tectonic and glacio-eustatic processes. But there also are a few Mediterranean ‘oceanic islands’ in the geological sense, such as the volcanic islands (see below) and notably Cyprus which emerged from the bottom of the sea and has probably never been

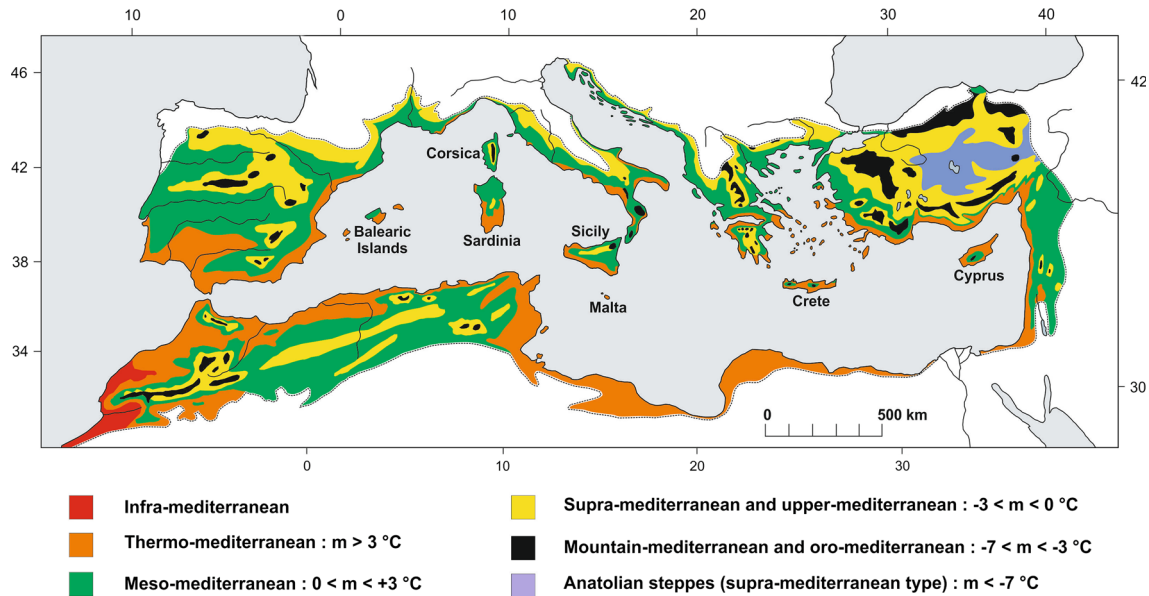


Fig. 1 Schematic distribution of major vegetation types in the Mediterranean region, according to vegetation and bioclimatic criteria, notably the mean minimum temperatures of the coldest month (m) of the year (see Quézel and Médail 2003; Médail 2008)

connected with the mainland. 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 (Fig. 2e). This category encompasses about 20 islands or archipelagos, including the five large islands (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 a land connection during the marine regression of the Würm glacial.

Climatic and eustatic changes of the Pleistocene

The onset of Mediterranean climate is relatively recent, and palaeoclimatic reconstructions demonstrate that cooling and drying, with a combination of summer drought and mild winter temperatures, have appeared quite rapidly in Late Miocene or Early Pliocene (c. 5–3 Ma) (e.g. Tzedakis 2009). Severe cooling episodes during the late Pliocene and the Early Middle Pleistocene have profoundly affected the biogeographical footprint of Mediterranean lineages with the extinction of several megathermic and warm-temperate taxa.

Drastic marine regressions that have occurred during the recurrent glacial episodes, between the end of the Pliocene and until the last glacial maximum (LGM, ca. 18,000 ± 2000 years BP), have induced more or less severe droppings of sea level (Fig. 2e). The last eustatic change in the LGM, with a lowering of sea level between

100 and 150 m below, has favoured the migration of a more competitive cool-temperate mainland flora to the offshore islands. This is the case of many Aegean islands, except Rhodes, the Cyclades and the Crete–Karthos island group, which remained completely isolated throughout the Pleistocene. These land-bridge connections explain some biogeographical affinities between floras that are currently distant and isolated. Although long-distance dispersals of seeds by wind, birds or marine currents almost certainly played a certain role in Mediterranean island colonization, well-documented evidence of these processes are quite rare, except for some common halophytes (Westberg and Kadereit 2009).

Glacial refugia for plants

Glacial refugia are areas sheltered from the strong climatic deteriorations during ice ages, where species could survive by avoiding the consequences of severe cold and aridity during glacial events like the LGM. Phylogeographic and palaeoecological studies show that these refugia represent crucial areas for the long-term persistence and dynamics of modern biodiversity in temperate regions such as the Mediterranean basin (Médail and Diadema 2009). The six large Mediterranean islands represent major refugia areas and sanctuaries of old, often mid-Tertiary floras with numerous ‘climate relicts’ (Woolbright et al. 2014), i.e. plants characterized by a prolonged evolutionary standstill. The relictual nature of Mediterranean island floras is well supported (1) by the

