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Climate changes in the central Mediterranean and Italian vegetation dynamics since the Pliocene

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ABSTRACT

Pollen records and pollen-based climate reconstructions from the Italian peninsula (central Mediterranean) show clear signals of vegetation change linked to variations in water availability in the Mediterranean basin over the past 5 million years. Profound vegetation changes occurred in four major steps from the Pliocene to the present. The subtropical taxa that dominate Pliocene assemblages declined and then disappeared between 3–2.8 and 1.66 Ma (at around 2.8 Ma in the North and later in the South), progressively being replaced by temperate *Quercus* forests at mid altitude. In the south Italy, *Quercus* expanded more at around 1.4–1.3 Ma and *Fagus* proportions increased after 0.5 Ma. Conifer forest (first mainly composed of *Tsuga* then by *Abies* and *Picea)* began to expand at 2.8 Ma, probably rather at high altitude, beginning at 2.8 Ma. Mediterranean-type forest, rare during the Early Pleistocene, developed and increased in diversity during the Middle Pleistocene. Open landscapes, with higher abundances of steppic taxa, became more frequent and extensive at the onset of Glacial/Interglacial (G/I) cyclicity around 2.6 Ma and gradually expanded with more and more marked glacials. Climate reconstructions done on selected pollen records from southern Italy suggest a decline in winter temperature and annual precipitation from the early Pleistocene to the Holocene. Specifically, both precipitation and winter temperature reconstructions show changes in interglacial maxima and glacial minima at around 3–2.8 Ma, 2 Ma, 1.3–1.4 Ma and 0.5 Ma.
This critical review provides evidence that the North–South precipitation gradient, with drier conditions in the South, has been a consistent feature of the Italian peninsula since the beginning of the Pleistocene.

1. Introduction

The Mediterranean basin is considered a global biodiversity hotspot (e.g. Médail and Quézel, 1997, 1999; Giorgi, 2006; Christensen et al., 2007). Given projections of future regional climate change, growing demographic pressures in coastal zones, and the particular importance of water resources in the region, the preservation of ecosystems within the basin is considered a key goal for governments (IPCC, 2007). Water availability is a key factor limiting plant growth and is an important driver of vegetation composition (Daget, 1977; Venetier et al., 2010). The future composition of Mediterranean ecosystems is thus clearly tied to water availability. While modern vegetation data from the region provide a baseline for understanding relationships between aridity and vegetation composition, paleoecological records provide support for

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understanding vegetation responses at longer time scales (e.g. Bertini, 2010; Joannin et al., 2012; Combourieu-Nebout et al., 2013; Peyron et al., 2013 and references therein). Paleoecological records show that aridity, as a feature of the Mediterranean basin, appeared recently, gradually increasing up to the present time (Pons et al., 1995). Even during the Messinian salinity crisis (MSC, 5.9–5.3 Ma), aridity did not play a major role in restructuring vegetation (Suc and Bessais, 1990; Bertini, 2006; Fauquette et al., 2006 and references therein). What we now call Mediterranean-type taxa have been present in the basin since the Paleocene, but only sporadically until they increased in importance during the last several thousand years. The development of modern Mediterranean ecosystems seems to be linked to increasing dryness and seasonality, with increasingly dry summers focusing moisture deficiency during the summer months (Pons et al., 1995; Quézel and Médail, 2003).

Researchers have documented a stepwise Pliocene–Pleistocene development of modern Mediterranean ecosystems and climate, although the rarity of records has hindered basin-wide reconstructions (Pons et al., 1995; Sadori et al., 2013a). Given the limited number of Mediterranean available records, reconstructing long-term (5 Myr) vegetation changes on the Italian peninsula will help to identify links between vegetation changes and increasing aridity in the region. The Italian peninsula stretches across the centre of the north Mediterranean basin, running in a northwest to southeast direction. The Apennine Chain forms the backbone of the peninsula, and within the peninsula generate heterogenous environmental conditions that support vegetation that varies with elevation and latitude. Several distinct climatic systems influence the Italian climate: polar air masses from the North; tropical air masses from the South; Atlantic Westerlies; and a monsoon system from the East (Lionello et al., 2006). This results in a climate gradient from north to south with a mosaic of local/regional situations, with usually higher humidity in the north and increasing aridity to the south. Italy thus represents one of the most informative Mediterranean areas to: (i) reconstruct the response of vegetation to various climatic stresses; and (ii) assess the likely future behaviour of Mediterranean plants. Furthermore, the Italy's rich geological and stratigraphical record makes it a significant source of information on the history of Mediterranean vegetation.

In this paper we describe vegetation reconstructions grouped in two areas: Northern and Southern Italy, placing the boundary between the two at 42.5°N. This latitude approximately splits the Italian peninsula according to the present duration of the dry season between areas to the south where this exceeds three months and those to the north where it is shorter. This division allows us to describe continuous long- and short-term climate and vegetation changes in the Mediterranean basin during the last 5 million years.

2. Present day Italian climate and vegetation

Italy is a mountainous country, bounded in the North by the Alps, and with the Apennines running as a backbone from northwest to southeast.

Located at mid-latitude (47°N to 37°N) and towards the western margin of the Eurasian landmass, the Italian peninsula exhibits a classic Mediterranean climate, with mild winters (especially in the hilly and coastal areas) and pronounced summer drought (Fig. 1). The influence of the Mediterranean climate on vegetation is most evident at lower altitudes and on the coasts, becoming attenuated with increasing altitude on the pre-Alpine chains and in the Apennines. In the Apennines, summers are cooler and moister with increasing altitude, whereas continentality increases towards and into the Alpine mountains, leading to increased annual temperature range, with colder winters and summers that are hot but not markedly dry. The Po Valley, a large plain situated in the north between the western Ligurian Alps and the Adriatic Sea, is relatively continental in climate. This is principally due to its proximity to the Alps and its separation from the Mediterranean proper by the Apennines. The Italian peninsula thus spans a clear and complex gradient from the southern warm-temperate Mediterranean climate, through the cool-temperate climate of the Apennines and pre-Alpine ranges, to the continental climate of the innermost Alps with its strong temperature seasonality. This complex topographic and climatic landscape has deeply affected the flora of the peninsula. The Italian vegetation is well documented (e.g. Tomaselli et al., 1973; Ozenda, 1975; Bonin, 1981; Ozenda, 1994; Pignatti, 1998; Quézel and Médail, 2003; Blasi, 2010). The European potential natural vegetation zones and the main physiognomic–ecological units for the Italian peninsula are summarised in Fig. 1 (modified from Pignatti, 2011).

3. Materials and methods

3.1. Pollen records

We use vegetation reconstructions based on palynology and paleobotanical information available from the Italian peninsula (Fig. 2, Table 1). These data help to reconstruct vegetation changes in Italy, and their links to increasing aridity since the Pliocene. The pollen records presented here are distributed unevenly across the region, and so each site has been assigned to either "Northern" or "Southern" Italy relative to latitude 42.5°N, the isocline for current dry season duration (longer or shorter than 3 months) (Figs. 1 and 2). Vegetation types inferred from pollen records and the literature are plotted for glacial and interglacial within six key geological intervals during the last 5 Myr: Pliocene (Zanclean, 5.332–3.600 Ma, and Piacenzian, 3.600–2.588 Ma); Early Pleistocene (Gelasian, 2.588–1.806 Ma, and Calabrian, 1.806–0.781 Ma); Middle Pleistocene ("*Ionian*", 0.781–0.126 Ma); Late Pleistocene ("*Tarantian*", 0.126–0.01 Ma); and Holocene (last 0.01 Ma) (Fig. 3a and b). Sixteen sites that combine long time series, coverage for key time intervals and consistent age models (Table 1 and Fig. 2 in red), provide the opportunity to develop a model of continuous vegetation change throughout Italy. Pollen diagrams for these sites have been plotted using Psimpoll (Bennett, 2008) for a subset of taxa selected to illustrate the major changes in Italian vegetation since the Pliocene (Fig. 4a and b).

The taxon "Taxodiaceae" is referred to in quotation marks throughout because many genera formerly assigned to this family are now placed in subfamilies of Cupressaceae, for example, Taxodioideae Endl. ex K. Koch (*Taxodium*, *Glyptostrobus* and *Cryptomeria*) and Sequoioideae (Luerss.) Quinn (*Sequoia*, *Sequoiadendron* and *Metasequoia*). The genus *Sciadopitys* is now generally placed in Sciadopityaceae (Brunsfeld et al., 1994; Farjon, 1998, 2005). However, the term "Taxodiaceae" has been commonly used in Italian records where it is generally assumed to represent *Sciadopitys*, *Taxodium* type (which includes *Taxodium* cf. *distichum* and *Glyptostrobus*) and *Sequoia* type (which includes *Cryptomeria*, *Cunninghamia*, *Metasequoia glyptostroboides*, *Sequoiadendron giganteum* and *Sequoia sempervirens*). Because of the ecological diversity of taxa represented by the term "Taxodiaceae" it is difficult to revisit the records and apply the new taxonomy; we have therefore chosen to keep the term "Taxodiaceae", as used in older publications, although providing greater clarity where possible.

3.2. Climate reconstructions

Climate reconstructions from pollen records allow us to understand the climate trends that have driven changes in Italian vegetation over the last 5 Ma. Depending on the period of interest we have used different methods for reconstructing climate. Annual precipitation and temperature have been reconstructed using: (1) probability mutual climatic spheres (PCS); and (2) the Modern Analogue Technique (MAT). The PCS method uses the modern climatic requirements of plant taxa, transposed to plant assemblages (Klotz, 1999; Klotz et al., 2006) and has been applied using 60 of the 110 taxa identified in fossil pollen floras from the Pliocene to Early Pleistocene (e.g. Fauquette et al., 1999; Klotz et al., 2006; Fauquette et al., 2007). The PCS method is

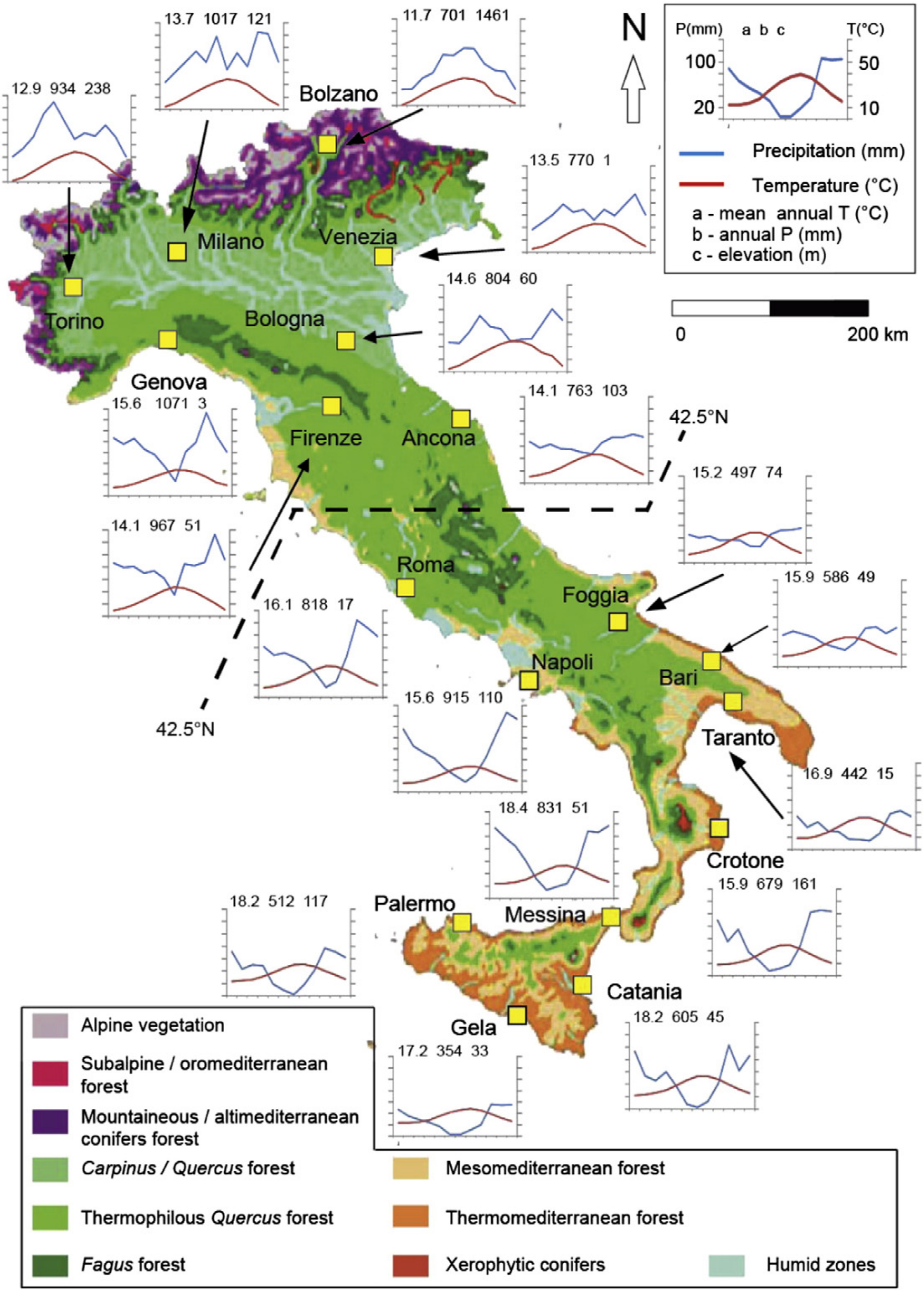

Fig. 1. Present-day vegetation and climate in Italy (modified from Pignatti, 2011). A selection of climate (ombrothermic) diagrams (calculated using the NewLocClim software, Grieser et al., 2006) illustrates the modern north–south climate gradient.

