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PIACENZIAN TO LATE PLEISTOCENE FLORA AND VEGETATION IN ITALY: A MOVING SKETCH

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ABSTRACT: The rich late Neogene and Quaternary stratigraphical record for the Mediterranean area is particularly useful for the reconstruction of palaeoenvironments and palaeoclimate changes. 66 Italian pollen sites (38 terrestrial and 28 marine) have been selected to cover the 3.60 - 0.0117 Ma time-interval. Pollen reveals evidence for the main changes in both flora composition and vegetation structure, tracing the imprint of increasingly cooler climates on Italian vegetation since the latest Pliocene. The role of both altitudinal gradients and physiographic reorganizations as well as of major taxa replacements and their extinctions-times is evaluated by the study of calibrated pollen records. The response of flora and vegetation to glacial/interglacial (G/I) cycles is especially well expressed from the beginning of the Pleistocene, and across the Early-Middle Pleistocene climate transition when a major decrease in temperature, during both G/I phases, occurred. Alternations of *Artemisia* steppe and thermophilous forest illustrate the overall vegetation changes during G/I cycles. However, different patterns in the G/I vegetational cycle have been detected in both northern and southern pollen sites. The Late Pleistocene high-resolution pollen records document the vegetation response to rapid climate changes such as the Dansgaard-Oeschger "cycles" and Heinrich stadials, associated with millennial to sub-millennial events.

Keywords: Quaternary palynology, palaeoenvironment, palaeoclimate, 3.60 - 0.0117 Ma, Mediterranean.

1. INTRODUCTION

Since the Neogene, the Mediterranean area has undergone palaeogeographic and palaeoclimatic changes that have gone hand in hand with significant orogenic activity, which led to the uplift of several chains including the Apennines, in Italy (e.g. Carminati & Doglioni, 2012). The collision of the African and Eurasian plates reduced the Tethys domain from the early Miocene onwards. Active Atlantic-Mediterranean water exchanges, through the Betic and Rifean corridors, assured open marine conditions and circulation until ca 7.2 Ma, while the progressive restriction of the corridors accentuated the isolation of the Mediterranean Basin and supported, at a regional scale, the development of the so-called Messinian salinity crisis, from 5.97 Ma (e.g. Clauzon et al., 1996; Roveri et al., 2014). At 5.33 Ma open marine conditions were restored at the base of the Pliocene (e.g. Van Couvering et al., 2000). Significant geomorphic modifications linked to the progressive uplift of the Apennines promoted the formation of numerous eastward-progressing and younger, marine and continental basins, extending WSW of the orographic divide (e.g. Martini & Sagri, 1993; Santangelo et al., 2012; Cosentino et al., 2017). At a global scale, the maximum extension of

the Arctic ice promoted the onset of well-expressed glacial/interglacial (G/I) cycles from 2.6 Ma (Berger & Loutre, 1991; Lisiecki & Raymo, 2005; Sarnthein et al., 2009). The set of previous changes gave rise, at a regional scale, to important reorganization and restructuring of the Italian vegetation, also affecting vertebrate communities, as attested by significant turnover events (e.g. Masini & Sala, 2007; Palombo, 2007, 2014; Magri & Palombo, 2013; Strani et al., 2021), and rearrangement of terrestrial ecosystem structures and patterns. The high number of Italian Neogene and Quaternary deposits has encouraged advances in several areas of geo-stratigraphical research, including palynological analyses. Terrestrial vegetation can be reconstructed from the rich pollen records preserved in marine and continental successions, providing a detailed picture of the spatial and temporal modifications of flora, vegetation and climate (e.g. Bertini, 2003, 2010; Sadori et al., 2013; Combourieu-Nebout et al., 2015; Magri et al., 2017 and references therein). By integrating previous summaries, the present pollen-based review provides an overview of Pleistocene Italian flora, vegetation, and climate as well as a coherent and comprehensive history of the Italian palaeoenvironments, according to a solid stratigraphic framework (Fig. 1; Tab. 1).



Fig. 1 - Location map of selected Piacenzian and Pleistocene marine and continental sites. See also Table 1 for the numbering of the sites and additional information. Heavy black dotted line traces the 42.5°N isocline.