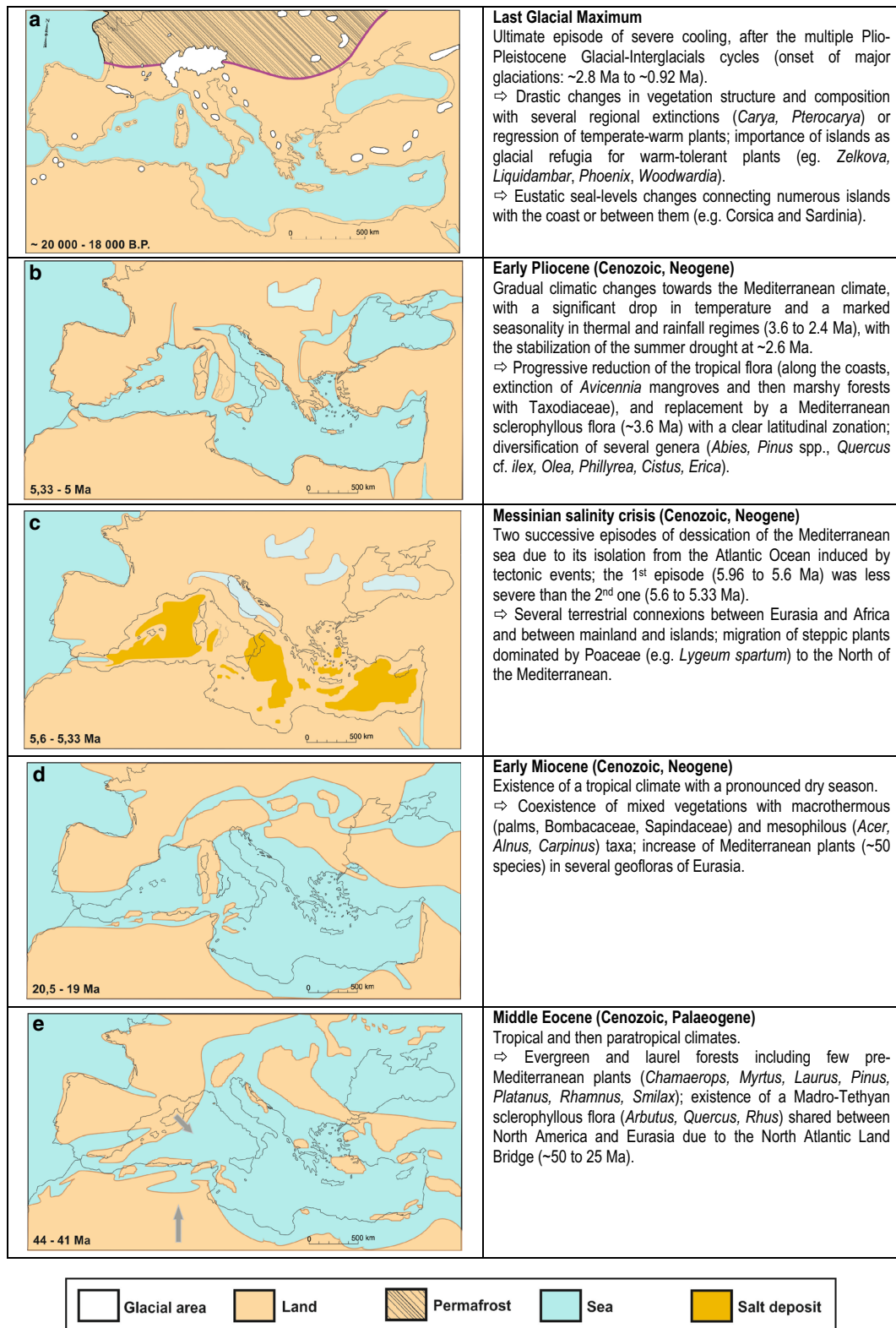


Fig. 2 Palaeogeographical maps of the Mediterranean basin between the first part of the Cenozoic (middle Eocene period, ca. 44 Ma) and the Last Glacial Maximum (Holocene, ca. 20,000 years BP) (after

Diadema and de Beaulieu 2011, modified), and correspondance with the main changes of flora and vegetation

presence of palaeoendemics restricted to one or few of these islands, notably several monotypic genera such as *Morisia*, *Naufraga* or *Petagnaea* (Table suppl.), and (2) by the existence of some relicts originating from the subtropical environments of the Tertiary, such as the Tethysian-Palaeotropical fern *Woodwardia radicans* in Corsica, Sicily and Crete or *Zelkova abelicea*, a relict tree endemic of the Cretan mountains (Bosque et al. 2014).

Recent plant diversification

While Mediterranean islands have served as important Tertiary and glacial refuges, their role in the local and more recent differentiation of plants is at least as important. All islands possess highly polymorphic species and vicariant endemic plants issued 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 adaptive radiation. Chromosomal rearrangements and hybridization have also played a key role in the rapid speciation of several endemic lineages in Mediterranean islands (Verlaque et al. 1995). In central Mediterranean islands, the taxa of the *Centaurea cinerea* group had long been assumed to be old relicts; however, molecular dating now indicates more recent (less than 250,000 years) allopatric diversification (Hilpold et al. 2011). Some well-studied examples are also found in the Aegean islands like the obligate chasmophytes of *Erysimum* sect. *Cheiranthus* (Snogerup 1967) and the *Nigella arvensis* complex, where the history of isolation of these multiple islands determines pronounced random plant differentiation by genetic drift following fragmentation of a former contiguous distribution area, or after long-distance dispersal (Bittkau and 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.

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 in the Holocene, vegetation dynamics have been strongly affected by human use and associated disturbances. Indeed, the history of the

Mediterranean island environment is intimately linked to that of human societies (e.g. Ghilardi 2016). The evidence of the earliest date of island colonizations by prehistoric people in the Mediterranean—a ‘Palaeolithic seafaring by Stone Age sailors’ (Simmons 2014)—is still disputed (Broodbank 2006; Leppard 2014; Runnels 2014), because it is often difficult to assess whether human occupation was only temporary along the coasts or has become more permanent. The first tangible traces of extended human presence on a Mediterranean island seem to exist on Cyprus around 12,500 years ago (Table 1) (Zazzo et al. 2015), and the development of agriculture has occurred between 11,200 and 10,600 years ago (Vigne et al. 2012). In the western Mediterranean, the oldest sporadic settlements on islands date back to the Mesolithic (ca. 10,000 years ago in Corsica, Sardinia), but with a gap until the Early Neolithic when these two islands were re-colonized during the initial phase of neolithization, around 7700 years ago (Rowley-Conwy et al. 2013). Genetic analysis of the genome of human populations bordering the Mediterranean also supports the hypothesis that a maritime route and island hopping was prominent and that Neolithic migrants have reached southern Europe, first through an Anatolian route and then, by the sea, through the Dodecanese islands, Crete and Italy (Paschou et al. 2014), in accordance with archaeological findings.