considered the best way to reconstruct climate parameters from geologically older pollen records representing vegetation associations including exotic or subtropical taxa and thus lacking a modern analogue. Mean temperature of the coldest month (MTCO) and mean annual precipitation (PANN) are presented here for PCS reconstructions performed on the older records. The MAT has been successfully applied to several Middle Pleistocene to Holocene records to produce pollen-based reconstructions of climate variables (e.g. Guiot, 1990; Joannin et al., 2011; Combourieu-Nebout et al., 2013; Peyron et al., 2013). The vegetation associations recorded in pollen diagrams for these intervals are compared to a collection of surface samples (database of >3000 surface pollen spectra from Europe and Mediterranean area) with their associated biomes and climate variables from various origin to reconstruct past climate variables (for details see Peyron et al., 1998, 2011, 2013). Mean temperature of the coldest month (MTCO), mean summer (June–July–August) precipitation (PSUM), mean winter (December–January–February) precipitation (PWIN) and mean annual precipitation (PANN) are presented here for MAT reconstructions.

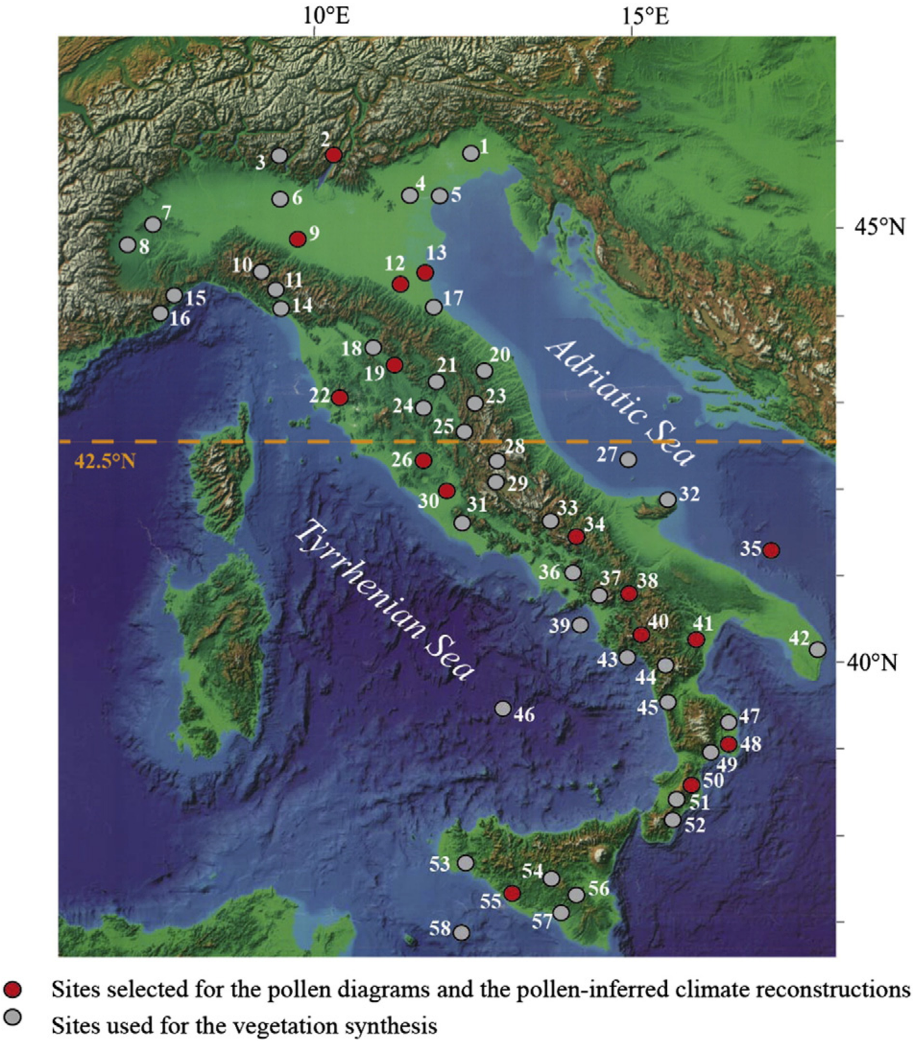

Fig. 2. Selected Italian sites: 1) Azzano Decimo; 2) Lago di Ledro; 3) Piànico–Sèllere, Leffe, Fornaci di Ranica; 4) Fimon; 5) Venice; 6) Pianengo; 7) Rio Ca' Viettone; 8) Villafranca RDB; 9) Stirone, Castell'Arquato (Campile), Monte Falcone–Rio Crevalese; 10) Compiano; 11) Aulla-Vallescura; 12) Monticino 1987, Lamone composite section; 13) Core S8 and core S13 (Po plain); 14) Sarzana; 15) Cava di Villanova; 16) Castel d'Appio; 17) Val Marecchia; 18) Lower Valdarno basin: San Quintino, Ponte a Elsa and other sections; 19) Upper Valdarno basin: Santa Barbara, Rena Bianca and other composite sections; 20) Maccarone; 21) Gubbio; 22) Lago dell'Accesa; 23) Pietrafitta, Tiberino basin: Fosso Bianco, Cava Toppetti and other composite sections; 24) Colle Curti–Cesi composite section; 25) Leonessa; 26) Lagaccione, Lago di Vico; 27) Marine core RF 93-30; 28) Madonna della Strada; 29) Corvaro, Borgorose and Marano de' Marsi; 30) Valle di Castiglione, Valle Ricca; 31) Fontana Ranuccio; 32) Lago Battaglia; 33) Sessano, La Pineta-Isernia; 34) Boiano; 35) Marine core MD 90-917, Marine core AD 91–17, Marine core KET 82-16, Marine core KET SA 03-1, Marine core IN 68-9; 36) Saticula (Sant'Agata de' Goti — BN); 37) Acerno; 38) Monticchio; 39) Salerno marine core C106; 40) Vallo di Diano; 41) Montalbano Jonico, Sant'Arcangelo; 42) Lago Alimini; 43) Camerota; 44) Mercure; 45) Lago di Trifoglietti; 46) core KET8003; 47) Valle di Manche; 48) Semaforo and Vrica sections, Santa Lucia; 49) Bianco; 50) Monte Singa; 51) Canolo Nuovo; 52) Le Castella; 53) Lago di Preola; 54) Lago di Pergusa; 55) Punta Piccola, Capo Rossello composite section; 56) Monte San Giorgio; 57) Monte San Nicola (Gela); 58) marine core MD 01-2797. Sites used for pollen diagrams (Figs. 3 and 8) and pollen based climate reconstructions (Fig. 7) are indicated in red. The orange dotted line represents the 42.5°N latitudinal limit between Northern and Southern Italy.

Our synthesis represents the first compilation of climate reconstructions from this region to span the entire Pleistocene, a time of major vegetation changes, and the first to separate cold and warm intervals during the Middle and Late Pleistocene. Because the temporal resolution is generally poor, reconstructed climate is presented as box-and-whisker plots for temperature and/or precipitation within the chosen intervals. For MTCO, PWIN, PSUM and TANN, separate plots were calculated for glacials and interglacials. Box-and-whisker plots were made using R software, the boxes representing the extent of the second and third quartiles, and the dotted delimited whisker lines representing extreme values. The median is indicated by a heavy line within the box.

3.3. Chronology

Published age models provided the chronologies used for the pollen records. Age models for the most recent time intervals were based on ^{14}C dates, links to Greenland ice-core records and tephra layer data, whereas for the geologically older records K/Ar dates, biostratigraphy (foraminifers and nanofossils), links to oxygen isotope records from Mediterranean or Atlantic marine sediment cores and astronomical tuning were variously used. It is not part of our review to discuss the individual age models, although we acknowledge that each has its own limitations. Instead, our aim is to reconstruct the general pattern of Italian vegetation changes from the Pliocene to the present day.

4. Italian vegetation and a trend towards increasing drought

4.1. Emergence of Mediterranean vegetation communities in Italy

Climate in the Mediterranean has changed repeatedly since the tropical, warm–humid conditions of the Eocene. The development of the Mediterranean climate regime, punctuated by a dry summer season, occurred in the late Pliocene (Suc, 1984), a time when cooling is observed in marine records (Poore and Berggren, 1975; Sprovieri et al., 2006).

Table 1
List of the sites used in this paper with their location, sediment type (P/L, peatbog and lacustrine sequences; T, other continental sequences; M, marine cores), the time interval covered and the main related bibliographic references (bold text indicates those with the site palynology included; italic text indicates other relevant references).