Knowledge of past palaeoenvironments and climate context is highly important in a geological perspective and is crucial for correctly evaluating the present-day ecological and biogeographical patterns; appropriately applied, this knowledge can contribute to biodiversity conservation and landscape restoration.

2. PRESENT-DAY CLIMATE AND VEGETATION

Italy extends at mid-latitude (between 47°N and 35°N) into the Mediterranean Sea, between the Balkan and Hellenic peninsula to the east, the Iberian Peninsula to the west, North Africa to the south and continental Europe, from which it is separated by the Alps, to the north. Three major sectors are recognised (Figs. 1, 2): a continental sector (northern Italy), between the Alps to

the north and the conventional line connecting La Spezia with Rimini to the south (Fig. 1); a peninsular sector (central and southern Italy, Fig. 1), which stretches into the Mediterranean in a north-west-south-east direction; and an insular sector encompassing the two largest islands of the Mediterranean, namely Sardinia and Sicily. Its territory is largely occupied by hills (up to ca 42 %) followed by mountain (35%), and flat areas (23%). Its highest point stands at 4811 m (Monte Bianco, Aosta) while the lowest point lies at -3.44 m (Contane, Ferrara). The Italian climate includes, according to the Köppen climate classification, a humid temperate climate (Cfa / Cfb) to the north and a Mediterranean climate with a dry summer period (Csa) in the centre-south. A complex climatic gradient is very evident moving 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 marked temperature seasonality. The Italian flora comprises more than 7000 species (Pignatti, 1982) whose distribution is strongly connected to the complex topographic and climatic features of its territory. Plant biodiversity is very high, and endemism is widespread. The Italian vegetation has been well documented in a large number of publications (e.g. Tomaselli et al., 1973; Ozenda, 1975, 1994; Bonin, 1981; Pignatti, 1998; Quézel & Médail, 2003; Blasi, 2010). The European potential natural vegetation zones and the main physiognomic-ecological units for the Italian peninsula are summarised in Fig. 2 (modified from Pignatti, 2011).

3. MATERIALS AND METHODS

Several Italian marine and continental pollen records have been selected for the time interval from the Piacenzian to Upper Pleistocene. The geographical distribution of the pollen sites is shown in Fig. 1. For each site, the main stratigraphical and geological information is summarized in Tab. 1 (see also Bertini, 2003, 2010; Combourieu-Nebout et al., 2015; Magri et al., 2017, and references therein). The most significant pollen evidence for selected single sites is summarized in section 4.

3.1. Pollen records

The abundance of pollen records permits the detection of past environmental changes and allows the reconstruction of the history of the flora, vegetation and climate throughout the Pleistocene in Italy. The Piacen-