Since the Neolithic revolution, landscapes have been profoundly shaped by humans for almost 10,000 years ago in the eastern Mediterranean, and for around 7500 years ago in the western part (Zeder 2008), in relation to the timing of human colonization (Table 1). The ecological consequences of these first human impacts on Mediterranean biodiversity can be seen in different perspectives. Broadly, two contrasting views have been proposed (Blondel 2006): the ‘ruined landscape’ or ‘lost Eden’ theory advocated by J.V. Thirgood and D. Attenborough for the whole Mediterranean biota versus the ‘pristine savanna-like landscapes’ proposed by O. Rackham after his historical landscape studies in Crete (Rackham and Moddy 1996). The ‘ecological reality’ is more complex and certainly positioned between these two extremes.

A second factor that has shaped plant diversity and landscapes on islands is the progressive aridification of the climate during the Holocene. Overall, human action, amplified by progressive warming and drying of the climate, has probably led to the extinction of several mesophilous species and communities, as well as to the disruption of formerly large plant populations into small and isolated fragments as a consequence of habitat deterioration. In Crete, some pollen assemblages suggest that the driest conditions occurred between 9375 and 8310 years ago, with a vegetation composed by open deciduous-oak forest (Bottema and Sarpaki 2003). In the central and western Mediterranean, dry

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

Island	Earliest date of sporadic human presence (years cal. BC)	Earliest date of permanent human settlement (years cal. BC)	References
Cyprus	10,200 cal. BC (Aetokremnos)	9200–8600 cal. BC (Shillouroukambos)	Vigne et al. (2012)
Crete		ca. 7000 BC (Knossos)	Efstratiou et al. (2013)
Sicily ^a	ca. 30,000 BP (Fontana Nuova, Ragusa)	14,640–13,760 cal. BP (Oriente cave, Favignana island)	Leighton (1999), Mannino et al. (2012)
Malta		ca. 5000 BC (5266–4846 BC) (Skorba)	Trump (2008)
Sardinia	ca. 7800 cal. BC	ca. 5700 cal. BC	Costa (2004) Rowley-Conwy et al. (2013)
Corsica	8000–6000 cal. BC (Monte Leone)	ca. 5700 cal. BC	Costa (2004) Rowley-Conwy et al. (2013)
Mallorca	ca. 7000 cal. BP?	2350–2150 cal. BC (or ca. 2700 cal BC?)	Alcover (2008)

^a Sicily is a special case due to its proximity with the Italian Peninsula and episodic terrestrial connections between them during the LGM (cf. Vigne 1999, 2014; Simmons 2014)

conditions arrived more recently during the middle Holocene, ca. 4500 years ago (Magny et al. 2012). In the Balearic Islands, aridification induces the replacement of mesophyllous forests with *Corylus*, *Alnus*, deciduous *Quercus*, *Buxus balearicus* and perhaps *Fagus*, by xeric-type communities combined with an increase in sclerophyllous species as this occurred in Sicily around 4500–4000 years ago, even if these ecological successions are not fully synchronous between the two islands (Pérez-Obiol and Sadori 2007).

Transformation of island landscapes during the Antiquity

During the Antiquity, human impact on island ecosystems was undoubtedly profound, affecting especially two types of natural habitats: forests and wetlands marshes. The ancient destruction of forests by humans for wood and the alteration of forest regeneration due to overgrazing constitute a common pattern in the whole Mediterranean area (Thirgood 1981; Quézel and Médail 2003). Alteration of forests first occurred in the low plains in order to increase cropland, and deciduous forests with various keystone species of oaks were particularly impacted. In Greece, deciduous forests were largely converted to permanent crops or olive groves during the first millennium before our era (Gerasimidis 2005). This is the case of the forests of Valonia oak (*Quercus ithaburensis* subsp. *macrolepis*) in the central Aegean islands. In the western Mediterranean, oak forests of *Quercus pubescens* in the Plaine orientale of Corsica were severely impacted by humans (Gamisans 1999). Also 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 and Médail 2003).

Coastal marshes were precociously drained and exploited because these flat areas with a deep fertile soil were coveted as farmland especially as malaria was rampant. In the Aegean islands, the originality of the impact on wetlands relies on its precocity, because the favourable lands were scarce compared to the vast areas of the continental Greece (Brun 1996). No one doubts that this early pattern of land use of wetlands has occurred also on many other Mediterranean islands. Moreover, coastal wetlands were impacted from ca. 7000 years ago onwards by a continued intrusion of sea water caused by the mid-Holocene marine transgression (see below) inducing salinization processes.

Another originality within the structure of agriculture on island is related to the space constraints imposed by the small proportion of the plains and the existence of often mountainous landscapes. These topographical constraints have led people, since the Antiquity, to arrange the slopes in cultivation terraces to stabilize the soil and to 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 also the Aegean islands (Brun 1996).

Probably, the main environmental changes on island landscapes were realized during the Antiquity, whereas the changes after the Middle-Ages till pre-industrial era vary considerably from one island to another and over time, depending on its topographical features and on the various practices of land uses.