n.	Sites	Lat N	Long E	Alt./depth	Locality	C/L	T	M	Age Interval	References *
1	**Azzano Decimo**	45°53'20"N	12°42'50"E	14 m asl	Friuli	■	■	■	Last 215 ka	**Pini et al., 2009a**
2	**Lago di Ledro**	45°51'46"N	10°44'46"E	860 m asl	Trentino	■			Holocene	**Joannin et al., 2013**
3	**Piànico-Sèllere**	45°51'06" N	10°03'35"E	1080 m asl	Lombardy	■			Controversial age: 1. Riss-Wurm Interglacial, 2. 779 ± 13 ka, 3. ca 400 ka (MIS 11)	**Moscariello et al., 2000; Rossi, 2003; de Beaulieu et al., 2006;** *Pinti et al., 2001; Roulleau et al., 2009, Brauer et al., 2007a, 2008*
3	**Leffe**	45°53'13"N	9°52′09"E	950 m asl	Lombardy	■			Olduvai (1.94–1.78 Ma) up to 0.87 Ma	**Lona, 1950; Lona and Follieri, 1957; Lona and Bertoldi, 1972; Ravazzi, 1993, 2003; Ravazzi and Rossignol-Strick, 1994; 1995; Ravazzi and Moscariello, 1998; Muttoni et al., 2007, Ravazzi et al., 2009;** *Cremaschi and Ravazzi, 1995; Martinetto, 2009*
3	**Fornaci di Ranica**	45°45'07"N	9°42'55"E	500 m asl	Lombardy	■			Late Calabrian	**Ravazzi et al., 2005**
4	**Fimon**	45°30'22"N	11°31'45"E	41 m asl	Veneto	■			Last 130 ka	**Pini et al., 2009b**
5	**Venice**	45°27'44"N	12°18'35"E	0 m asl	Veneto	■		■	Quaternary	**Mullenders et al., 1996;** *Kent et al., 2002* **; Canali et al., 2007; Massari et al., 2004**
6	**Pianengo**	45°25'43"N	9°41'34"E	142 m slm	Lombardy	■		■	Late Matuyama to the early Brunhes	**Muttoni et al., 2003**
7	**Rio Ca' Viettone**	45°12'N	7°35'E	N/A	Piedmont	■			Pliocene (? Most probably Late Zanclean)	**Allason et al., 1981; Bertoldi and Martinetto, 1995**
8	**Villafranca RDB**	44°48'46"N	7°29'38"E	380 m asl	Piedmont	■			Zanclean-Piacenzian	**Francavilla et al., 1970; Lona and Bertoldi, 1972; Carraro et al., 1996;** *Martinetto and Vassio, 2010*
9	**Stirone**	44°50'N	9°58'E	140 m asl	Emilia-Romagna			■	Zanclean to Calabrian	**Lona and Bertoldi, 1972; Becker-Platen et al., 1977; Bertolani-Marchetti et al., 1979; Bertini, 1994, 2001; Fauquette and Bertini, 2003;** *Mai, 1995; Martinetto et al., 2007*
9	**Castell'Arquato** (Campile)	44°51'13"N	9°52'14"E	224 m asl	Emilia-Romagna			■	Gelasian	**Lona, 1962; Lona and Bertoldi, 1972;** *Mai, 1994: Martinetto et al., 2015*
9	**Monte Falcone-Rio Crevalese**	44°51'13"N	9°52'14"E	N/A	Emilia-Romagna			■	Late Piacenzian	**Monegatti et al., 1997, 2002**
10	**Compiano**	44°33'34"N	9°39'09"E	332 asl	Emilia-Romagna	■			Early Pleistocene (?)	**Bertoldi, 1985b;** *Martinetto et al., 2015*
11	**Aulla-Vallescura**	44°14'13"N	9°47'57"E	547 m asl	Tuscany	■			Pliocene (Zanclean or Piacenzian?)	**Bertoldi, 1988; Bertoldi and Castello, 1990**
12	**Monticino 1987**	44°23'53"N	11°34'20"E	148 m asl	Emilia-Romagna		■	■	Late Messinian to Zanclean	**Bertini, 1994, 2006;** *Vai, 1988 and references therein*
12	**Lamone composite section**	44°18'35"N	11°54'41"E	26 m asl	Emilia-Romagna			■	Calabrian, MIS 64 to MIS 46	**Fusco, 1996, 2007, 2010;** *Vaiani and Venezia, 1999*
13	**Po Valley : core 240-S8**	44°18'35"N	12°E	N/A	Emilia-Romagna			■	Holocene	**Amorosi et al., 2004;** *Cibin et al., 2005*
13	**Po Valley : core 240-S13**	44°18'35"N	12°E	N/A	Emilia-Romagna			■	Late Pleistocene to Holocene	**Amorosi et al., 2004**
14	**Sarzana**	44°08'20"N	9°57'30"E	298 m asl	Ligury	■			Pliocene (Zanclean or Piacenzian?)	**Bertoldi et al., 1994;** *Federici, 1973*
15	**Cava di Villanova**	44°02'27"N	8°06'09"E	194 m asl	Ligury			■	Zanclean	**Zheng, 1990; Zheng and Cravatte, 1986** *and references therein*
16	**Castel d'Appio**	43°48'12"N	7°34'31"E	287 m asl	Ligury			■	Zanclean	**Zheng, 1990; Zheng and Cravatte, 1986** *and references therein*
17	**Val Marecchia**	43°58'39"N	12°18'08"E	300 m asl	Emilia-Romagna			■	Piacenzian-Gelasian	**Rio et al., 1997**
18	**Lower Valdarno basin**: San Quintino, Ponte a Elsa and other sections	43°41'15"N	10°53'55"E	60 m asl	Tuscany		■		Piacenzian-Gelasian	**Valleri et al., 1990; Benvenuti et al., 2007;** *Bossio et al., 1993; Benvenuti and Degli Innocenti, 2001; Martinetto et al., 2015*
19	**Upper Valdarno basin**: Santa Barbara, Rena Bianca and other composite sections	43°33'47" N	11°28'33"E	143 m	Tuscany	■			Gelasian to Calabrian	**Follieri, 1977; Albianelli et al., 1995; Bertini and Roiron, 1997; Bertini, 2002, 2003, 2010, 2013; Napoleone et al., 2003;** *Ghinassi et al., 2004; Mai, 1994*
20	**Maccarone**	43°25'31"N	13°06'55"E	225 m asl	Marche		■	■	Late Messinian to Zanclean	**Bertini, 1994, 2006;** *Carloni et al., 1974*
21	**Gubbio**	43°22'40"N	12°33'56"E	358 m asl	Umbria	■			Pleistocene	**Lona and Ricciardi, 1961a; Ricciardi, 1965; Fusco, 2010**
22	**Lago dell'Accesa**	42°59'19"N	10°53'37"E	260 m asl	Tuscany	■			Holocene	**Drescher-Schneider et al., 2007**
22	**Pietrafitta**	43°01'17"N	12°12'36"E	318 m asl	Umbria	■			MIS 58 to MIS 28	**Ricciardi, 1961; Ge.Mi.Na, 1962; Lona and Bertoldi, 1972; Fusco, 2010**
23	**Colle Curti - Cesi composite section**	43°01'N	12°53'E	850 m, 820 m asl	Umbria	■				**Bertini, 2000; Ficcarelli et al., 1997; Coltorti et al., 1998**
24	**Tiberino basin**: Fosso Bianco, Cava Toppetti and other composite sections	42°36'N	12°30'57"E	187 m asl	Umbria-Marchean Apennines	■			Upper Early to lower Middle Pleistocene	**Pontini, 1997; Pontini and Bertini, 2000; Pontini et al., 2002;** *Basilici, 1997; Martinetto et al, 2014*
25	**Leonessa**	42°35'11"N	12°57'37"E	930 m asl	Rieti	■			MIS 62 (?) to MIS 28, according to Fusco (2010)	**Ge. Mi.Na., 1962; Ricciardi, 1965**

in red, pollen data included in this paper

wd: water depth N/A not found
asl: above sea level

* References including palynology are in bold;
other references in italic

(*continued on next page*)

n.	Sites	Lat N	Long E	Alt./depth	Locality	C/L	T	M	Age Interval	References *
25	**Lagaccione**	42°34'N	11°51'E	355 m asl	Latium	■			Last 130 ka	**Magri, 1999**; *Narcisi and Anselmi, 1998*
26	**Lago di Vico**	42°20'18"N	12°09'56"E	557 m asl	Latium	■			Last 90 ka	**Leroy et al., 1996**; **Magri and Sadori, 1999**
27	**Marine core RF 93-30**	42°40'01"N	15°40'03"E	77 m wd	central Adriatic Sea			■	Holocene	**Oldfield et al., 2003; Piva et al., 2008**
28	**Madonna della Strada**	42°20'55"N	13°15'16"E	1590 m asl	Abruzzi	■			Calabrian	**Magri et al., 2010**
29	**Corvaro**	41°12'36"N	13°13'55"E	1074 m asl	Latium				Middle-Late Pleistocene	**Chiarini et al., 2007**
29	**Borgorose and Marano de' Marsi**	42°08'56"N	13°15'59"E	720 m asl	Latium	■			Early Pleistocene	**Sadori et al., 2010**; *Chiarini et al., 2007, 2009*
30	**Valle di Castiglione**	42°N	12'E	44 m asl	Latium	■			Last 250 ka	**Follieri et al., 1988**; **Di Rita et al., 2013**; *Narcisi et al., 1992*
30	**Valle Ricca**	42°N	12'E	50 m asl	Latium			■	Early Pleistocene	**Urban et al., 1983; Arias et al., 1990**; *Borzi et al., 1998; di Bella et al., 2005*
31	**Fontana Ranuccio**	41°53'33"N	13°06'13"E	235 m asl	Latium			■	Early Pleistocene	**Corrado and Magri, 2011**
32	**Lago Battaglia**	41°53'N	16°10'E	20 m asl	Apulia	■	■		Late Holocene	**Caroli and Caldara, 2007**
33	**Sessano**	41°38'44"N	14°19'51"E	700 m asl	Molise	■			MIS 15 to MIS 12	**Russo Ermolli et al., 2010a**; *Amato et al., 2011*
33	**La Pineta-Isernia**	41°37'06"N	14°13'34"E	450 m asl	Molise	■			~700-800 ka	**Lebreton, 2002;** *van Otterloo and Sevink, 1983; Cremaschi, 1983; Cremaschi and Peretto, 1988; Delitala et al., 1983; von Koenigswald and Kolfschote, 1996; Belluomini et al., 1997*
34	**Boiano**	41°29'46"N	14°28'11"E	660 m asl	Molise	■			Middle Pleistocene	**Orain et al., 2013** *and reference therein; Aucelli et al., 2011*
35	**Marine core MD 90-917**	41°17'N	17°37'E	1010 m wd	south Adriatic Sea			■	Last deglaciation and Holocene	**Combourieu-Nebout et al., 1998, 2013**
35	**Marine core AD 91-17**	40°52'17"N	18°38'15"E	845 m wd	south Adriatic Sea			■	Holocene	**Sangiorgi et al., 2003; Giunta et al., 2003**
35	**Marine core KET 82-16**	41°31'N	17°59'E	1166 m wd	south Adriatic Sea			■	Last deglaciation and Holocene	**Rossignol-Stick et al., 1992**
35	**Marine core KET SA 03-1**	41°30'25"N	17°10'77"E	567 m wd	south Adriatic Sea			■	Last deglaciation and Holocene	**Favaretto et al., 2008**
35	**Marine core IN 68-9**	41°47'5'N	17°54'5"E	609 m wd	south Adriatic Sea			■	Last deglaciation and Holocene	**Zonneveld, 1996**
36	**Saticula** (Sant'Agata de' Goti - BN)	41°06'14"N	14°30'10"E	200 m asl	Campania	■			late Early Pleistocene	**Russo Ermolli et al., 2010b**
37	**Acerno**	40°49'50"N	15°02'44"E	650 m asl	Campania	■			MIS14 to MIS12	**Russo Ermolli, 2000; Munno et al., 2001; Petrosino et al., 2014a**
38	**Monticchio**	40°56'N	15°35'E	681 m asl	Basilicata	■			Last 127 ka	**Watts et al., 1996, 2000; Allen and Huntley, 2000, 2009; Brauer et al., 2000, 2007b**
39	**Salerno marine core C106**	40°28'22"N	14°42'24"E	292 m asl	South Tyrrhenian Sea			■	Last 30 ka	**Russo Ermolli and Di Pasquale, 2002; Di Donato et al., 2008;** *Buccheri et al., 2002*
40	**Vallo di Diano**	40°16'17"N	15°37'06"E	450 m asl	Campania	■			650 to ca 450 Ka (MIS 16 to 13) (Karner et al., 1999)	**Russo Ermolli, 1994; Russo Ermolli et al., 1995; Russo Ermolli and Chedaddi, 1997**
41	**Montalbano Jonico**	40°17'N	16°34'E	226m asl	Basilicata			■	1.240 to 0.900 Ma (MIS 37 to 23)	**Joannin et al., 2008**
41	**Sant'Arcangelo**	40°15'51"N	16°16'30"E	236 m asl	Basilicata	■			Jaramillo subchron to Brunhes chron	**Sabato et al., 2005**
42	**Lago Alimini**	40°11'27"N	18°26'34"E	35 m asl	Apulia		■		Late Holocene	**Di Rita and Magri, 2009**
43	**Camerota**	40°02'33"N	15°22'30"E	300 m asl	Campania	■			Early Pleistocene	**Baggioni et al., 1981; Brenac, 1984; Russo Ermolli, 1999**
44	**Mercure**	39°58'07"N	16°02'04"E	300 m asl	Basilicata /Calabria	■			Middle Pleistocene	**Lona and Ricciardi, 1961b;** *Petrosino et al., 2014b; Robustelli et al., 2014*
45	**Lago di Trifoglietti**	39°32'34"N	16°00'14"E	400 m asl	Calabria	■			Holocene	**Joannin et al., 2012**
46	**core KET8003**	38°49'N	14°29'E	1900 m wd	South Tyrrhenian Sea			■	Tarantian-Holocene	**Rossignol-Stick et al., 1989**
47	**Valle di Manche**	39°05'35"N	16°55'14" E	205 m	Calabria			■	MIS 22 to MIS 18.3	**Capraro et al., 2005;** *Massari et al., 2002*
48	**Semaforo and Vrica sections**	39°N	16°42'E	50 m asl	Calabria			■	Semaforo (2.46 to 2.11 Ma) and Vrica (2.2-1.36 Ma)	**Combourieu-Nebout et al., 1990, 2000; Combourieu-Nebout and Vergnaud-Grazzini, 1991; Combourieu-Nebout, 1993; 1995; Klotz et al., 2006**
48	**Santa Lucia**	39°N	16°42'E	161 m asl	Calabria			■	Late Early Pleistocene	**Joannin et al., 2007**; Lourens et al., 1996
49	**Bianco**	38°04'25"N	16°08'21"E	61 m asl	Calabria			■	Pliocene (ca 3.7-3 Ma)	**Bertoldi et al., 1989;** *Howell et al., 1988; Rio et al., 1989*
50	**Monte Singa**	38°10'N	16°08'18"E	61 m asl	Calabria			■	Early Pleistocene (2.5-2.45 Ma)	**Combourieu-Nebout et al., this paper;** *Lourens et al., 1996*
51	**Canolo Nuovo**	38°18'43"N	16°09'56"E	660 m asl	Calabria	■			Holocene	**Gruger, 1977; Schneider, 1985**
52	**Le Castella**	38°1'47"N	16°04'11"E	231 m asl	Calabria			■	Pleistocene	**Bertoldi, 1977; Bertoldi et al., 1989;** *Raffi and Rio, 1980; Rio, 1982*
53	**Lago di Preola**	37°38'19"N	12°37'08"E	20 m asl	Sicily	■			Holocene	**Sadori et al., 2011**
54	**Lago di Pergusa**	37°31'13"N	14°17'56"E	570 m asl	Sicily	■			Holocene	**Sadori et al., 2013b**
55	**Punta Piccola**	37°16'47"N	13°38'24"E	9 m asl	Sicily			■	Zanclean to Piacenzian	**Combourieu-Nebout et al., 2004;** *Brolsma, 1978; Hilgen, 1987; Castradori et al., 1998*
55	**Capo Rossello composite section**	37°17'47"N	13°29'24"E	77 m asl	Sicily			■	Pliocene to Early Pleistocene	**Bertoldi, 1985a; Guerrera et al., 1984; Bertoldi et al., 1989;** *Cita and Gartner, 1973; Hilgen and Langereis, 1988; Caruso, 2004; Cita et al., 2008*
56	**Monte San Giorgio**	37°14′55″N	14°30′34″E	496 m	Sicily			■	1.23 to 1.095 Ma	**Dubois, 2001**
57	**Monte San Nicola (Gela)**	37°15'34.5" N	14°12'48.2" E	394 m asl	Sicily			■	Early Pliocene	**Bertoldi, 1985a; Bertoldi et al., 1989**
58	**Marine core MD 01-2797**	36°57'N	11°40'E	771 m wd	Siculo-tunisian strait			■	Tarantian-Holocene	**Desprat et al., 2013**

