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Palynology and Mediterranean vegetation history*

Abstract

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The history of Mediterranean vegetation can be outlined using pollen grains contained in lacustrine, marine and other sediments. These sediments have recorded very important vegetation changes during recent geological times. For example, during the last 6 Ma (million years), the effects of different events acting at regional (e.g. the Messinian salinity crisis between 5.96 Ma and 5.33 Ma) and global (expansion of the Arctic ice at ca 2.6 Ma) scales produced a progressive decrease and final disappearance of tropical and subtropical taxa. However, prior to the start of the Quaternary the Mediterranean flora still included a consistent number of tropical and subtropical arboreal taxa accompanying deciduous and partly evergreen trees that have persisted until today. The most important features of the vegetation history of the Quaternary consist in the fact that vegetation adapted to climate changes due to changes in orbital cyclicity, alternating between glacial and interglacial periods. The more widespread vegetation types were steppe and grassland formations during the dry and cold glacial periods whereas either deciduous or evergreen forests were characteristic of interglacial periods. These cold-dry to warm-humid climate cycles became more and more intense towards the present. During the second half of the present interglacial, after the mid-Holocene, joint actions of increasing dryness, climate oscillations and human impact led to the present day Mediterranean plant landscape. It is however not clear how far the causation of this spread of evergreen taxa was climatic or human. One of the most exciting challenges is the prediction of the future course of Mediterranean vegetation. In this perspective a consistent help, not fully explored yet, can be found in aeropalynology, recording the pollen transported in the air. Together with modern surface samples, these data act as modern analogues. Though it probably does not represent the same past vegetational composition, the current pollen rain is the only basic reference on which our comparative approach can rely. Present trends are interpreted and future scenarios can be hypothesized just using a combination of aero- and archaeo-/palaeo-palynological approaches.

Key words: flora and vegetation history, palynology, climate change, human impact.

Introduction

The Mediterranean basin has always featured, and still has, extremely rich environmental biodiversity (Fig. 1), based both on climate, geology and orography. A huge set of

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biological archives provides evidence of the flora and vegetation changes that occurred in the Mediterranean regions over geological times. The natural richness and variety of plants have been enriched and conditioned by the development of human cultures. These changes have occurred not only during the distant past, but also in the recent one. Together they have determined the shape of the present-day plant landscape. Even if plant macrofossil analysis is quite precise in taxonomic determination of local finds, palynology has been most extensively used to reconstruct different scenarios through the long-term perspective.

The Mediterranean has been impacted by several climate and environmental changes, since before Quaternary times. For example, during the "Messinian salinity crisis", which occurred after the cut off of the connection between the Atlantic Ocean and Mediterranean Sea (ca. 5.9 Ma ago), terrestrial and marine ecosystems were subject to important modifications. During this event, warm and dry climate conditions were prevalent in southern areas. They were associated with an important occurrence of open vegetation taxa followed by the occurrence of subtropical to warm-temperate arboreal taxa. However, at the same time, humid conditions prevailed on the northern areas where precipitation was sufficiently high for the persistence of a "subtropical humid forest". Some tropical taxa were especially abundant in southern areas, and Mediterranean taxa were already present even if sporadic. Pollen records show north to south gradients (e.g. Bertini & Martinetto 2011) attested also by temperature and precipitation quantifications obtained by palaeoclimate methods (Fauquette & al. 2006).