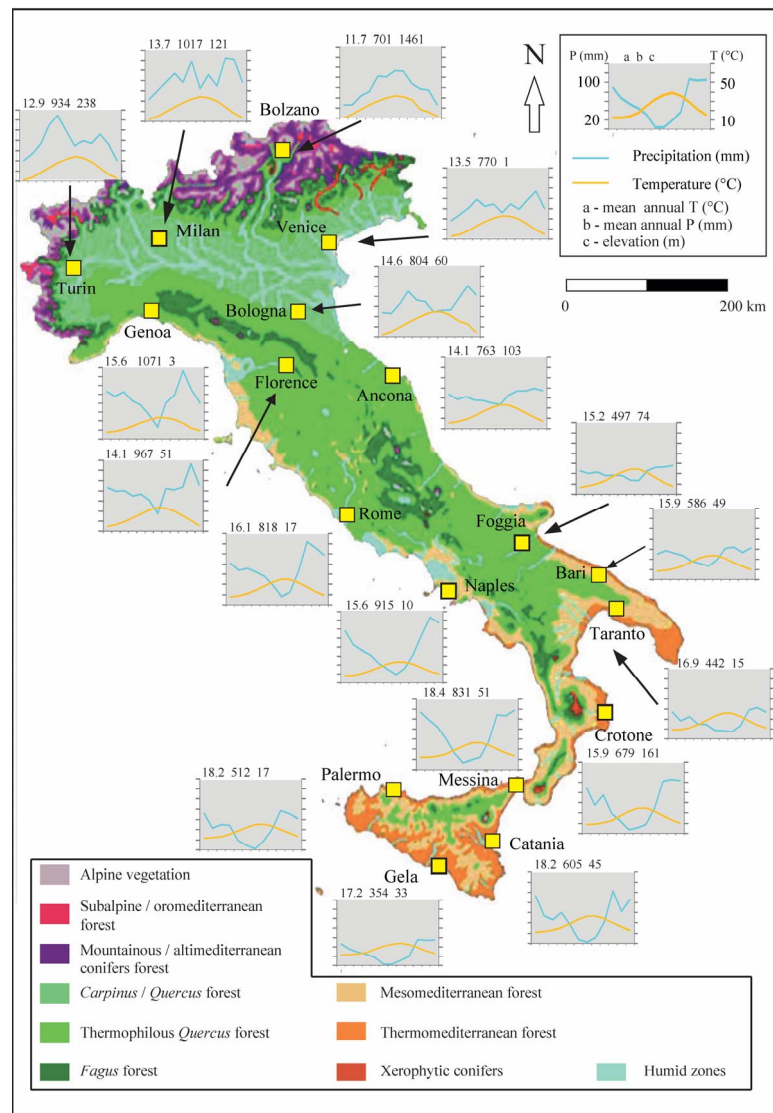


Fig. 2 - Present-day vegetation and climate in Italy (modified from Pignatti, 2011). A selection of climate (ombrothermic) diagrams (calculated using the NewLocClim software, Grieser et al., 2006) illustrates the modern north-south climate gradient.

zian is also part of this revision, particularly for documenting the last warm period preceding the installation of the G/l cycles at 2.6 Ma. The main palaeoenvironmental events, acting at both global and Mediterranean scales, are taken into account in the reconstructions. Each pollen site and its associated record have been assigned to either "Northern" or "Southern" Italy, relative to latitude 42.5°N, according to the isocline for current dry season duration (longer or shorter than 3 months) (Fig. 1 - heavy black dotted line). Pollen-inferred vegetation from available well calibrated records (Tab. 1 and Figs. 3-7) is used to illustrate the succession of climatic and environmental changes within six key stratigraphical intervals during the last 3.6 Myr: Piacenzian (3.6 - 2.58 Ma), Gelasian (2.58 - 1.80 Ma), Calabrian (1.80 - 0.774 Ma), Chibanian (0.774 - 0.129 Ma), and Late Pleistocene (0.129 - 0.0117 Ma). In the text