in red, pollen data included in this paper

wd: water depth N/A not found
asl: above sea level

* References including palynology are in bold; other references in italic

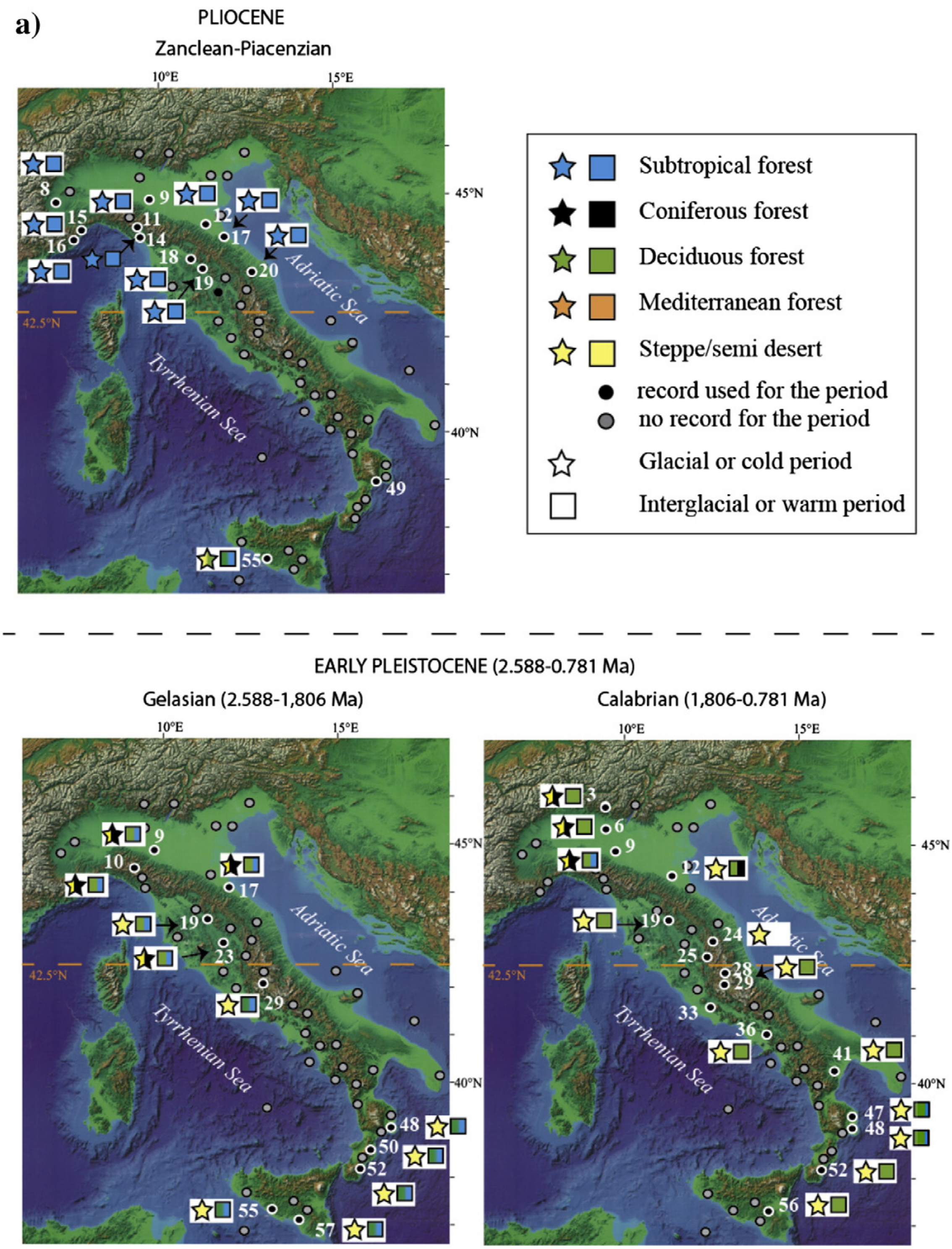

Fig. 3. a: Dominant vegetation during warm (interglacial, squares) and cold (glacial, stars) stages in Italy for the three main sub-series from Pliocene to Early Pleistocene. Orange line corresponds to the latitudinal limit of 42.5°N.

Glacial/Interglacial (G/I) cycles, beginning in the Pleistocene, contributed to the individualization of the Mediterranean climate conditions during the mesic interglacials and dry glacials (Pons et al., 1995).

Modern Mediterranean taxa were present, but only sporadically, during the Paleogene (Fig. 5). Mediterranean taxa have been present in the western Mediterranean since the Paleocene, although diversification of the Mediterranean flora followed the end of the Oligocene (Quézel and Médail, 2003 and references therein). Oligocene fossils of Oleaceae (pollen and leaves) have been reported from Northern Italy (Sachse, 2001). However, development of truly Mediterranean vegetation occurs only later, during the Miocene, with the weak onset of summer aridity favouring establishment of such vegetation in Italy and throughout the Mediterranean basin (Pons et al., 1995; Quézel and Médail, 2003 and references therein).

Although xerophytic taxa have been reported from Miocene deposits in the northern Mediterranean area (e.g. de Saporta, 1889;

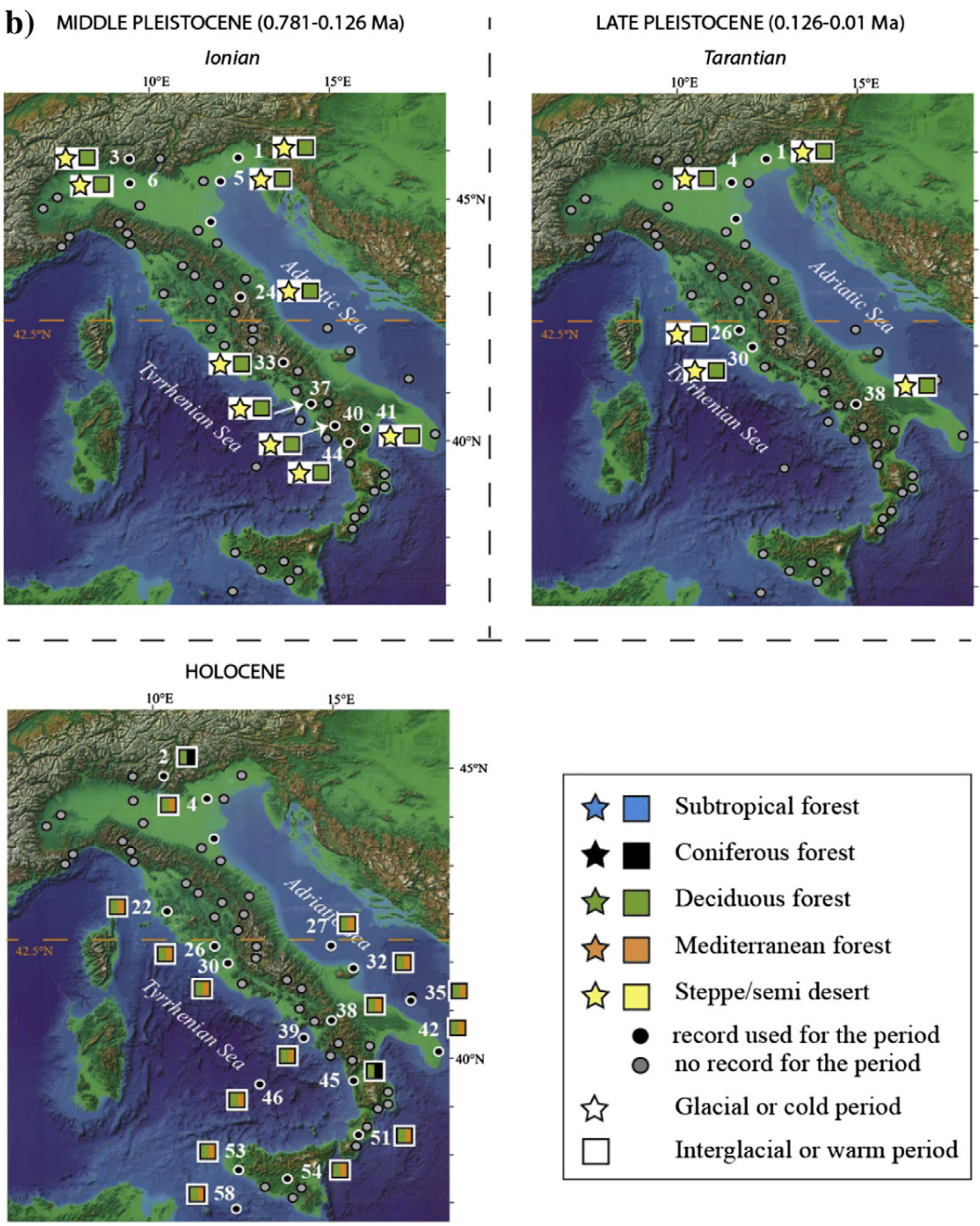

Fig. 3 b: Dominant vegetation during warm (squares) and cold (stars) stages in Italy for the three main sub-series from the middle Pleistocene to modern. Orange line corresponds to the latitudinal limite of 42.5°N.

Bessedik, 1985), semi-arid associations were a minor component in the rich tropical vegetation that occupied the Mediterranean region at that time. Arid or semi-arid associations are not a major feature during the MSC (e.g. Bertini, 2006; Fauquette et al., 2006, 2007; Bertini and Martinetto, 2008, 2011) either, although in some intervals (e.g. close to 5.5 Ma) aridity appears to have promoted the expansion of open vegetation including steppe taxa such as *Lygeum* (Bertini, 2006). The expansion of semi-arid associations across the Mediterranean region is likely related to: (1) the development of a Mediterranean climate during the Pliocene; and (2) the periodic occurrence of aridity since the onset of the Pleistocene (Pons et al., 1995). Semi-arid plant communities developed during the Pliocene and expanded at low to middle altitudes during the middle Pleistocene.

4.2. The Pliocene: setting the stage

Although a diverse Pliocene flora is found in Italian sites after the MSC, while pollen data are available from several sites in Northern Italy they are scarce in Southern Italy (Fig. 3a and b; Table 1) rendering difficult any vegetation synthesis across the entire peninsula (e.g. Bertini, 2010; Bertini et al., 2010 and reference therein).