It is not surprising that a consistent contingent of subtropical taxa such as *Taxodium/Glyptostrobus* type, *Engelhardia*, *Symplocos* was still present in the Italian Pliocene/lower Pleistocene flora (e.g. Bertini 2010; Bertini & Sadori 2010; Sadori & al. 2010a; Bertini & Martinetto 2011) and that steppe and grassland formations covered on most occasions the Mediterranean lands during glacial times (e.g. Combourieu-Nebout 1993; Klotz & al. 2006; Joannin & al. 2007, 2008; Suc & al. 2010) despite different patterns in some areas (e.g. expansion of "mountain" conifers near the Po Plain area - Bertini 2001; Fusco 2007 – and in the central Apennines – Sadori & al. 2010a) have been described (Bertini 2010, and references therein). The climate reconstruction based on pollen data from southern Italy shows that, during the lower Pleistocene, the temperature and precipitation distribution pattern of glacial times was similar to that of recent ones. Interglacials were characterised by either higher annual precipitation (homogeneously distributed during the year) or summer-winter temperatures several degrees higher than today (Klotz & al. 2006). Such features allowed the persistence of subtropical taxa. Recurrent glacial/interglacial oscillations were characterized by the regular intensification of dryness and cooling during glacials, and by warming during interglacial periods. The progressive reduction of temperature maxima occurred during the following interglacials caused the progressive impoverishment of the old flora and the increase of the typical Mediterranean trees and shrubs taxa associated to the temperate forest (Fig. 2; e.g. Russo-Ermolli & Cheddadi 1997; Klotz & al. 2006; Joannin & al. 2008, 2011; Combourieu-Nebout & al. 2009). To predict Mediterranean vegetation's response to future climate changes it becomes now crucial to understand better the behaviour of Mediterranean taxa through its complex history. In fact Mediterranean vegetation today matches a Mediterranean bioclimate characterized by long dry summers and mild-wet winters. From older to recent times, the Mediterranean environment was very sensitive not only to extreme events, but even to