Island plant biodiversity in the face of current global environmental change

The dynamics of landscape and vegetation on Mediterranean islands depend both on specific environmental constraints (climate and soil types) and on local socio-economic trends induced by humans. First, the particular vulnerabilities of Mediterranean climate are related to its seasonality and the severe dry summers. This induces severe and contrasted stress on species and communities, since organisms must often cope with drastic temporal unpredictable variations in climate and resource availability of soils (e.g. Médail 2008). In addition to this harsh environmental context, the ancient impact of man since the Neolithic has profoundly altered the composition, structure and function of these island ecosystems. With the current global environmental trends, the situation is now changing rapidly with a new magnitude of impacts on island ecosystems and biodiversity.

Widespread human impacts and land use changes

Most of the ups and downs in Mediterranean ecosystems are closely linked with human population pressures which 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 and Médail 2009).

Beginning in the nineteenth century and with 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 tryptich' named *ager-saltus-sylva* (agriculture, pastoralism, forestry) which had moulded insular landscapes during several centuries, and even millennia. Until the mid-twentieth century, natural resources were indeed crucial for island population, notably for food, livestock, nutraceutical and healing compounds, or various usages (fibre, weaving, resin). These needs were huge when one considers, for example, that only during one year (1867) more than 7000 tonnes of wood and coal were consumed in Palma de

Mallorca for domestic and artisanal uses (Mayol 1995). Caused by the end of the nearly specific economies on islands, changes in agricultural and livestock farming extending inland have induced in many cases a reduction in pressures on natural resources. Therefore, there is a general increase in areas covered by sclerophyllous shrubs (*ma-torrals*) and forests, induced by 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 in Tuscany; Petanidou et al. 2008, for Nisyros in the Aegean).

Today, the major islands are usually characterized by a slight increase in permanent human population, whereas the medium-sized islands—except some hotspots of tourism such as Corfu and Djerba—are subject to demographic decline. But even for large islands, disparities are strong between a very densely populated island like Malta (1330 people/km²) and a less-populated island as Corsica (36 people/km²). Furthermore, since the 1960s, tourism on islands has increased everywhere, with a paroxysm on some Balearic Islands (Mallorca and Ibiza) where a peak was reached in 2000–2001 with 11 million tourists. This pressure has induced strong urban development, concentrated along the coasts, which is 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 caused a 80% reduction in these coastal ecosystems (Economidou 1995).

Nevertheless, these environmental trends cannot be generalized for all islands. For example, the ecosystem dynamics after land abandonment and increased grazing pressure are still uncertain in many Mediterranean islands (e.g. Rühl and Pasta 2008; Schaich et al. 2015). In some cases, the vanishing of traditional agricultural activities and landscapes has induced severe soil erosion or the rapid extinction of many ruderal endemics and several particular archaeophytes (La Mantia et al. 2011). Throughout the Aegean archipelago, the collapse of cultivation practices on terraces after the beginning of the twentieth century has induced major 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). On most of these islands, the unique terraced landscapes have significantly decreased. In the western part of Crete, human immigration from arid mountains has led to the decline in agricultural land area by almost 40% between 1945 and 1990, favouring the recovery of forest ecosystems dominated by the coniferous *Cupressus sempervirens* and *Pinus brutia*. The same process occurs on the Balearic Islands where drastic changes have occurred (Marull et al. 2015). Forests covered by

Aleppo pine (*Pinus halepensis*) multiplied their surface by more than five in Mallorca during the last century. Between 1971 and 1999, pinewoods increased from 55,000 to 115,000 ha in the Balearic Islands (Gil and Díaz-Fernández 2003). Similarly, holm-oak (*Quercus ilex*) forests have increased from 5000 ha to more than 10,000 ha in Mallorca, and from 900 to 2600 ha in Menorca since 1860 (Mayol 1995). In contrast, high shrublands and natural forests of eastern Sardinia have diminished by 35% between 1955 and 1996, whereas pastures, burned low shrublands and reforested areas are progressing. Landscape dynamics are more heterogeneous in Corsica, and since the beginning of the twentieth century, land abandonment has induced a global increase in 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 in the surface of Corsican forests over a period of 150 years (Panaïotis et al. 2015). But this increase can be locally counterbalanced by frequent illegal fires, often linked to pastoral practices. Corsican rural area occupies still 80% of the land and sectors of traditional moving herds (*transhumance*) span more 130,000 ha throughout the mountain range (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 intensified on most Greek islands, where large flocks of sheep and goats are usually free to graze. The case of small islets deserves mention. On many Aegean islets where no permanent inhabitants are present, people still leave herds of goats and sheep to graze for several periods of time (Bergmeier and Dimopoulos 2003). Until the last century, this practice was common in several other Mediterranean islets. These apparently uncontrolled practices can lead to overgrazing and even to desertification, i.e. land degradation under arid and semi-arid climates, of these fragile ecosystems (e.g. Arianoutsou-Faraggiraki 1985; Papanastasis et al. 2002). Nevertheless, we must be cautious with the apparent desertification of the Mediterranean environments on larger islands. As demonstrated for the assessment of the natural environment in Cyprus between 1878 and 1960 (Harris 2012), the ‘classic degradation thesis of deforestation’ is often a simplified story of presumed desertification in order to justify the environmental policies of colonial authorities or centralized governments.