Pliocene forests in the north were composed of rare tropical to common subtropical taxa, such as *Taxodium*-type, mixed with temperate trees (Zheng and Cravatte, 1986; Zheng, 1990; Bertini, 2001; Fauquette and Bertini, 2003) (Figs. 3a and 4a). Swamp environments were widespread and herbs were a minor component of the vegetation (Fig. 6a and b). After 3 Ma, following marine evidence of cooling, forest of a montane character developed, with major increases in *Picea*

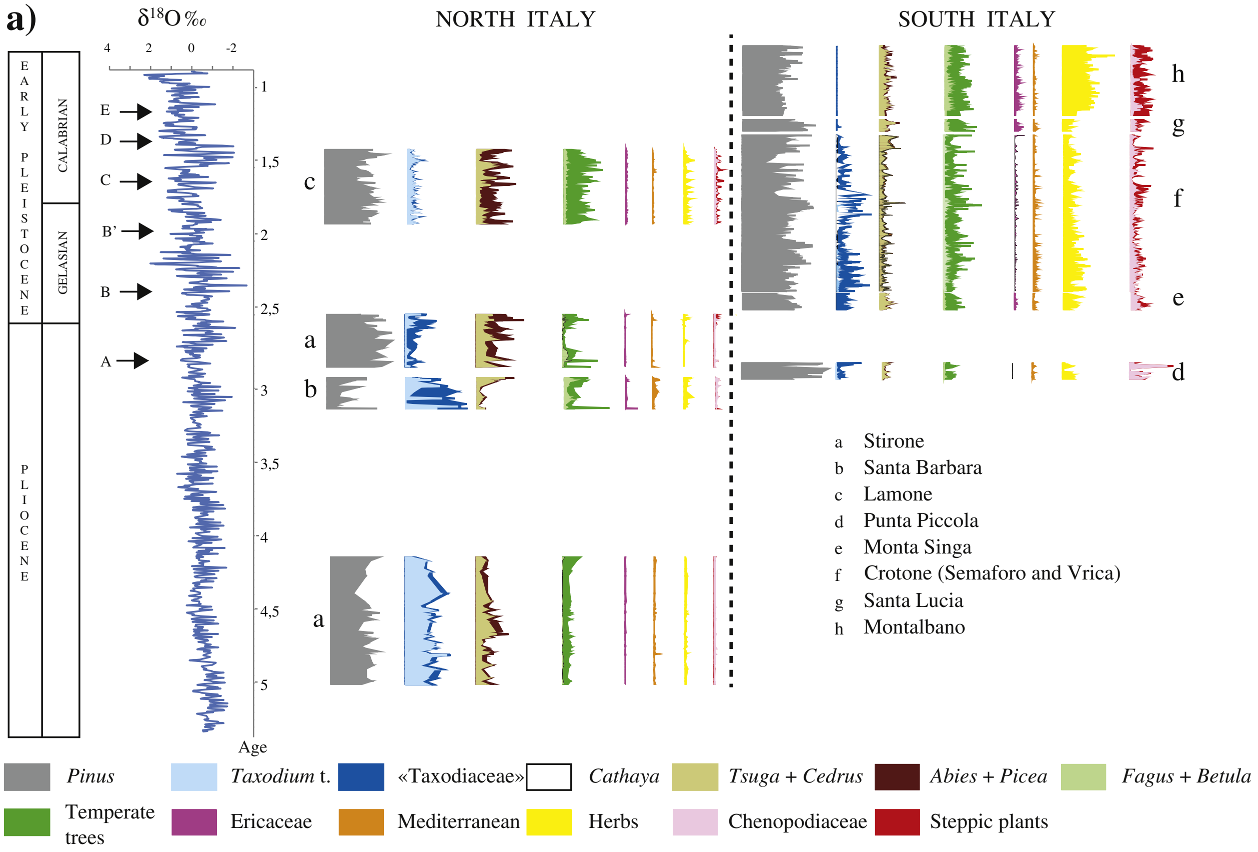

Fig. 4. a: Vegetation changes in Northern and Southern Italy using representative pollen diagrams from 5 Ma to 0.9 Ma. A, decrease in Taxodium-type and increase in montane trees; B, onset of decrease in "Taxodiaceae" (*Sequoia-type*) and increase in steppic vegetation; B′, extinction of "Taxodiaceae" and development of *Cathaya*; C, extinction of tropical forest and *Cathaya*, increases of *Tsuga* and *Quercus*; D, increase in *Quercus* forest and increased representation of Ericaceae; E, increase in herbs.

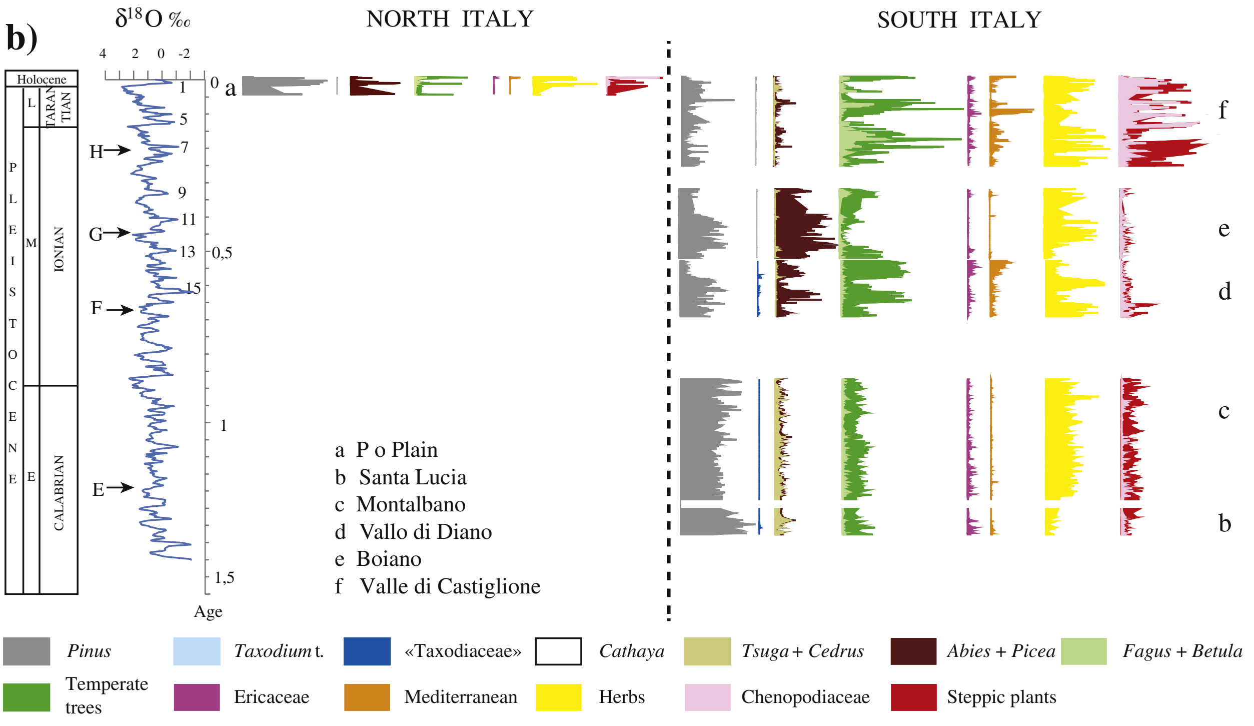

Fig. 4 b: Vegetation changes in Northern and Southern Italy using representative pollen diagrams from 1.2 Ma to 0 Ma. E, increase in herbs; F increase in Quercus and extinction of Tsuga; G, increase in Abies and Picea; H, increase in Fagus, development of Mediterranean forest, expansion of open vegetation and steppic vegetation.

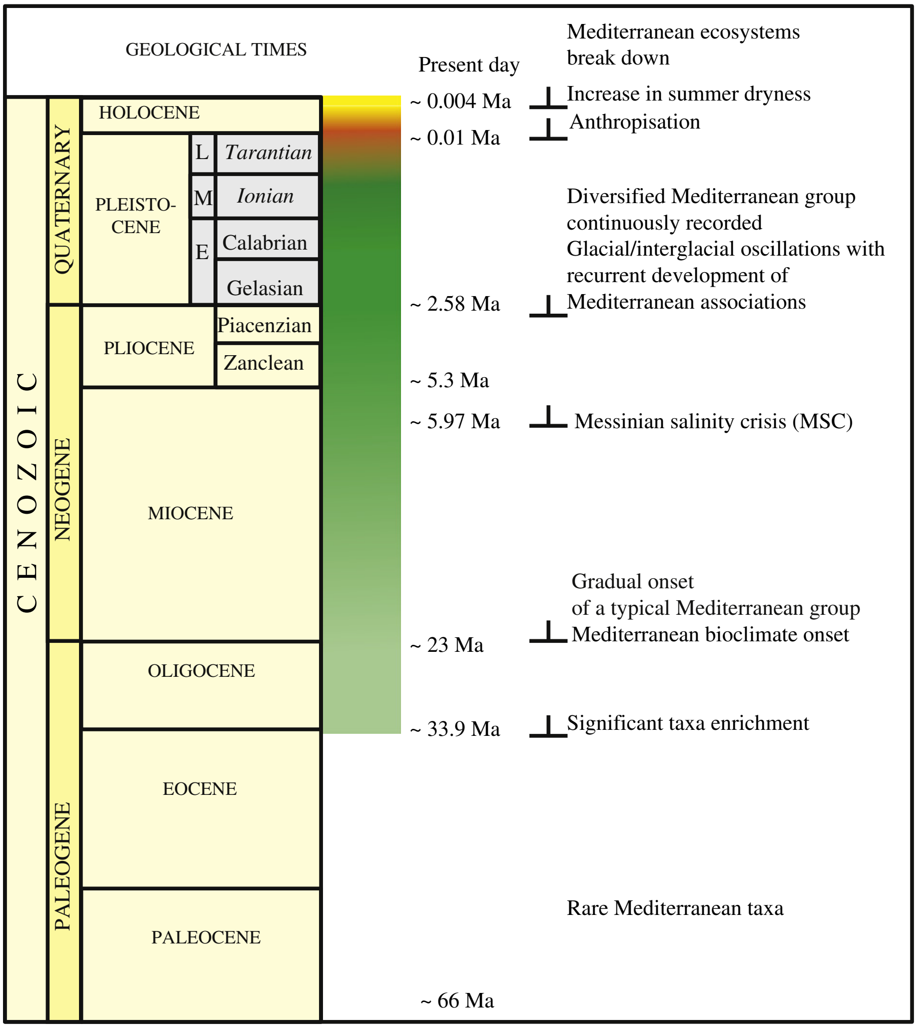

Fig. 5. Development of the Mediterranean flora and climate in the Mediterranean basin (modified from Quézel and Médail, 2003; Sadori et al., 2013a,b).

followed by *Cedrus* and *Tsuga*, while *Taxodium*-type forest declined (Bertini, 2001, 2010).

There are few Pliocene vegetation records from Southern Italy, mostly from parts of the far south. Thus, on the island of Sicily (the southernmost region of Italy) at Punta Piccola (Combourieu-Nebout et al., 2004) and Capo Rossello (Guerrera et al., 1984; Bertoldi, 1985a; Bertoldi et al., 1989; Suc et al., 1995) open herbaceous vegetation already had expanded during the Pliocene, although steppic taxa remained sporadic. *Quercus* forest was here restricted to mountains, and contained relict subtropical taxa. Further information is needed to improve our understanding of change in Southern Italy during this interval, in particular to reveal the extent of open vegetation at this time. The contrast between northern and far southern records supports the existence of a north–south climate gradient in Italy during the Pliocene, similar to the broader Mediterranean climate pattern at this time (Fauquette et al., 2007). These records also support the existence of an east–west climate gradient in the Mediterranean basin suggested by other Neogene palynological records (Suc et al., 1995; Bertini, 2006; Fauquette et al., 2006, 2007; Bertini, 2010). Climatic conditions during the Early Pliocene were predominantly subtropical, with year-round moisture and warm temperatures (e.g. Fauquette and Bertini, 2003). Mean annual temperatures were between 12 and 20 °C in Northern Italy and exceeded 22 °C in Sicily (Fauquette et al., 1999, 2007). Annual precipitation ranged from 1100 to 1400 mm in the north to ~600 mm in the south (Fauquette et al., 1999, 2007). Thus while the extent of seasonality is unknown, mean annual climate values were similar to modern values.