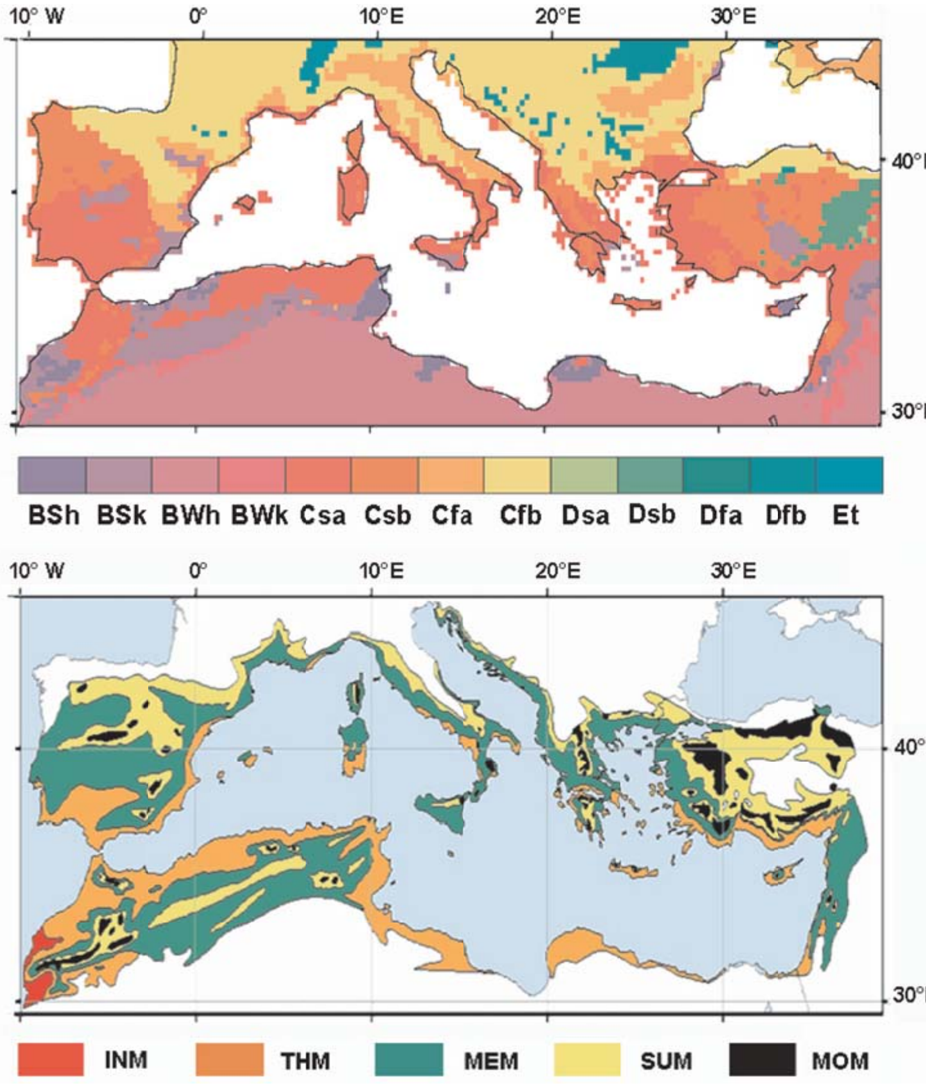

Fig. 1. A) Köppen climate types in the Mediterranean region: subtropical steppe (BSh), midlatitude steppe (BSk), subtropical desert (BWh), midlatitude desert (BWk), Mediterranean climate with hot/warm summer (Csa/b), humid subtropical with no dry season (Cfa), maritime temperate (Cfb), humid continental with hot/warm summer (Dfa/b), continental with dry hot/warm summer (Dsa/b), and tundra (Et) (from Lionello 2012, modified). B) Types of Mediterranean vegetation: infra-Mediterranean (INM), Thermo-Mediterranean (THM), Meso-Mediterranean (MEM), Sub-Mediterranean (SUM), Mountain-Mediterranean (MOM) (from Quézel & Médail, 2003, modified).

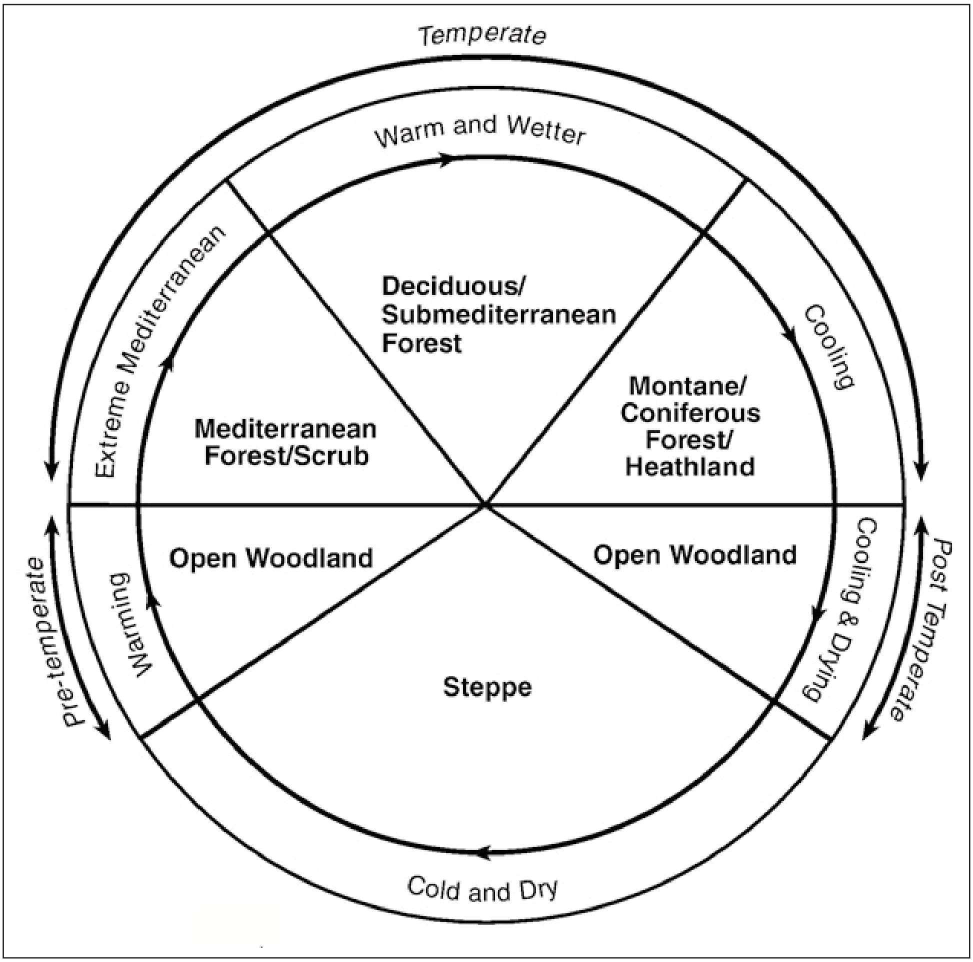

Fig. 2. Scheme of glacial and interglacial vegetation cycle in southern Europe (from Tzedakis & al. 2009).

weaker climate changes with precipitation and/or winter temperature changes acting as the main limiting factors (Lionello 2012).