Number	Sites	Lat N	Long E	Altitude (m asl) Depth (m wd)	Locality	FLP/ L	M/Lg/ D	Time slice	P	G	Ca	Ch	LPS	References
1	Azzano Decimo	45°53'20"N	12°42'50"E	10 m asl	Fraili			0-215 ka						Pini et al., 2009a
2	Lefte	45°49'13"N	9°51'09"E	500 m asl	Lombardy			Olduvai (1.94-1.78 Ma) up to 0.87 Ma						Lona, 1959; Lona & Folleri, 1957; Lona & Bertoldi, 1972; Ravazzi, 1993, 2003; Ravazzi & Rossignol-Strick, 1994, 1995; Ravazzi & Moscarello, 1998; Muttoni et al., 2007; Ravazzi et al., 2009; Cremaschi & Ravazzi, 1995; Marinetto, 2009
3	Pianico-Selere	45°48'10"N	10°02'35"E	280-350 m asl	Lombardy			Controversial age: 1. Riss-Wurm Interglacial, 2. 779 ± 13 ka, 3. ca 400 ka (MIS 11)						Moscarello et al., 2000; Rossi, 2003; de Beauville et al., 2006; Pini et al., 2014; Pini et al., 2001; Brauer et al., 2007b, 2008; Roddica et al., 2009
4	Fornaci di Ranica	45°43'58"N	9°42'35"E	290-310 m asl	Lombardy			Late Calabrian						Ravazzi et al., 2005
5	Pinon	45°46'22"N	11°53'45"E	23 m asl	Veneto			27-138 ka						Pini et al., 2009b, 2010, 2022
6	Venice	45°27'44"N	12°18'35"E	2.3 m asl	Veneto			Quaternary						Mullenders et al., 1996; Kent et al., 2002; Canali et al., 2007; Massari et al., 2004
7	Pianengo	45°25'43"N	9°41'34"E	83 m asl	Lombardy			Late Matuyama to the early Brunhes						Muttoni et al., 2003
8	Castell'Arquato (Cumple)	44°51'13"N	9°52'14"E	224 m asl	Emilia-Romagna			Gelsian						Lona, 1962; Lona & Bertoldi, 1972; Mai, 1994; Marinetto et al., 2015
9	Monte Falcone-Rio Crevallese	44°51'13"N	9°52'14"E	N/A	Emilia-Romagna			Late Piacenzian						Monegatti et al., 1997, 2002; Marinetto et al., 2015
10	Sirone	44°50'N	9°58'E	140 m asl	Emilia-Romagna			Zanclean to Calabrian						Lona & Bertoldi, 1972; Becker-Platen et al., 1977; Bertolini-Marchetti et al., 1979; Bertini, 1994, 2001; Fauquette & Bertini, 2003; Mai, 1995; Marinetto et al., 2007
11	Villafanca RDB	44°48'46"N	7°29'38"E	380 m asl	Piedmont			Zanclean-Piacenzian						Fraccavilla et al., 1976; Lona & Bertoldi, 1972; Carraro et al., 1996; Marinetto & Vassio, 2010; Forno et al., 2015
12	Compiano	44°32'40"N	9°20'09"E	332 m asl	Emilia-Romagna			Early Pleistocene (?)						Bertoldi, 1985b
13	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; Vacini & Venezia, 1999
14	Po Valley, core 240S-13	44°18'35"N	12°E	N/A	Emilia-Romagna			Late Pleistocene to Holocene						Amorosi et al., 2004
15	Aulla-Vallesaura	44°14'13"N	9°47'57"E	547 m asl	Tuscany			Pliocene (Zanclean or Piacenzian?)						Bertoldi, 1988; Bertoldi & Castello, 1990
16	Sarzana	44°08'20"N	9°57'30"E	298 m asl	Liguria			Pliocene (Zanclean or Piacenzian?)						Bertoldi et al., 1994; Federici, 1973
17	Buca dell'Onice	44°07"N	10°20"E	570 m asl	Tuscany			MIS 13-10?						Bertini et al., 2022