4.3. The Pleistocene: the onset of recurrent drought and its influence on Mediterranean ecosystems

4.3.1. The Early Pleistocene (EP, 2.588–0.781 Ma, Gelasian and Calabrian) and the regression of subtropical trees

The development of the Arctic ice cap at the beginning of Pleistocene had significant impacts on global climate. The EP corresponds to the initiation of the G/I cycle that has largely driven climate variability on multi-millennial time-scales and that is clearly represented in $\delta^{18}O$ records from marine sediment cores (for the Mediterranean Sea, see Lourens et al., 1996, 2004) (Fig. 4a). In the Mediterranean, especially in Italy, geological processes, such as Apennine uplift and sea level change, further modified these cyclic processes, resulting in further changes in vegetation composition and structure. Several records have illustrated the occurrence and dynamics of climate cycles during this interval (Combourieu-Nebout, 1993, 1995; Fusco, 1996; Combourieu-Nebout et al., 2000; Bertini, 2001, 2003; Capraro et al., 2005; Fusco, 2007; Joannin et al., 2007; Bertini, 2010, 2013; Bellucci et al., 2014). The start of G/I cycles, and especially the occurrence of cold glacial stages, favoured an increase in steppic taxa that has continued throughout the Pleistocene and up to the present. Over the same interval, forest diversity declined as a result of a progressive decline in, and loss of, subtropical taxa during the Early and Middle Pleistocene (Fig. 3a). As noted above, the north–south climate gradient, marked by increasing aridity towards the south, was already well established by this time (Figs. 3a and 4a) (Fusco, 2007).

During the EP, Mediterranean taxa (mainly *Quercus ilex* accompanied by *Olea*, *Pistacia* and *Cistus*) were present although not abundant in fossil pollen assemblages, (e.g. Combourieu-Nebout, 1995; Magri et al., 2010; Corrado and Magri, 2011). These taxa were not a major component of the vegetation during either interglacial or glacial stages of the EP and probably occurred only at low altitude and/or near the coast. They may, however, have also occurred scattered through the warm-temperate forest and have persisted there during glacial stages.

In the north, moist conditions along the Po valley enabled persistence of swamp environments within the Po valley during interglacial, supporting *Taxodium*-type forests. These swamps were also occasionally present during glacial of the EP (Fusco, 1996, 2007; Fig. 3a, see event A in Fig. 4a; Fig. 6a and b, Table 2). Conifer forests with *Picea* and *Tsuga* extended from higher towards lower altitudes (Fig. 6a; e.g. Fusco, 2010 and references therein). Declines in subtropical swamp forest began around 2.8 Ma, at the time of the first expansion of high altitude conifer forest (Fig. 4a see event A, Table 2). This expansion was marked especially by increased *Picea* observed at sites such as Stirone (Bertini, 2001), and, in central Italy, at sites in the Upper Valdarno (Bertini, 2010, 2013). The expansion of conifers in the north reflects cooling, but the sparse occurrence of open vegetation even during peak glacial stages indicates that there was no marked increase in aridity there. According to Fusco (2010), expansions and contractions of the conifer forests mimic marine δ^{18}O variations which are mainly controlled by worldwide temperature changes. In Northern Italy, however, glacial stages saw significant expansions of steppic taxa, especially *Artemisia* (e.g. Bertini, 2010, 2013), indicating relatively arid conditions at those times. Deciduous trees and conifers dominated forests in the north at 2 Ma, marking a second step in vegetation change (e.g. Fusco, 2007). After around 1.4 Ma, interglacial in the Alps were marked by the presence of Juglandaceae (mainly *Carya*), reflecting increased humidity during these stages after that time (e.g. Ravazzi and Rossignol-Strick, 1995; Fusco, 2007).

Subtropical forests associated with elements of the deciduous forests (especially *Quercus*), in the south expanded at low to middle altitudes during interglacial. Conifer forests continued to develop at high

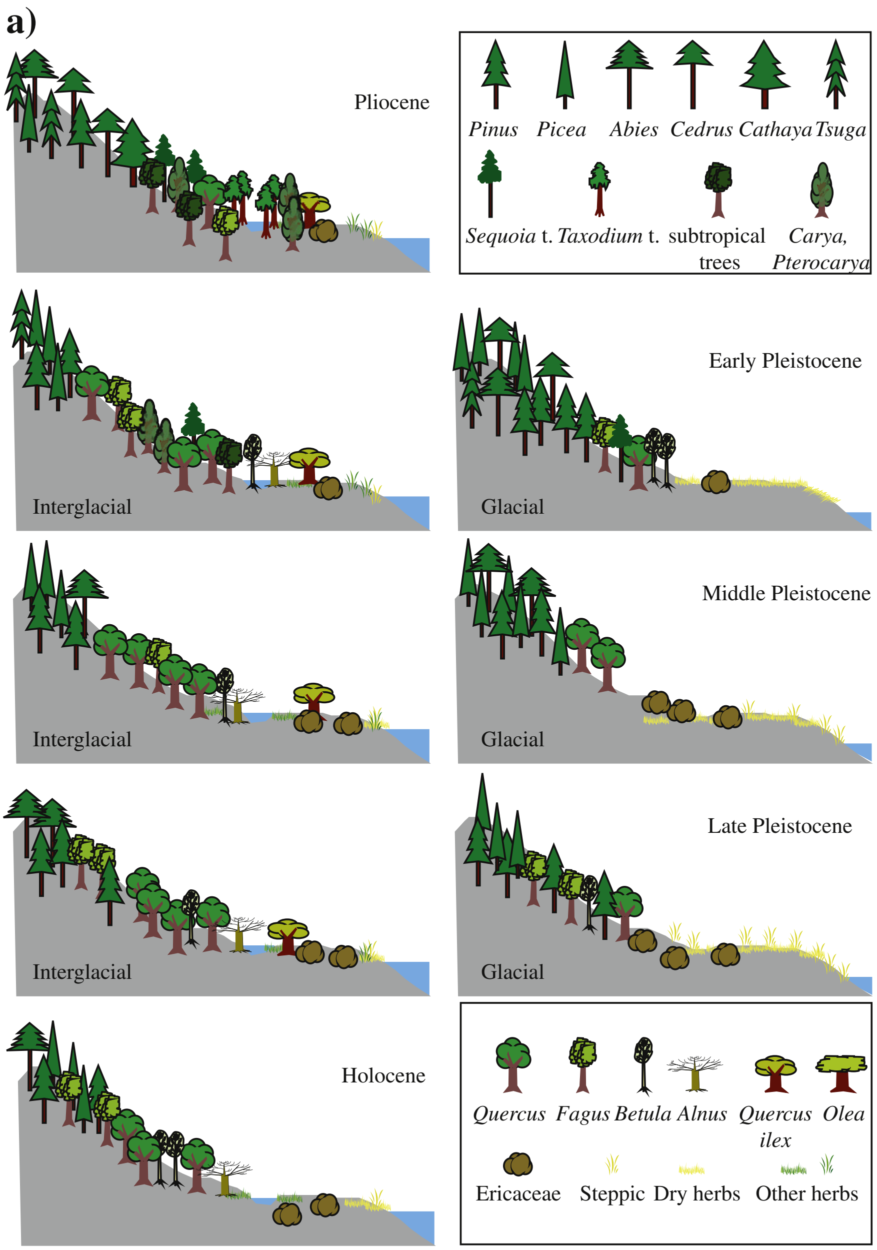

Fig. 6. a: Altitudinal vegetation profiles from the Pliocene to the Holocene at latitudes above 42.5°N.

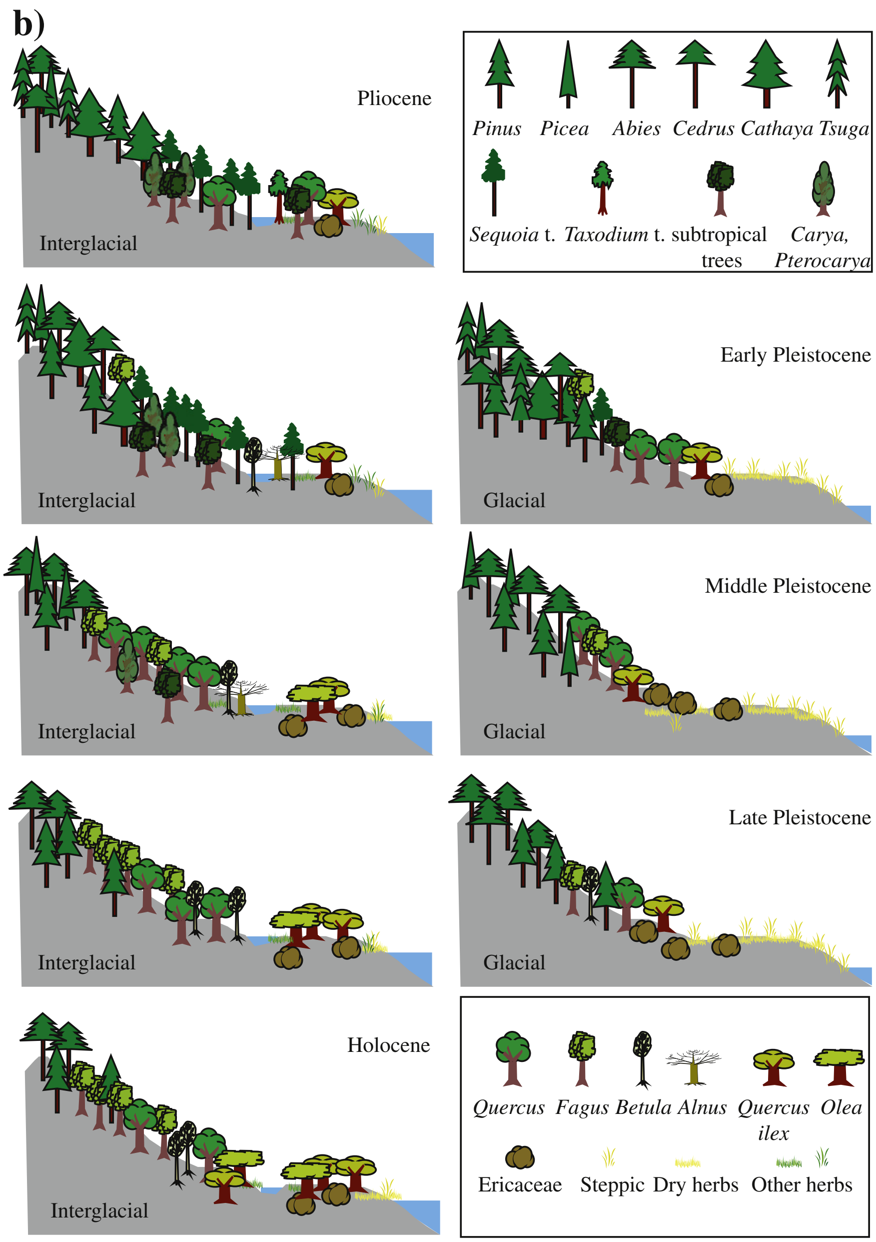

Fig. 6 b: Dominant vegetation during warm (squares) and cold (stars) stages in Italy for the three main sub-series from the middle Pleistocene to modern. Orange line corresponds to the latitudinal limite of 42.5°N.

altitudes, while herbaceous taxa were limited to coastal fringes (Fig. 6b; Combourieu-Nebout et al., 2000). During glacials, steppic taxa colonised low altitudes, subtropical and deciduous forests were patchy at middle altitudes, and conifer forests dominated at high altitudes, expanding from higher mountain sites occupied during interglacial stages (Fig. 6b). Mountain elevations were still too low to permit the development of alpine tundra (Fauquette and Combourieu-Nebout, 2013). Climate oscillations were the principal (but not exclusive) driver of vegetation change (e.g. Bertini, 2003; Capraro et al., 2005; Bertini, 2010). Shifts between forest and open vegetation clearly following the G/I cycles driven, during the EP, by obliquity (Fig. 4a; Fig. 6a and b; Combourieu-Nebout et al., 1990; Combourieu-Nebout and Vergnaud-Grazzini, 1991; Combourieu-Nebout, 1993, 1995; Fusco, 2007; Joannin et al., 2007; Leroy, 2007; Tzedakis, 2007; Joannin et al., 2008).