Increasing forest fires

Like grazing, forest fire has been a major driving force of Mediterranean ecosystem dynamics since the emergence of the Mediterranean climate, from 3.6 Ma ago. For the

emblematic Corsican pine (*Pinus nigra* subsp. *laricio*), fires have played a key role in the functioning of these mountainous woodlands since this tree has survived mean fire-return intervals of 80 years over the last 13,200 years (Leys et al. 2014). Palaeo-fires contributed to the frequent dominance of shrubland on islands during the mid-Holocene (ca. 8000–7000 years ago) under dry conditions, as is the case of the *Pistacia* matorrals in Sicily and Malta (Djamali et al. 2013), and 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, since ancient woodlands are scarce because of recurrent fires, shrub communities or steppic grasslands, still often dominate islands’ landscapes. In Greece, the situation has been of particular concern for the last few decades given the increase in frequent intense wildfires. On Thasos Island, for example, a series of wildfires since 1984 has reduced forest cover from 61.6 to almost 20% (Ranis et al. 2015). Furthermore, there often is spatial congruence between the most fire-affected microregions and the main cattle-rearing regions, like in Corsica. On this fire-prone island, 28,000 starting fires occurred between 1973 and 2004 (i.e. ≈ 1000 starting fires/year) and a third of the total surface area of Corsica was burned in a period of 30 years.

Fire regime changes and the occurrence of extreme fire events (or ‘megafires’) are related to both land use change and climate change and involve multiple biotic and socio-economic drivers (e.g. Pausas and Keeley 2014). It is difficult to disentangle their relative importance because the management of Mediterranean landscapes plays a major role to explain the probabilities of outbreak and spread of forest fires. In the western Mediterranean basin, a fire regime shift has occurred and fires are now less fuel limited and more drought-driven than before the 1970s (Pausas and Fernández-Muñoz 2012). In the future, increased drought could increase fire activity on most Mediterranean islands, with secondary effects of land degradation and erosion.

The aforementioned separation of key drivers related to global change is somewhat artificial. Their effects on plant biodiversity and ecosystem dynamics must be considered in interaction in order to better estimate the real consequences of these future changes.

Biological invasions

Worldwide, islands are known 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 trigger or accelerate the local extinction of indigenous plants. Also Mediterranean islands and islets are, in some places, seriously threatened by invasive plants, notably along coasts, in lowlands and riparian habitats (Hulme et al. 2007). But invasions in Mediterranean insular ecosystems are highly idiosyncratic and mainly depend on propagule pressure linked to human-mediated factors and water availability conditions (Vilà et al. 2006). The impacts depend on both the identity of the invasive plant and of the invaded island, suggesting that 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 and 9.5% (Table 2).

Some of the most invasive plants are the trees *Acacia* spp., *Ailanthus altissima*, the shrub *Nicotiana glauca*, the perennial herbs *Cortaderia selloana* and *Oxalis pes-caprae*, the succulent plants *Carpobrotus* spp. and *Opuntia* spp., and the liana *Senecio angulatus*. If larger islands are generally characterized by a greater habitat diversity and can support a wider richness of non-native plants, small Mediterranean islands are the most threatened by plant invasions (Pretto et al. 2012), because any invasion will induce disproportionate effects on the local carrying capacity of the ecosystems, including the persistence of narrow endemic plants. This is for example the case of the problematic survival of *Silene hicsesiae* (Caryophyllaceae) on Panarea island (Aeolian archipelago, Sicily) that is currently threatened by the vegetative expansion of *Ailanthus altissima*, and of *Limonium sommierianum* (Plumbaginaceae) on the island of Giglio (Tuscan archipelago, Italy) whose future persistence is jeopardized by

the expansion of the succulent mat-forming *Carpobrotus edulis*.

All available data show the increasing importance of the alien flora in Mediterranean islands during the past century, with a higher proportion of introduced woody species (phanerophytes and chamaephytes) (Jeanmonod et al. 2011). Future scenarios suggest an exponential increase in naturalized and invasive plants on islands due to human activities and global warming. In Corsica, the number of naturalized plants ($n = 117$ taxa) could exceed the number of endemic ones ($n = 284$ taxa) in the next 30–50 years, and that of introduced plants could exceed the number of native ones in the next centuries (Jeanmonod et al. 2011).

Impacts of current climatic change

The Mediterranean basin is considered to be one of the regions that will face the largest changes in climate worldwide (e.g. Giorgi and Lionello 2008). Scenarios of the IPCC show that this region will be particularly affected by temperature increase, decrease in rainfall and changes in seasonal patterns. With an expected temperature increase of 3–5 °C in the Mediterranean over twenty-first century, the potential evapotranspiration is expected to reach an average of 200 mm annually, which is equivalent to a loss of 50 mm in annual rainfall (Le Houérou 1990). The expected shifts in vegetation belts resulting from increased aridity and a 3 °C increase in temperature will be an upward shift of ca. 545 m (i.e. almost the amplitude of a vegetation belt) and a 50–80 km northwards shift in latitude (Médail and Quézel 2003). These impacts will be exacerbated on islands where no (or insufficient) areas are available for such shifts. The flora and vegetation of the alpine areas (i.e. mostly the oro- and alti-mediterranean belts: see Table suppl.) and the spatially restricted summit areas of mountain ranges will probably be the most threatened, as mentioned in the Lefka Ori massif in Crete

Table 2 Specific richness of native, endemic and alien plants of the six largest Mediterranean islands (Médail unpublished data from various sources)

Island	Area (km ²)	Native plant richness	Endemic richness	Endemism level (%)	Endemic genera	Number of alien plants	% alien flora/total flora
Sicily	25,426	2793	322	11.5	<i>Petagnaea, Siculosciadium</i>	292	9.5
Sardinia	24,090	2149	290	13.5	<i>Castroviejoa, Morisia, Nananthea, Soleirolia</i>	508	17.4
Cyprus	9251	1633	142	8.7	<i>Lindbergella</i>	152	8.5
Corsica	8679	2237	284	12.7	<i>Castroviejoa, Morisia, Nananthea, Soleirolia</i>	466	17.2
Crete	8261	2240	395	17.6	<i>Horstrissea, Petromarula</i>	162	6.7
Balearic islands	4987	1551	140	9	On eastern islands: <i>Femeniasia, Naufraga, Soleirolia</i>	124	7.3

Native plant richness includes the endemic richness

(Kazakis et al. 2007). In Corsica, this is particularly the case of arctic-alpine species (ca. 25 taxa) located in the alpine vegetation belt (Contandriopoulos and Gamisans 1974).