In general, a huge amount of data demonstrates that if we consider the vegetation changes that have occurred in the last millennia, the long-term relationships between human cultures, climate changes and landscape ecologies have elicited complex human responses to environmental change since prehistoric times (Kuper & Kröpelin 2006; Mercuri 2008; Berger & Guilaine 2009; Mercuri & al. 2010a; Munoz & al. 2010; Brooks 2011; Mercuri & Sadori 2013). In particular, Mediterranean habitats have been continuously transformed by both climatic changes occurring at a global scale and interlaced environmental and cultural changes at local and micro-habitat scale. The environment has been exploited and the landscape shaped by different human groups and societies (Sadori & al.

2010b,c; Mercuri & al. 2011, 2013a; Kouli 2012). Joint actions of increasing dryness, climate oscillations, and human impact are hard to disentangle, and this becomes particularly true after the mid-Holocene (Carrión & al. 2010; Roberts & al. 2011a, b; Sadori & al. 2011, 2013). As a matter of fact important changes in Mediterranean vegetation seem to have coincided either with enhanced aridity or with marked increases in social complexity during the Holocene, or with both of them.

The origin of the Mediterranean vegetation

Mediterranean typical vegetation as usually observed today is the outcome of the influence of geological and climatic history of the Mediterranean area. The present-day Mediterranean biodiversity was not present during the Paleogene (ca. 65-23 Ma ago) and the first probable precursors of a Mediterranean group occurred during the Oligocene (33.9-23 Ma ago). Thereafter, during the Neogene (ca. 23-2.6 Ma ago), the Mediterranean vegetation unit was already individualized and then progressively enriched (Fig. 3) to become a distinct and perennial group of taxa. At this time, the Mediterranean bioclimate probably began to take its place especially with the onset of Mediterranean seasonality even if it was not so marked.

The contribution of palynology in the understanding of causes and effects of the Mediterranean Salinity Crisis (MSC) can be summarized in the sentence: “the climate was dry before, during and after the MSC” inferred from the first palynological studies carried out in Sicilian deposits (e.g. Suc & Bessais 1990; Suc & al. 1995; Bertini & al. 1998). The stratigraphic record of vegetational and climatic changes for the area of northern and central Italy (e.g. Bertini 2006; Roveri & al. 2008; Gennari & al. 2013), dominated by taxa of the subtropical humid forest (e.g. *Taxodium/Glyptostrobus* type and *Engelhardia*), completes the picture and demonstrates that more complex climate scenarios characterized the Mediterranean since the Messinian. Subsequently, the Pleistocene glacial/interglacial cycles have periodically impacted the Mediterranean vegetation through the progressive onset of droughts more and more intense towards the present (Pons & al. 1995). The interglacials were mainly characterized by the spread of subtropical taxa such as *Sequoia* during the oldest cycles and of the deciduous forest taxa in the recent ones, while the glacials were generally characterised by non arboreal steppe and grassland taxa (Combourieu-Nebout 1993; Leroy, 2006; Tzedakis & al. 2006, 2009; Tzedakis 2007), and locally by expansions of conifer montane taxa (e.g. Bertini 2001; Tzedakis 2007; Bertini 2010; Sadori & al. 2010a). The response of tree populations of each site to climatic amelioration during the interglacials correlates directly with the proximity of glacial refugial areas (Tzedakis 1993). Tzedakis & al. (1997, 2001) considering many terrestrial pollen European records showed that, in the last 430 ka, besides a broad correspondence between long pollen sequences and the deep-sea oxygen isotope record, pollen sequences display a higher degree of climate sensitivity.