18	Val Marecchia	43°58'39"N	12°18'08"E	300 m asl	Emilia-Romagna			Piacenzian-Gelsian						Rio et al., 1997
19	Lower Valdarno basin: San Quintino, Ponte a Elsa and other sections	43°41'15"N	10°53'55"E	60 m asl	Tuscany			Piacenzian-Gelsian						Valteri et al., 1990; Benvenuti et al., 2007; Bossio et al., 1993; Benvenuti & Degli Innocenti, 2001
20	Upper Valdarno basin: Santa Barbara, Rena Bianca and other composite sections	43°33'47"N	11°28'33"E	143 m asl	Tuscany			Piacenzian to Chibanian						Falheri, 1977; Albani et al., 1995; Bertini & Rotron, 1993; Bertini, 2002, 2003, 2010, 2013; Napoleone et al., 2003; Ghinassi et al., 2004; Mai, 1994; Faldini et al., 2013
21	Bagnoli, Val d'Elsa	43°26'39"N	11°03'13"E	200 m asl	Tuscany			upper late Pleistocene (L.G.I. YD)						Bertini et al., 2014; Ricci et al., 2015
22	Gubbio	43°22'40"N	12°36'E	348 m asl	Umbria			Pleistocene						Lona & Ricciardi, 1961a; Ricciardi, 1965; Fusco, 2010
23	Rapolano	43°15'N	11°33'56"E	310 m asl	Tuscany			Late Pleistocene						Bertini et al., 2014
24	Pietrafitta	43°01'17"N	12°12'36"E	318 m asl	Umbria			MIS 58 to MIS 28 according to Fusco (2010)						Ricciardi, 1961; Ricciardi in Ge.Mi.Na, 1962; Lona & Bertoldi, 1972; Fusco, 2010; Marinetto et al., 2014
25	Colle Curti - Cesi composite section	43°01'N	12°53'E	850, 820 m asl	Umbria			Upper Early Pleistocene to Lower Middle Pleistocene						Ficcarelli et al., 1997; Colliori et al., 1998; Bertini, 2000
26	Tiberino basin: Fosso Bianco, Cava Toppetti, Dunarobba and other composite sections	42°36'N	12°30'57"E	187 m asl	Umbria-Marche Apennines			Piacenzian-Gelsian						Pontini, 1997; Pontini & Bertini, 2000; Pontini et al., 2002; Marinetto et al., 2014; Basile, 1997
27	Leonessa	42°35'11"N	12°57'37"E	930 m asl	Lattium			MIS 62 (?) to MIS 28, according to Fusco (2010)						Ge. Mi.Na., 1962; Ricciardi, 1965
28	Lagaccione	42°57'N	1°08'E	355 m asl	Lattium			4-100 ka						Magri, 1999; Nasci & Anedda, 1998
29	Torrevecchia	42°22'67"N	14°22'59"E	20 m asl	Abruzzi			MIS 17?						Pieruccini et al., 2016
30	Lago di Vico	42°52'18"N	12°28'56"E	507 m asl	Lattium			0-50 ka						Leroy et al., 1996; Magri & Sadori, 1999
31	Madonna della Strada	42°20'53"N	13°15'16"E	720 m asl	Abruzzi			Calabrian						Magri et al., 2010
32	Rignano Flaminio	42°11'26"N	12°31'13"E	243 m asl	Lattium			MIS 13 (513 ± 3 ka-499 ± 3 ka)						Di Rita & Sorfili, 2019
33	Borghese and Mirano de' Marsi	42°08'56"N	13°15'59"E	720 m asl	Lattium			Early Pleistocene						Sadori et al., 2010; Charim et al., 2007, 2009
34	Valle di Castiglione	42°11'26"N	12°31'13"E	44 m asl	Lattium			0-250 ka						Falheri et al., 1988, 1989; Di Rita et al., 2013; Nasci et al., 1992
35	Valle Ricca	42°N	12°E	50 m asl	Lattium			Early Pleistocene						Urban et al., 1983; Ahas et al., 1990; Borzi et al., 1998; di Bella et al., 2005