But it is too simplistic to consider a single range shift of plant communities in response to global warming. As suggested for Mediterranean mammals, the effects of climate change on species distribution and communities may consist of changes in community structure (Maiorano et al. 2011). The extent to which many organisms will be able to cope with climate change is still largely an open question, especially because it is now taking place at an unprecedented rate in known climatic records during recent periods. Microevolutionary changes may occur rapidly in fitness related traits such as the flowering time of Mediterranean plants (Penuelas et al. 2002). Differential responses of organisms interacting in complex food chains or symbiotic associations may also disrupt interactions that are essential for ecosystem functioning such as pollination or seed dispersal by animals. This mutualism disruption was assessed for two declining relict plants of the Balearic Islands, *Daphne rodriguezii* and *Cneorum tricoccon* (Rotllan-Puig and Traveset 2016).

Climatic change is also a threat for the long-term persistence of island plant populations and communities linked to humid or mesophilous habitats, including some endemics that constitute the cornerstone of Mediterranean plant diversity. This is the case of two endemic species of the Apiaceae family restricted to the Balearic Islands. *Apium bermejoi*, a narrow endemic of Menorca located in a single area of 50 m² where the ca. 100 individuals occupy only one square metre. As this critically endangered plant is vulnerable to prolonged droughts, its present decline is probably related in part to a series of dry summers (Moragues and Mayol 2013). The narrow ecological niche of the palaeoendemic *Naufraga balearica*, only distributed along a short section (ca. 15 km) of the north facing slopes of the northern Majorcan coast, explains its current extreme rarity (Fernández-Mazuecos et al. 2014). Narrow microclimatic conditions of shade and humidity are crucial for the survival of *Naufraga*, and rapid climatic shifts could jeopardize its survival. In Cyprus, several populations of narrow endemics (e.g. *Onosma caespitosa*, *Salvia veneris*, *Sideritis cypria*) are also threatened by reduced rainfall by 20–40% and warming (Kadis, unpublished), both of which could modify their germination window in the fall like for other Cyprian endemics (Kadis and Georgiou 2010).

So far, despite multiple threats and the fact that a large number of endemic plant species are narrowly distributed on a single island with few small populations, there is only still few evidence for direct depletion or extinction of populations due to climate change. About six endemic

species are known to have become extinct on the Mediterranean islands, of the 26 Mediterranean plants presumed to be totally extinct in this region (Médail and Iriondo, unpublished). Recent studies focused on the Cretan endemic Ulmaceae tree *Zelkova abelicea* (Fazan et al. ined.), and on some entire plant communities (e.g. Henne et al. 2015) showed that the ecological amplitude of many so-called ‘temperate’ species that thrive on Mediterranean mountains may have been underestimated since they could tolerate drier and warmer climates. Local persistence of Mediterranean plants, notably perennials, in diverse microhabitats may be due to multiple demographic strategies of persistence by longevity or regeneration, depending on the local or regional conditions (García and Zamora 2003). This is corroborated by the important role played by glacial refugia on islands (Médail and Diadema 2009), especially as the ecological and evolutionary implications of Pleistocene microrefugia or cryptic refugia (Mee and Moore 2014) are still underestimated on this large Mediterranean patchwork of islands. However, most plants interact with bioclimatic characteristics at a physiological rather than macroclimatic level (Curtis et al. 2016). Differences in small-scale habitats in a landscape may therefore explain species’ ability to cope with drastic and changing climate. The high habitat heterogeneity of Mediterranean-type ecosystems may thus represent an ‘ecological insurance’ for the future persistence of plant species at local scale, allowing species to migrate locally in more favourable ecological niches. Nevertheless, at the scale of small islands, this may not be sufficient to ensure the survival of highly specialized plants. The future persistence of ‘islet specialists’ such as the small annual *Nananthea perpusilla* (Asteraceae) in some shady and humid patches under granitic rocks of some islets around Corsica and Sardinia may well be at risk if aridity is going to increase.

Impact of sea-level rise

Sea-level rise (SLR) is another important component of climate change threatening coastal ecosystems of large islands and the totality of terrestrial environments of flat islets. At the end of the last glacial period, a major consequence of climatic oscillation from cold to warm conditions was the melt of the Northern Hemisphere ice sheets causing a continuous eustatic sea-level rise worldwide. In the Mediterranean Sea, the main part of this marine transgression occurred before ca. 6000 years ago, with major disparities between areas. A recent review based on 917 relative sea-level data-points offers a strong and high-quality Holocene relative sea-level framework for the western Mediterranean (Vacchi et al. 2016). Between ca. 7200 and 6200 years ago, the relative sea-level rose in

south-eastern France from -6.4 ± 0.5 to -4.7 ± 0.5 m a.s.l., but in southern Corsica and northern Sardinia the sea-level was lower: -15.5 ± 1.6 m at c. 7100 years ago. The last 5000 years are characterized by a sub-linear sea-level rise (SLR) of about 2.5–1.5 m, with a rapid elevation until 1500 years ago, and then a stabilization close to the modern sea-level 500 years ago. Some intra-island phylogeographies—such as for the narrow Balearic endemic *Senecio rodriguezii* (Molins et al. 2009)—indicate an ‘island beneath island syndrome’, i.e. a split of populations into several isolated and genetically divergent lineages that are explained by the repeated cycles of sea-level changes during the Quaternary.