Ca. 120 ka (thousand years) ago, during the Eemian (the previous interglacial) an important spread of Mediterranean taxa (mainly evergreen oaks and olive) characterized the vegetation near Rome, at Valle di Castiglione (Follieri & al. 1988, 1989). High resolution long pollen records from Greece documented considerable regional and temporal variability during the last

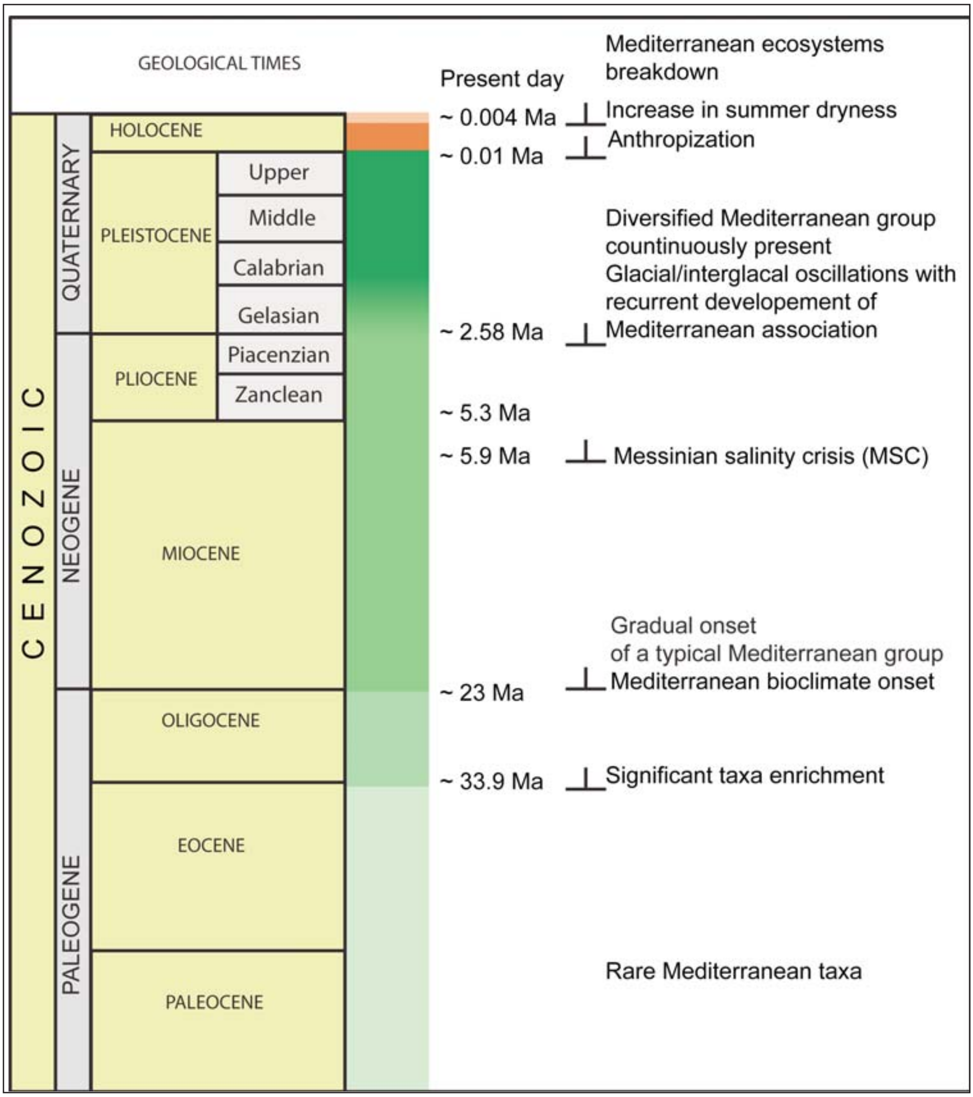

Fig. 3. Installation of Mediterranean taxa during the Cenozoic era (ca. 65 Ma-present).

interglacial, suggesting the occurrence of spatial climatic regimes (Tzedakis 2000, Tzedakis & al. 2004). Already from the beginning of last Interglacial (ca. 128 ka ago), Mediterranean taxa expanded in the area of Ioannina and Tenaghi Philippon but they retreated earlier than deciduous taxa in the later part of the interglacial cycle (Tzedakis & al. 2003; Milner & al. 2013). In the Iberian Peninsula, pollen records show the expansion of Mediterranean trees and shrubs during the first part of Eemian indicating that Mediterranean climate was established close to the beginning of this interglacial period (Sanchez-Goni 2006).