TABLE 1A

Number	Sites	Lat N	Long E	Altitude (m asl) Depth (m wd)	Locality	F/P/L M/Lg/D	Time slice	P	G	Ca	Ch	LPs	References
36	Fontana Rannuccio	41°45'33"N	13°06'13"E	235 m asl	Lafium		Calabrian						Corrado & Magri, 2011
37	Core IN 68-9	41°47'5"N	17°54'5"E	609 m wd	south Adriatic Sea		Last deglaciation and Holocene						Zonneveld, 1996
38	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
39	La Pineda-Isernia	41°37'06"N	14°13'34"E	451 m asl	Molise		870 to 520 ka						Lebreton, 2002; van Oortelo & Sevink, 1983; Cremaschi, 1983; Cremaschi & Perotto, 1988; Dell'Ala et al., 1983; von Koenigswald & Kolfschone, 1996; Bellomini et al., 1997
40	Carpino	41°31'48.37"N	13°28'56.29"E	97 m asl	Lafium		MIS 13						Margari et al., 2018; Manz et al., 2010
41	Core KET 82-16	41°31'N	17°59'E	1166 m wd	south Adriatic Sea		Last deglaciation and Holocene						Rosso Ermolli et al., 2012
42	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
43	Boiano	41°29'00"N	14°28'25"E	660 m asl	Molise		MIS 13 to MIS 9						Orain et al., 2013; Amato et al., 2010; Anzelli et al., 2011
44	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
45	Corvaro	41°12'36"N	13°13'55"E	805 m asl	Lafium		Late Pleistocene						Chiarrini et al., 2007
46	Satocula (Sant'Agata de' Goti)	41°06'14"N	14°30'10"E	200 m asl	Campania		late Early Pleistocene						Russo Ermolli et al., 2010b
47	Monticchio	40°56'N	15°35'E	681 m asl	Basilicata		0-132 ka						Watts et al., 1996, 2000; Allen & Huntley, 2000, 2009; Brauer et al., 2000, 2007a; White et al., 2015
48	Core AD 91-17	40°52'17"N	18°38'15"E	845 m wd	south Adriatic Sea		Latest Pleistocene and Holocene						Sangiorgi et al., 2003; Giunta et al., 2003
49	Acerno	40°49'50"N	15°02'44"E	650 m asl	Campania		MIS 14 to MIS 12						Russo Ermolli, 2000; Munno et al., 2001; Petrosino et al., 2014a
50	Salerno core CI 06	40°28'22"N	14°42'24"E	292 m asl	South Tyrrhenian Sea		0-30 ka						Russo Ermolli & Di Pasquale, 2002; Di Donato et al., 2008; Buscheri et al., 2002
51	Montalbano Jonico	40°17'N	16°34'E	226 m asl	Basilicata		MIS 37 to MIS 16						Joannin et al., 2008; Bertini et al., 2015; Toti & Bertini, 2018; Vonnade et al., 2019
52	Vallo di Diano	40°16'17"N	15°37'06"E	450 m asl	Campania		650 to ca 450 Ka (MIS 16 to 13)						Russo Ermolli, 1994; Russo Ermolli et al., 1995; Russo Ermolli & Chedadi, 1997; Karner et al., 1999
53	Sant'Arcangelo	40°15'31"N	16°16'30"E	236 m asl	Basilicata		Jaramillo to Brunhes						Sabato et al., 2005
54	Camera	40°02'33"N	15°22'30"E	300 m asl	Campania		Early Pleistocene						Baggioli et al., 1981; Brenac, 1984; Russo Ermolli, 1993; Suc & Popescu, 2005
55	Mercurio	39°58'07"N	16°02'04"E	300 m asl	Basilicata / Calabria		Middle Pleistocene (MIS13)						Lona and Ricciardi, 1961b; Petrosino et al., 2014b; Robustelli et al., 2014
56	Valle di Manche	39°05'35"N	16°55'14" E	205 m asl	Calabria		MIS 22 to MIS 18.3						Massari et al., 2002; Capraro et al., 2005, 2015, 2017, 2022
57	Semafaro and Vrica sections	39°N	16°42'E	50 m asl	Calabria		2.46 to 1.36 Ma Semafaro (2.46 to 2.11 Ma) and Vrica (2.2-1.36 Ma)						Combourieu-Nebout et al., 1990, 1993, 1995, 2000; Combourieu-Nebout & Vergnaud-Grazzini, 1991; Klotz et al., 2006
58	Santa Lucia	39°N	16°42'E	161 m asl	Calabria		Late Early Pleistocene						Joannin et al., 2007; Lourens et al., 1996b
59	core KET8003	38°49'N	14°29'E	1900 m wd	South Tyrrhenian Sea		Late Pleistocene and Holocene						Rossignol-Stick et al., 1989
60	Monte Singa	38°10'N	16°08'18"E	61 m asl	Calabria		Early Pleistocene (2.5-2.45 Ma)						Combourieu-Nebout et al., 2015
61	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
62	Le Castella	38°14'47"N	16°04'11"E	231 m slm	Calabria		Pleistocene						Bertoldi, 1977; Bertoldi et al., 1989; Ruffi & Rio, 1980; Rio, 1982
63	Capo Rossello composite section	37°17'47"N	13°29'24"E	77 m asl	Sicily		Pliocene to Early Pleistocene						Bertoldi, 1985a; Guerrero et al., 1984; Bertoldi et al., 1989; Cita & Gartner, 1973; Hilgen & Langereis, 1988; Caruso, 2004; Cita et al., 2008
64	Punta Piccola	37°16'47"N	13°38'24"E	9 m asl	Sicily		Zanclean to Piacenzian						Combourieu-Nebout et al., 2004; Brakma, 1978; Hilgen, 1987; Castradori et al., 1998
65	Monte San Giorgio	37°14'55"N	14°30'34"E	496 m asl	Sicily		1.23 to 1.095 Ma						Dubois, 2001
66	Core MD 01-2797	36°57'N	11°40'E	771 m wd	Sicula-Tunisian strait		Late Pleistocene and Holocene						Desprat et al., 2013