For the coming decades, a significant and rapid rise in global sea level (Galassi and Spada 2014). Tide gauge observations during the 1901–2010 period shows an average rate of SLR of 1.7 ± 0.2 mm per year (Church and White 2011). For the period 1993–2014, altimetric data show that the global sea-level has risen with an average of 3.3 ± 0.4 mm per year (Cazenave et al. 2014). However, this accelerated rise remains difficult to accurately estimate at the regional and local scales, because current SLR is the result of complex processes, with disparities between the different parts of the Mediterranean basin. Here, future regional scenarios by 2050 suggest that the total averaged SLR will be comprised between 9.8 and 25.6 cm. This means that the regional rates of SLR may increase by a factor of 1–6 relative to the observed long-term rates.

Among the many harmful effects of SLR are the exacerbation of coastal erosion, the submersion of low elevation islands and flat coasts, and the salinization of coastal wetlands (Nicholls et al. 2016). For several oceanic islands of the world, Weigelt et al. (2016) suggest that current pattern of island biodiversity depends not only on the ‘classical’ process of immigration–extinction dynamics, but also of changes in island area, isolation and connectivity due to the SLR since the last glacial period (LGM). These past physiographical changes have strongly affected the composition of biodiversity, specially the number and proportion of endemic species.

A robust estimation of the biological consequences of these past SLR can be furnished by palaeoecological studies. On a small Mediterranean island (Cavallo, S. Corsica), Holocene sea-level changes played a significant role in loss of wetland biodiversity and ecosystem changes because of the increase in salinity caused by marine intrusions (Poher et al. 2017b). Analysis of coleopteran fossils preserved in a 7000 year sedimentary record showed that 60% of past wetland beetle fauna became locally extinct as a result of regime shift in this freshwater pond. The largest impoverishment occurred 3700 years ago when the relative Mediterranean sea-level rose more than 1.5 ± 0.3 m (Poher et al. 2017a).

The effects of SLR might be less harmful for plant biodiversity on rocky island or coasts, because a slight altitudinal rise of halophilous communities and species towards the salt-tolerant habitats present just above could take place. Nevertheless, this shift may be limited by the presence of more disturbed habitats inland. Another worrying case is the vulnerability of ‘pocket beaches’ on islands. In Provence (France), Brunel and Sabatier (2007) found an 12.1 ± 3.5 m retreat in the shoreline between 1896 and 1998, of which 5.8 ± 3.5 m was caused by SLR. On small islands like Porquerolles (Port-Cros National Park) pocket beaches could almost completely disappear (from 75 to 97% regression of their present surface area) by 2100. Because of frequent coastal cliffs or rocky slopes blocking landward migration, typical plant communities and species of fixed maritime sands (e.g. the psammophytes *Eryngium maritimum*, *Otanthus maritimus*, *Pancratium maritimum* of the ‘grey dunes’) could become locally extinct on numerous small islands.

Small Mediterranean islands, laboratories of global environmental changes

The small islands (i.e. size < ca. 1000 ha) and islets (less than 1 ha) represent the most common insular realm of the Mediterranean basin with several thousands of units. If most of the ecological studies carried out were devoted to large or medium islands (Médail 2017), smaller ones encompass a large range of environmental and biogeographical situations, forming suitable ‘experimental laboratories’ to test the putative consequences of global environmental changes in the face of several drivers. This is explained by the fact that, compared to the continent and larger islands, small insular communities and ecosystems are more sensitive to exogenous disturbances (storms, nesting seabirds, invasive species) and to environmental stochasticity which often promote rapid and contrasted ecological dynamics. The detailed example of the small islands of south-eastern Tunisia provides a good illustration of the vulnerability of an insular system to both a global driver (here the sea-level rise) and local human impacts (Box 1).

Finally, compared to large islands and continent, small islands often house large seabird colonies, notably gulls, that exert specific disturbance with a high pressure on ecosystems by modifying patterns and dynamics of plant communities. Seabirds are responsible for the energy inflow from sea to terrestrial ecosystems through guano, fish scraps and various rubbish. They often induce severe impacts because of physical (trampling, pulling-up, soil erosion, burrowing) and chemical (soil manuring induced by guano rich in phosphorous and nitrogen compounds, salt

Box 1 Collapse of terrestrial biodiversity on the islands of Eastern Tunisia induced by sea-level rise and human impact

In the Gulf of Gabes (south-eastern Tunisia), there are thirty flat and sandy islands and islets distributed into three archipelagos: (1) the Kerkennah archipelago, located about eighteen km from the coastal town of Sfax and including two main islands (Gharbi, 48 km² and Chergui, 99 km²), and thirteen small satellite islands or islets for a surface area of around 4.5 km² (Médail et al. 2015); (2) the Kneiss archipelago, consisting of one main island (El Bessila, 440 ha) and four vegetated islets, situated near the coast south of Mahare's (Médail et al. 2016); (3) the Djerba archipelago including the eponymous island, the greatest one of Tunisia (526 km²) situated at 1.5–2 km from the coast and surrounded by nine satellite islands or islets with vascular vegetation (Médail, unpubl. obs.). Maximum altitudes reach only 51 m a.s.l. for Djerba, and 13 m for the Kerkennah where lowland less than 2.5 m represents more than 50% of the islands' areas. The bioclimate is classified as upper-arid (with annual rainfalls between 200 and 300 mm) according to the Emberger's classification. The current vegetation is mainly composed by halophilous plant communities with several shrubs of the Amaranthaceae family (genera *Anabasis*, *Arthrocnemum*, *Atriplex*, *Halimione*, *Halocnemum*, *Salsola*, *Sarcocornia*, *Suaeda*, etc.), some steppes with the Poaceae *Lygeum spartum* or *Stipa capensis*, and palm groves of *Phoenix dactylifera*.