The aridity increase occurred during the mid-late Holocene has been largely strengthened by the anthropic impact over the Mediterranean area. Such a history drives the present-day Mediterranean vegetation puzzle that is and will be particularly vulnerable to human pressure and future climate change. Collins & al. (2012) compared pollen data 0 ka and 6 ka from ~200 southern European sites to reconstruct mid-Holocene and present-day distribution and relative abundance of 11 tree taxa. At 6 ka, *Olea*, *Fagus* and *Juniperus* had smaller distributions and/or abundances than at present, while *Abies, Cedrus* and both deciduous and evergreen *Quercus* have become less abundant or widespread since the mid-Holocene. It was around 4 ka BP that the Mediterranean vegetation spread in most pollen sites, but a doubt still remain on its origin (Combourieu Nebout & al. 2013; Mercuri & Sadori 2013; Mercuri & al. 2013a; Sadori & al. 2013).

Archaeo-palynology of Greek and Italian records

The long and composite history of human presence and activities in Mediterranean countries is documented in detail by long-standing archaeological research. In the Hellenic peninsula, as well as in the Italian peninsula, excavation and survey of archaeological sites show intense habitation since the early Holocene and increasing social complexity during the middle and late Holocene. The emergence and collapse of cultures, urban centers and states, establishment of exchange and trade routes can bee deeply investigated through archaeobotanical research. Several major cultural changes that have been observed in archaeological records offer the opportunity of comparing human societies and activities with recorded climate variability in a given area.

Holocene vegetation record of Greece displays remarkable temporal and spatial variability, revealing the heterogeneity of the landscapes. The Pindos mountain ridge separates the Greek peninsula into different climatic regions: a western “maritime” region, with significantly higher precipitation, and an eastern typical Mediterranean one. In addition, pollen records confirm a north-south climatic trend by documenting the occurrence of mixed deciduous oak forests alternating with mountainous conifer and later beech forests in the northern areas and enhanced schlerophyllous evergreen vegetation in the south (Bottema 1974; Willis 1992; Jahns 1993; Lawson & al. 2004; Kouli & al. 2012). Prehistoric human activities like cultivation, grazing or lumbering, have left an imprint on local plant communities without altering the regional flora until about 4000 years BP (Athanasiadis & al. 2000; Lawson & al. 2005; Kouli & Dermitzakis 2008). Bearing in mind that the tracing of human impact on Holocene plant communities is rather complex, as the expansion of Mediterranean sclerophyllous vegetation can be both the response of human clearance, grazing/pastoralism and shift toward drier climates, the several abrupt short-term episodes of retreat of woodlands are recorded (e.g. 8700, 7600, 5600 and 4300 BP) have been explained as the result of either human activity and/or climatic fluctuations (Jahns & van den Bogaard 1998; Lawson & al. 2004; Jahns 2005; Peyron & al. 2011; Panagiotopoulos & al. 2013).

Correlations and syntheses of past vegetation records with the cultural context in times of independently known climatic conditions elucidates the shaping factors of vegetation dynamics and connect vegetation fluctuations to human and/or climatic fluctuations in an effort to decode human–environment relationships in the past (Kouli 2012). In that perspective, the comparison of terrestrial high-resolution palaeovegetation records with pollen and other multiproxy climatic data from marine sediment cores of the landlocked seas, contribute to the discussion on the main shaping factor of palaeovegetation patterns (Kotthoff & al. 2008; Bellini & al. 2009; Combourieu-Nebout & al., 2009, 2013; Triantaphyllou & al. 2009, 2013; Mercuri et al. 2010a; Kouli & al. 2012; Zanchetta & al. 2013).