Subtropical trees still represented the principal forest component at the onset of the EP. Thereafter “Taxodiaceae” progressively declined, with *Taxodium*-type decreasing markedly at the Pliocene/Pleistocene boundary followed by *Sequoia*-type at the transition to the middle Calabrian (Fig. 3a, see events A and B in Fig. 4a; Fig. 6a and Table 2). The onset of the decline in *Sequoia*-type in southern Italy at around 2.45 Ma coincides with an intensification of sea surface cooling in the Mediterranean, marked by recurrent increases in $\delta^{18}O$ values (see B event in Fig. 4a; Lourens et al., 1996). Successive cold intervals at the beginning of the Pleistocene likely stressed subtropical trees, resulting in their progressive decline, although they persisted in some localities until at least 1.66 Ma (e.g. *Cathaya*; Combourieu-Nebout et al., 1990; Combourieu-Nebout and Vergnaud-Grazzini, 1991; Bellucci et al., 2014), and possibly even later (Capraro et al., 2005; Corrado and Magri, 2011) (Fig. 4a see changes from events B to B′). In China today, where *Cathaya* and “Taxodiaceae”, including *Sequoia*-type (e.g. *Metasequoia*), occur in the same areas, they are found in distinct altitudinal belts, with *Cathaya* in a higher altitude belt than that occupied by “Taxodiaceae” (Wang, 1961, 1986). Thus, *Cathaya* development at the expense of “Taxodiaceae” in Italy during the EP probably reflects a progressive cooling of interglacial optima (Combourieu-Nebout and Vergnaud-Grazzini, 1991). This inference corresponds to increased

Table 2
Principal vegetation changes in Italy from early Pleistocene to Holocene, along with the inferred climate.

	Event	Age	Vegetation of North Italy	Vegetation of South Italy	Climate
🟨 🟡	–	Holocene	Mixed temperate forest	Mediterranean forest	Temperate to Mediterranean
🟧	H	~0.2 Ma	↑ *Abies* and *Picea* in Alps ↑ herbs and steppic taxa during G	↑ *Fagus* and ↑ Mediterranean taxa during IG, ↑ steppe and open xeric vegetation during G	IG, temperate to Mediterranean G, cold and dry
	G	~ 0.4–0.5Ma	–	↑ *Abies* and *Picea*	
	F	~ 0.7 Ma	Extinction of the last exotic subtropical taxa and deciduous forest domination during IG ↑ Conifers (*Abies* and *Picea*) in the Alps during G	↑ *Quercus* forest taxa during IG Extinction *Tsuga* ↑herbs during G	IG, temperate G, cool and dry
🟫	E	~1.2 Ma	–	↑ Herbs	
	D	~1.3–1.4 Ma	exotic subtropical taxa still present (*Carya*) during IG	↑ Ericaceae ↑ montane taxa *Tsuga*	
	C	~1.6 Ma	–	Extinction *Cathaya* and slight ↑ *Quercus* during IG	IG, temperate G, cool–temperate and/or dry
	B'	~ 2 Ma	↑ *Quercus* forest taxa, persistence of *Taxodium*–type in the Po valley	Extinction “Taxodiaceae” (*Sequoia*–type) and ↑ *Cathaya* during IG Steppic taxa during G	IG, temperate to subtropical G, cool–temperate and/or dry
	B	~ 2.4 Ma	↓ *Sequoia*–type during IG, Onset ↑ Steppic taxa during G ↑ *Picea* and *Tsuga*	Onset ↓ *Sequoia*–type during IG, Onset ↑ Steppic taxa during G	IG, subtropical G, cool–temperate and/or dry
🟩	A	~ 2.8 Ma	↑ montane trees (*Abies, Picea, Tsuga,*), ↓“Taxodiaceae” (*Taxodium*–type and *Sequoia*–type)	↓ *Taxodium*–type and ↑ *Sequoia*–type	IG, subtropical G, cool–temperate and/or dry
		Before 3 Ma	Humid subtropical forest, swamps with *Taxodium*–type	Open vegetation (Sicily) and *Quercus* forest with subtropical taxa on the mountains	tropical to subtropical

🟨 Holocene
🟡 Late Pleistocene
🟧 Middle Pleistocene
🟫 Early Pleistocene
🟩 Pliocene

G, Glacial
IG, interglacial

interglacial δ^{18}O values seen in marine records indicating cooler sea surface temperatures during interglacial optima (see the Oxygen isotope record in Fig. 3a). At the beginning of the Pleistocene, conifers were probably confined to the highest altitude sites in the mountains of Southern Italy, with *Abies*, *Picea*, *Cedrus* and *Tsuga* increasing during the Calabrian, and *Cathaya* declining around 1.6 Ma (Combourieu-Nebout et al., 1990; Combourieu-Nebout and Vergnaud-Grazzini, 1991). Today, when both are found in the same region, *Tsuga* is found at higher elevations than *Cathaya* (Wang, 1961). Thus, as with Taxodiaceae and *Cathaya*, the changing vegetation composition indicates a cooling of interglacial optima that again coincided with increases in interglacial δ^{18}O values. Vegetation was again reorganized during the middle Calabrian, around 1.3–1.4 Ma, with the expansion of *Quercus* mixed forest (see events C and D in Fig. 4a; Fig. 4b and Table 2). Higher altitude forests with *Tsuga* persisted and Ericaceae increased in parallel with herbs, while *Carya* declined rapidly after 1.3 Ma (see event E in Fig. 4b; e.g. Dubois, 2001; Joannin et al., 2007, 2008; Corrado and Magri, 2011).

EP climate reconstructions from pollen indicate a subtropical climate sites in Southern Italy. Winters were mild during both glacial and interglacial stages, with mean temperatures above 5 °C (Klotz et al., 2006 and this paper), although glacials were slightly cooler and drier than interglacials (Fig. 7, box plots 52–76 and 81–100). Temperatures declined around 2 Ma (Fig. 7), with a slight cooling during interglacial winters and sharp declines in precipitation during both glacial (between box plots 52–78 and 80–100) and interglacial stages (between box plots 43–79 and 81–101). Climate reconstructions indicate another cooling, between 1.4 and 1.3 Ma, with winter temperatures decreasing at both interglacial maxima (Fig. 7, see difference between box plots 41–43 and 45–79) and glacial minima (Fig. 7, see difference between box plots 42–46 and 52–78). During the same interval, annual precipitation during both interglacial and glacial stages decreased (Fig. 7).

4.3.2. The middle Pleistocene (MP — 0.781–0.126 Ma, Ionian) and the development of lowland deciduous and montane forests

The 41 kyr G/IG cycles of the EP were replaced by 100 kyr cycles during the MP, with the length of glacial stages increased (Tzedakis, 2005, 2007; Leroy, 2007; Tzedakis et al., 2012). This change is evident in several Italian records (e.g. Follieri et al., 1988, 1989; Russo Ermolli et al., 1995; Russo Ermolli and Cheddadi, 1997; Magri, 1999; Magri and Sadori, 1999; Muttoni et al., 2007; Ravazzi et al., 2009; Fusco, 2010; Magri, 2010; Russo Ermolli et al., 2010a; Magri and Palombo, 2013;

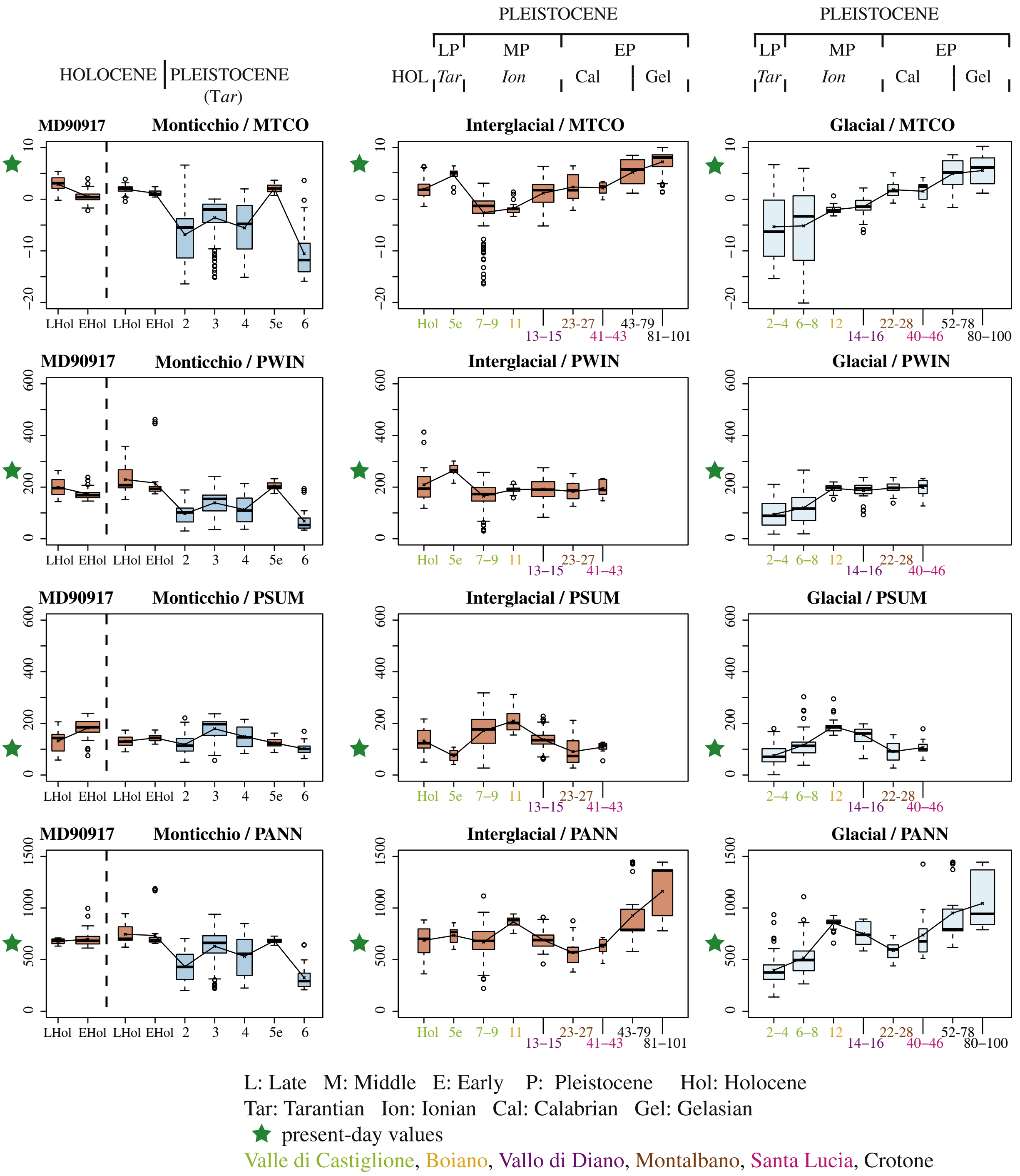

Fig. 7. Climate changes in Southern Italy from Early Pleistocene to present day. Inferred values are presented as box plots summarising interglacials: Holocene (Hol); sub-stage 5e (0.123–0.130 Ma); stages 7–9 (0.191–0.337 Ma); stage 11 (0.374–0.424 Ma); stages 13–15 (0.478–0.563 Ma); stages 23–27 (0.900–0.970 Ma); stages 41–43 (1.320–1.362 Ma); stages 45–79 (1.405–2.103 Ma); and stages 81–101 (2.146–2.554 Ma); and for glacials: stages 2–4 (0.014–0.071 Ma); stages 6–8 (0.130–0.300 Ma); stage 12 (0.424–0.478 Ma); stages 14–16 (0.533–0.676 Ma); stages 22–28 (0.866–1.014 Ma); stages 40–46 (1.286–1.405 Ma); stages 52–78 (1.530–2.043 Ma); and stages 80–100 (2.125–2.540 Ma). Ages of the boxplot-intervals are from Lisiecki and Raymo (2005). Interglacials are plotted in red and glacials in blue in two separate diagrams. Interglacials and glacials are shown for the whole time series in the central and righthand columns respectively; the lefthand column shows the last G/IG cycle at Monticchio and the Last deglaciation and Holocene for core MD 91-917. Bold lines represent the median, fine lines connect the means. The dotted line marks the extreme value interval (interquartile range no more than 1.5) and outliers are indicated by small empty circles.

Orain et al., 2013). Plant communities during the MP were very different from those of the late Calabrian, with deciduous *Quercus* forests extending across the peninsula during interglacial stages and increased herbaceous cover during glacial stages. Mediterranean taxa were present, with *Quercus ilex* as the principal taxon, and they increased in representation during interglacial stages.

Deciduous forests dominated in Northern Italy during the MP. The increased length and severity of glacial stages effectively extirpated subtropical taxa from the region and supported the expansion of conifer forests in the Alps (e.g. Muttoni et al., 2007; Ravazzi et al., 2009) (Fig. 4b; Fig. 3a and b). Conifers expanded downslope during cold intervals while at lower elevations there was an open herbaceous vegetation mixed with steppic elements (Fig. 4b see event F, Table 2). Ericaceae became now a significant component of the open vegetation (Fig. 6a).