Geo-archaeological studies on these islands mention significant flooding of coastal lands and antique remains, up to two metres 2000 years ago (Slim et al. 2004). The magnitude of sea-level rise is currently estimated to 5.7 mm per year (Pirazzoli 1986). It is mainly explained by the active subsidence of the northern part of the Gabes Gulf (Oueslati 1995) and is exacerbated by the general rise in sea-level for over a century.

The lithological context explains the high vulnerability to coastal erosion with 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. On the Kerkennah islands, land salinization has led first to a sharp increase in *sebkhas* (+20% between 1984 and 2011) and a 27% decline in palm groves equivalent to 26 km² (Etienne et al. 2012). The next environmental phase was the increase in coastal marshes in place of *sebkhas* and the coastal indentation by channels (Slim et al. 2004). An even greater environmental collapse has occurred in the Kneiss archipelago: the four southern islets with a current total area of less than one hectare, surrounded by very reduced marine depth, comprise only 9 vascular plant species. In the Middle-Ages, though, they constituted a single elongated island, which hosted the monastery of Fulgence de Ruspe and a fairly large religious community (Troussset et al. 1992). The reconstruction of the contour of this 'palaeo-island El Laboua' based on the isobath –2 m shows that its surface area was around 205 hectares, 1500 years ago (Médail et al. 2016). The collapse of terrestrial biodiversity induced by this huge surface retraction was probably considerable.

Because of the scarcity of palaeoecological data, it is difficult to estimate the potential vegetation of these islands during the post-glacial times, with the onset of long-term aridification occurring between 5700 and 4600 years ago (Jaouadi et al. 2016). Nevertheless, the presence of ancient woody remnants of juniper (*Juniperus phoenicea* subsp. *turbinata*) and lentisc (*Pistacia lentiscus*) from a site of Djerba dated to 4200–4300 years ago (Damblon and Vanden Berghen 1993), and the occurrence of several bio-indicator plants suggests the former existence of sclerophyllous matorrals or open pre-steppic forests, with the possible presence of native Aleppo pine (*Pinus halepensis*) and olive tree (*Olea europaea*) on some of the largest islands (Médail et al. 2015). At present, keystone steppic shrubs (e.g. *Lycium schweinfurthii*, *Periploca angustifolia*, *Rhus tripartita*) are very rare on some islands or absent. The spiny summer-deciduous shrub *Ziziphus lotus*—the probable famous *lotos* of the Lotophagous island (Djerba) haunted in Homer's *Odyssey*—has totally disappeared from this large island during the first half of the twentieth century mainly because of wood collection by humans.

Thus, if the natural flora and vegetation were precociously modified by humans, sea-level rise since at least 2000 years is about to lead to the ultimate *coup de grace* for the persistence of these original ecosystems of Eastern Tunisia.

deposition) disturbances (e.g. Vidal et al. 2000; García et al. 2002). These impacts favour generally plant turnover, selection of some functional types with the massive establishment of annual, ruderal and cosmopolite or non-native species (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). Detailed studies of these 'natural island microcosms' could indeed enhance our knowledge of functional and evolutionary processes induced by rapid environmental changes, at least for the biotic-simplified communities of the Mediterranean coasts.

Conclusion

Phylogenetical and phylogeographical results support the complex historical biogeography of the Mediterranean basin and also the importance of islands as reservoirs of

unique genetic lineages, notably for most endemics and narrowly distributed plants (Médail and Diadema 2009; Nieto Feliner 2011). Nevertheless, the time frame and evolutionary consequences of biogeographical events linked to repeated cycles of connections and isolation of these continental islands, due to marine regressions–transgressions, remain largely unknown compared to oceanic islands (Weigelt et al. 2016). This is of particular concern for efficient evolutionary conservation of these heterogeneous insular floras. With the ongoing biome crisis of the Mediterranean basin (Hoekstra et al. 2005), islands constitute indeed key ecological systems and 'current refugia' to ensure the conservation of coastal plant biodiversity. They are also key entities to disentangle the role of environmental versus human pressures in the long-term preservation of these biodiversity hotspots.

Because of increased threats across the Mediterranean region and the complex consequences of climate change

(Klausmeyer and Shaw 2009), it is crucial to observe, monitor and analyse changes in vegetation and plant biodiversity across ecological and biogeographical gradients. Mediterranean islands, notably the small ones, are favourable sites for such long-term observations as well as for monitoring at various spatial scales. These ‘natural island microcosms’ are indeed appropriate systems to study adaptation to climate change by species or communities, and the functional biogeography approach (Violle et al. 2014) is undoubtedly an interesting topic that needs further research. The diversity of situations facing Mediterranean islands should facilitate their integration as laboratories or testing grounds of extinction in relation to global change and human pressures.

To this end, it would be useful to combine reactive approaches on the most threatened (often largest) islands, and proactive approaches on relatively less threatened islands, notably small islands and islets. Multi-disciplinary collaboration among prehistorians, archaeologists, palaeoecologists, historians, socio-economists, soil scientists, ecologists and biogeographers is needed to disentangle the complex interactions between past human societies and specific island environments. Enhancing these interdisciplinary research efforts is a prerequisite for the design of sound policies and practices concerning the conservation of these unique and fragile floras and plant communities (Médail 2013). The smallest islands should not be neglected, as they are often isolated territories where microspeciation processes occurs, offering modern refugia for diversity that is put at risk by the impacts of human activity on the coasts of the adjacent mainland.

Owing to their high biotic originality and vulnerability to global change, Mediterranean islands and islets urgently require integrated and ambitious conservation planning aimed at the long-term preservation of their outstanding biodiversity and cultural heritage.

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