The integration of terrestrial and marine pollen data have given pieces of evidence for the timing and intensity of climate-human forces that shaped the cultural landscapes in the Italian peninsula at least in the last four millennia. During the progressive climate aridification occurred in the mid and late Holocene, the reduction in the natural woodland vegetation, composed by both deciduous and evergreen trees, was visible as a combined and synergic effect of increasing climate instability and human pressure (Mercuri & al. 2012; Combourieu-Nebout 2013; Sadori & al. 2013). In central Italian lake cores, human activities left more or less evident traces in pollen diagrams. At Lago di Mezzano they consist of forest natural opening followed by clearance or cutting of specific trees, increase of anthropogenic indicators and use of fire from Bronze Age times onwards (Sadori & al. 2004). In some cases human traces are unambiguous: e.g. the abrupt chestnut increase in pre-Roman times, hemp retting at Lago Albano and Lago di Nemi dating back to ca. 1800 cal BP (Mercuri & al. 2002, 2013a: p. 29) and tamarisk intensive plantation in the imperial port of Rome (Sadori & al. 2010b). In southern Italy, pastoralism favoured the development of shrubby - macchia - vegetation in arid environments, which became especially visible in rural sites (Mercuri & al. 2010b, 2013b; Florenzano & Mercuri 2012; Florenzano & al. 2013).

Pollen records of Holocene vegetation change and the conservation of Mediterranean biodiversity

Pollen data provide the main way of reconstructing long-term vegetation change but, to be most useful, they need to be converted into a form that is comparable with phyto-geographical evidence. The pseudo-biomisation (PBM) approach (Fyfe & al. 2010) was developed to provide a simple and easily applied transformation of fossil pollen data into land-cover classes in order to reconstruct changes in landscape ecology through time. Within this method pollen taxa are assigned to one of a range of possible Land Cover Classes (LCC) based on modern community assemblages using the indicator species approach. For each pollen sample, a modified pollen sum is calculated based on the taxa assigned to each LCC. The PBM has been tested and refined through application to an extensive modern pollen dataset and comparison with Corine remote-sensed land cover maps for Europe. In the circum-Mediterranean region modern vegetation assemblages were established during the early-mid Holocene and they have subsequently been transformed into a mosaic of different land cover types, agricultural, semi-natural and (more or less) natural by a combination of human actions and climatic change.

Site-specific reconstructions may be especially valuable in distinguishing between ecosystems which have experienced major anthropogenic disturbance during their histories and those which have maintained overall land cover continuity during the Holocene, even if species assemblages have often altered. For example, Malo Jezero on the Dalmatian island of Mljet in Croatia lies in a protected reserve comprising *Pinus halepensis* - *Quercus ilex* woodland. Pollen analysis by Jahns and van den Bogaard (1998) has shown that there has been continuous tree cover around this lake throughout the Holocene, even if taxa composition has altered over time. By contrast, at Gölhisar in southwest Turkey, the present-day residual conifer forest is secondary in origin. Pollen analysis by Eastwood & al. (1999) showed that the mid-Holocene forests were cleared during Classical times and replaced by tree crops, grazing land and cereals, with secondary pine-dominated woodland developing when these were abandoned after ~700 AD. Palaeoecological data can therefore play an important role in identifying key areas and sites for biological conservation in the Mediterranean (Zanchetta & al. 2012).

The contribution of aerobiological data to palaeoenvironmental reconstructions in Mediterranean contexts

Links between the different fields of palynology have given extremely interesting insights to solve problems of pollen representation in past and present contexts (e.g., Prentice 1988; Davis & al. 2013). In order to understand the relationships between deposited pollen and past vegetation that produced it, modern surface samples are known to have a central role in the translation of fossil assemblages into the most probable plant communities (e.g. Gaillard & al. 1992; Broström & al. 2008; Hjelle & Sugita 2012). Pollen collected from spore trap may further contribute because artificial traps permit control on the time interval over which the pollen is collected. Moreover, pollen production and transport, seasonality, monthly and daily variations in pollen concentrations can be observed (e.g., Montali & al. 2006). The current airborne pollen is usually monitored through continuous sampling by artificial spore-traps (Hirst volumetric sampler) as included in large datasets of national and international networks (EAN-European Aeroallergen Network).