Deciduous forest dominated in the South during MP interglacials and *Fagus* began to increase in relative abundance. Subtropical trees were absent. *Tsuga* was present sporadically as a relic of the older subtropical humid vegetation (Fig. 4b see event F, Fig. 3a and b; Fig. 6b and Table 2). *Carya* and *Pterocarya* were still found, although rarely, possibly in refuge areas (e.g. Orain et al., 2013). Conifers, including *Abies*, became established at higher altitudes and expanded at middle altitudes during glacial stages (Fig. 4 see event G, Fig. 6b) (Orain et al., 2013). During the longer, colder and drier glacial stages herbs colonised lower elevations and land that was exposed by falling sea levels. Steppic vegetation proportions increased during the glacial stage after 0.3–0.2 Ma, a signal of increasing drought intensity (Fig. 4b see after event H).

Pollen-inferred climate indicates low temperatures in both glacial and interglacial stages. Maxima for MP interglacial stages are near the lowest values observed during the LP glacials. MP glacial stages experienced much lower temperatures (Fig. 7). Cool interglacials that were longer than previous interglacials (Tzedakis, 2007; Tzedakis et al., 2012) may explain the increase in conifers, the expansion of *Quercus* forest at mid-altitude and the increase in *Fagus* (e.g. Russo Ermolli et al., 1995; Russo Ermolli and Cheddadi, 1997; Magri, 1999; Magri and Sadori, 1999; Russo Ermolli et al., 2010a). The increase in Ericaceae and herbs in Southern Italy may also be related to the longer glacials (Fig. 6a and b). Pollen inferred climate reconstructions show near-modern annual precipitation values during interglacials, whereas glacials were dry. Precipitation seasonality is inferred for the interglacials (Fig. 7).

Although pollen based reconstructions exhibit climate oscillations, with warm/humid interglacials and cold/dry glacials during the MP, some interglacials appear to have experienced cooler winters than the glacials, especially marine isotope stage (MIS) 11 (Fig. 7). Precipitation during MIS 11 appears to have been slightly lower during winter and higher in summer comparing to other interglacials from the same period. Reconstructed MTCO values for MIS 11 are the lowest of the interglacial box plot series, whereas reconstructed precipitation is greater than for preceding stages. The MIS 11 reconstructions come from pollen assemblages in the Boiano section and need to be confirmed by more analyses of other time-series since this is not a common feature in G/I alternation. The Boiano basin may have been a refuge for vegetation during MIS 11, potentially biasing estimates because of the presence of taxa such as *Carya* that persisted at this site characterised by its topographic situation, whereas regional climate was less suited to their presence (Orain et al., 2013). More recent G/I cycles show the expected patterns of opposition between interglacial and glacial climatic conditions, although the contrast in reconstructed climate between glacial and interglacial stages is less than expected. The lowest reconstructed glacial MTCO values fall during MIS 6–8 (Fig. 7).

4.3.3. The Late Pleistocene (LP — 0.125–0.01 Ma, Tarantian) and the persistence of drought

Several pollen records capture the LP in Italy (e.g. Mullenders et al., 1996; Follieri et al., 1998; Allen et al., 1999; Magri, 1999; Magri and Sadori, 1999; Allen and Huntley, 2000; Kent et al., 2002; Ravazzi, 2002; Brauer et al., 2007b; Allen and Huntley, 2009; Pini et al., 2009a, b) and demonstrate the increasing extent, duration and recurrence of drought through the regular expansion of steppe/semi-desert over large areas in Italy since MIS 11. The LP interglacial/glacial cycle was expressed as an alternation between deciduous forest and steppe both in Northern and Southern Italy (Fig. 4b). Mediterranean taxa were well represented during the warm interglacials but restricted during the last glacial.

In Northern Italy the proportion of conifers increased from the Po valley towards the Alps (Fig. 3a and b; e.g., Mullenders et al., 1996; Pini et al., 2009a,b). *Picea* and *Abies* occupied upper elevations and were mixed with deciduous *Quercus* at middle to lower altitudes during the last interglacial (Ravazzi, 2002). Herbaceous and steppic vegetation occupied northern valleys during glacials. Mediterranean taxa were rarely present in Northern Italy, even though they may be considered to be part of the regional vegetation.

In Southern Italy the last interglacial was marked by the development of deciduous *Quercus* forest at middle altitudes, with a strong increase in *Fagus* (Fig. 3b see after event H, Figs. 6b and 8; e.g. Watts et al., 1996; Follieri et al., 1998; Magri and Sadori, 1999; Watts et al.,

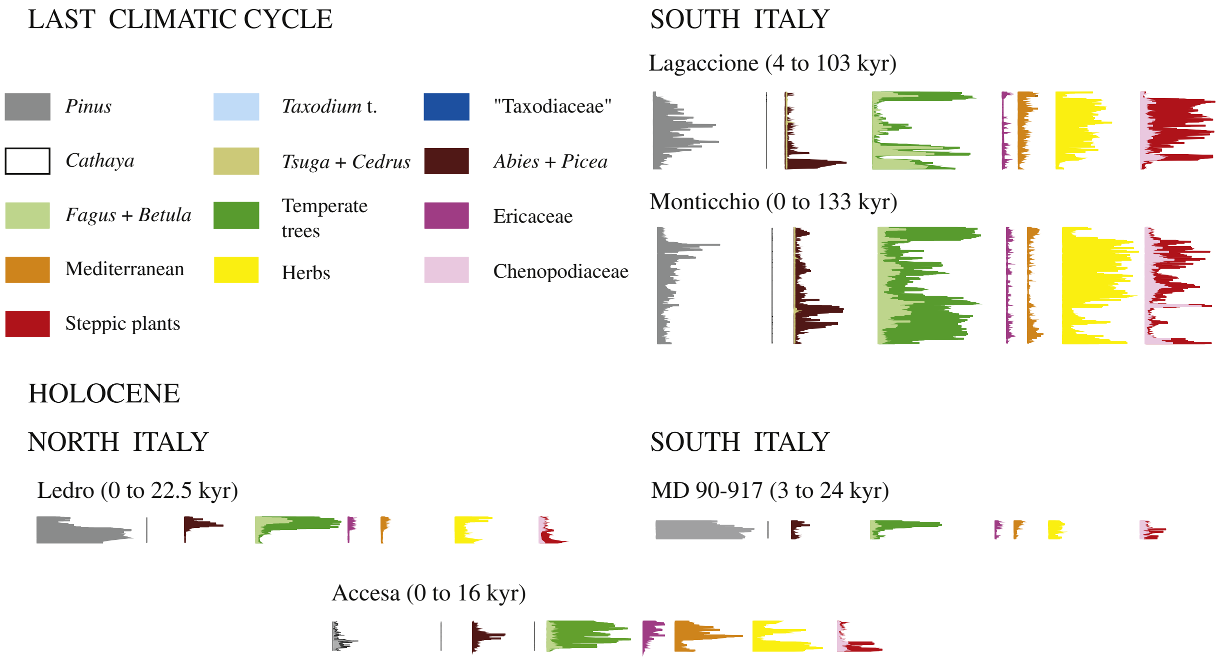

Fig. 8. Representative vegetation changes during the last climate cycle in Northern and Southern Italy.

2000; Allen and Huntley, 2000; Allen et al., 2002; Brauer et al., 2007a,b). *Abies* and *Fagus* both increased at higher altitudes in the Apennines, while at low altitudes Mediterranean communities expanded. Herbs and steppic taxa were probably restricted to the coast. Chenopodiaceae increased in importance within the open vegetation assemblages, especially during glacials, probably expanding in an edaphic fringe near the coast and over the land exposed by sea level decreases (Fig. 4b; e.g. Follieri et al., 1998; Allen et al., 1999; Magri and Sadori, 1999; Allen and Huntley, 2000; Brauer et al., 2007b; Allen and Huntley, 2009). Mediterranean forest was established and remained stable at middle altitude, especially south of 43°N. During MIS 3, peaks in abundance of steppic elements regularly indicated changes in vegetation associated with arid intervals (Allen et al., 1999; Fletcher et al., 2010) recognised from the western Mediterranean and concurrent with North Atlantic Heinrich Events observed in the western Mediterranean (e.g. Combourieu Nebout et al., 2002; Sánchez Gòni et al., 2002). This clearly indicates the ability of vegetation in the central Mediterranean to respond quickly to abrupt climate events.

Pollen-based climate reconstructions for Southern Italian sites show that MTCO during marine isotope sub-Stage 5e was nearly as warm as during the EP interglacials (Fig. 7). Nevertheless, annual precipitation remained low compared to the earlier interglacials. During the glacial stage, both temperature and precipitation values were very low, corresponding to the lowest values obtained in the box plot record (Fig. 7). This was probably linked to recurrent Mediterranean cooling, along with increased aridity induced by the global climate effects of Heinrich Event discharges in the North Atlantic (e.g. Combourieu-Nebout et al., 2002; Sánchez Gòni et al., 2002).

4.3.4. The Last deglaciation and Holocene: the installation of the Mediterranean climate seasonality and human pressure on Mediterranean environments

The last deglaciation and the Holocene in Italy are well described by pollen records. These records show the step-wise development of deciduous *Quercus* forests in Northern Italy (e.g. Joannin et al., 2013, 2014) and of its partial replacement by Mediterranean mixed forests in Southern Italy (e.g. Grüger, 1975, 1977; Rossignol-Strick and Planchais, 1989; Rossignol-Strick et al., 1992; Zonneveld, 1996; Combourieu-Nebout et al., 1998; Magri and Sadori, 1999; Sadori and Narcisi, 2001; Allen et al., 2002; Oldfield et al., 2003; Drescher-Schneider et al., 2007; Sadori et al., 2011; Di Rita and Magri, 2012; Joannin et al., 2012; Mercuri et al., 2012; Combourieu-Nebout et al., 2013; Di Rita et al., 2013; Mercuri et al., 2013; Sadori et al., 2013b and references therein) (Fig. 3a, b; Figs. 4b and 8). The early Holocene summer insolation maximum was marked by a humid event, expressed by increases in Po discharges into the Adriatic Sea and increases in high elevation forests (e.g. Combourieu-Nebout et al., 1998, 2013). After 4.2 kyr BP, pollen records show increasing dryness, expressed as an expansion of herbs and Mediterranean taxa. We see the onset of present-day precipitation seasonality and increases in human impacts expressed through deforestation and agriculture which can induce a possible bias in the pollen-based reconstructions for this period (e.g. Sadori et al., 2004; Di Rita and Magri, 2009; Sadori et al., 2011, 2013b; Combourieu-Nebout et al., 2013; Mercuri et al., 2013; Joannin et al., 2014). Pollen-based reconstructions show the modern Mediterranean climate regime establishing, with an inversion of winter and summer precipitation trends after 4.2 kyr BP, well illustrated by the regional record from marine core MD 90-917 (Fig. 7; Combourieu-Nebout et al., 2013). Italian precipitation regime changes and aridification fit the scenario of Mediterranean Holocene climatic changes outlined in Pons and Quézel (1985); Jalut et al. (2000, 2009). The combination of aridification and increasing seasonality have played a major role in driving major and all too recent vegetation changes in Italy and, along with human impacts, will influence Mediterranean ecosystems in the future.

5. Conclusion

Pollen records are used to show the step-wise changes in vegetation patterns on the Italian peninsula over the past 5 million years. These pollen records show the relationships between successive vegetation changes and climate variations (temperature and precipitation) in the Mediterranean region.

Based on vegetation composition, a north–south climate gradient has existed on the Italian peninsula since at least the Pliocene. After a warm and humid Pliocene, the Early Pleistocene, characterised by the beginning of G/I cycles, experienced a progressive decline in subtropical taxa in the sequence: first *Taxodium*-type (~3–2.8 Ma); *Sequoia*-type (~2 Ma); and finally *Cathaya* (after 1.6 Ma). Steppic associations occurred cyclically, expanding during glacial stages. The first step-wise decreases in humidity and winter temperature occurred at around 2 Ma and 1.4–1.3 Ma.

During the Middle and Late Pleistocene, new vegetation communities assembled, marked by conifer forest expansion in the north and the expansion of deciduous *Quercus* forest, with *Fagus* and *Betula*, in the south. Herbaceous and steppic taxa also expanded over a large area, to a more pronounced extent during glacial stages. Further cooling occurred at 0.4–0.5 Ma, with decreasing precipitation and winter temperatures during glacials. Interglacials remained relatively humid.

Modern Mediterranean summer drought was established during the Holocene after 4.2 kyr BP, following humid early- to mid-Holocene climates, the humid character of which was more pronounced in summer.

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