Data of airborne pollen of chestnut and yew collected for 18 years from one aerobiological monitoring station of Modena, a small centre of northern Italy, have been recently published (Mercuri & al. 2012, 2013c). The data from typical aerobiological analyses have been elaborated to produce a set of modern reference pollen values that are useful for the understanding of the development of plant landscape in Italy and for past environmental reconstructions. As for chestnut, long-distance transport of this pollen is well-known (Conedera & al. 2004, and references therein), but studies on modern pollen rain show that a relatively small amount of pollen is compatible with the presence of chestnut trees living in the area. The data obtained from modern surface samples collected from monospecific woods show very high values, up to 90%. Such examples cannot be found in past records. Data from the monitoring station of Vignola, however, shows that chestnut pollen is important in the summer airborne rain but it falls to 6% on average - from 0.7 to 10% per year - when its value is calculated on yearly basis. Therefore, though chestnut is a high pollen-producer species, and though chestnut woods are important and common on the hills today, such pollen grains are a minor part of the regional annual pollen rain in northern Apennines (Mercuri & al. 2012).

As for yew, pollen production has decreased, while total woody pollen abundance in air has increased in the studied time period (1990-2007; Fig. 4). The trend of the yew pollen season shows a delay at the beginning, a shortening of the pollen period, and an advance of the end of the pollen season. This was interpreted as a response to the current global climate warming. In particular, yew follows the behaviour of winter-flowering plants, and therefore earlier pollination is favoured at low autumn temperatures, while late pollination occurs more often, most likely after warm autumn temperatures. The decrease of pollen production and the shortening of the flowering season point to the decline of yew pollen in the air during the global warming of the last few years. Accordingly, *Taxus* has the highest percentages in past pollen diagrams from cold or cool periods, and it is generally considered a good index to infer such climate features from past records. Current trends in pollen production may support this inference. Palaeoenvironmental data show that, in southern Europe, yew was a declining tree as the climate has become less oceanic and as the activity of the Bronze agriculture increased. This decline has been attributed to different, possibly complementary, ecological causes including competition for light against *Fagus* and *Carpinus*, adverse soil conditions, poor soil water, fungal diseases, deforestation, selective cutting, heavy grazing, and transition from fen-carr environment to ombrotrophic bogs (Thomas & Polwart 2003; Deforce & Bastiaens 2007).

The application of aerobiological studies to past palaeoenvironmental reconstructions is, therefore, a very interesting field of investigation that, though not still completely explored, may be vector of new important inferences about past, present and future of climate change.

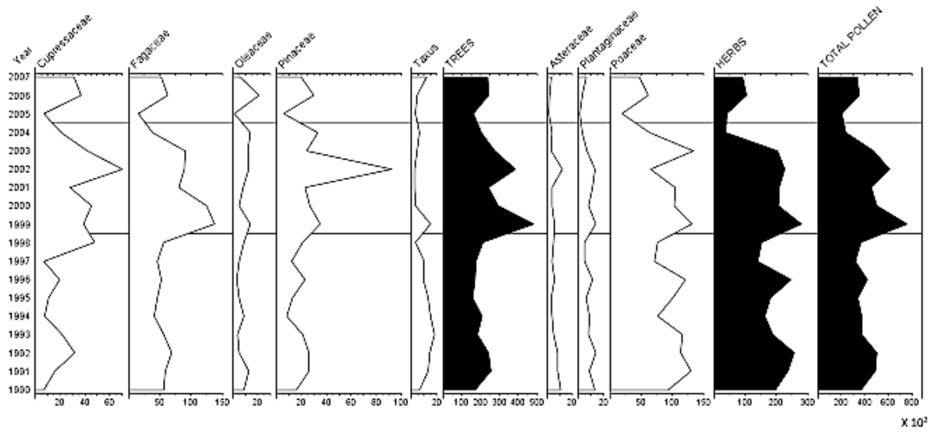

Fig. 4. Aerobiological monitoring: station of Vignola-Modena. Pollen rain of the years 1990-2007 (from Mercuri & al. 2013c, modified).

Conclusions

The Mediterranean flora and vegetation as we know it at present, originated quite recently. Even if already recorded earlier, e.g. during the last interglacial, the spread of typical Mediterranean vegetation is impressive in the last few thousand years, namely in the second half of the present interglacial, the Holocene. It remains a subject of debate how far the causes of the spread of evergreen and sclerophyllous taxa was climatic or human in the Mediterranean. It was in fact a probable synergy of natural and anthropic factors that led to the present-day environment dominated by Mediterranean vegetation.

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