TABLE 1B

Tab. 1 - (A and B). List of the selected Piacenzian and Pleistocene sites with the main stratigraphical, geological and palynological references. Numbers on the left refer to the geographical location of sites as reported in Fig. 1. F/P/L: Fluvial-Peat-Lacustrine; M/Lg/D: Marine-Lagoonal-Deltaic; P: Piacenzian, G: Gelasian, Ca: Calabrian, Ch: Chibarian, LPs: Late Pleistocene. References including palynology are in bold; other references in italic. The heavy black dotted line in Table 1A traces the 42.5°N isocline.

“Taxodiaceae” is in quotation marks; many genera formerly assigned to Taxodiaceae are now grouped in subfamilies of Cupressaceae, for example Taxodioidae Endl. ex K. Koch (*Taxodium*, *Glyptostrobus*, and *Cryptomeria*) and Sequoioidae (Lueres.) Quinn (*Sequoia*, *Sequoiadendron*, and *Metasequoia*) whereas the genus *Sciadopitys* is now generally placed in Sciadopityaceae (Brunsfeld et al., 1994; Farjon, 1998, 2005). In the Italian pollen records, “Taxodiaceae” are mainly represented by *Sciadopitys*, *Taxodium* type (which includes *Taxodium* cf. *distichum* and *Glyptostrobus*) and *Sequoia* type (which includes *Sequoiadendron giganteum*, *Sequoia sempervirens*, *Metasequoia glyptostroboides*, *Cunninghamia* and *Cryptomeria*).

A sketchy reconstruction of vegetation distribution is proposed for the Piacenzian to Late Pleistocene, according to different transects from non-specific areas of high relief to coastal areas (Figs. 3 - 7). The arboreal plant cover is in accordance with AP (arboreal plants) / NAP (non-arboreal plants) percentages values in pollen diagrams. However, the density and distribution of vegetation are not based on accurate estimates, they only provide a snapshot of vegetation in various areas at different times. The distribution of main taxa is illustrated by informal “plant symbols” and is supplemented by the evidence from previous works integrating pollen and macroflora (Bertini & Martinetto, 2008, 2011; Combourieu-Nebout et al., 2015).

3.2. Chronology

Age models for the most recent time intervals are based on ¹⁴C dates, links to Greenland ice-core records and tephra dates. For the geologically older records K/Ar dates, biostratigraphy (foraminifers and nannofossils), tuning to oxygen isotope records from Mediterranean or Atlantic marine sediment cores and astronomical tuning were variously used (Tab. 1). The chronological framework for terrestrial sites was often provided by biochronology (mammal fauna and palaeomagnetism; e.g. Napoleone et al., 2003). It is undoubted that the chronological control of all published age models is quite critical, especially for the older sites (e.g. Sarzana and Compiano sites; Fig. 1, Tab. 1). It is not part of our review to discuss the individual age models, and in Tab. 1 all sites are noted whether they have a reliable chronology or not.

4. AN OVERVIEW OF THE ITALIAN POLLEN EVIDENCE

4.1. Piacenzian (3.6 - 2.58 Ma): the last subtropical forests (Fig. 3)

During the Piacenzian a transition from relatively warm to cooler climates starts to develop until the instauration of high-magnitude G/I oscillations during the Quaternary. Short-lived cooling episodes punctuated this interval reflecting a progressive decline of temperature. Just after glacial marine isotope stage M2, at ~ 3.3 Ma, during the last climate phase that was warmer than today, known as mid-Piacenzian Warm Period (mPWP; e.g., Dowsett et al., 2012; Haywood et al., 2013; De Schepper et al., 2013; De La Vega et al., 2020, 2021),

sea surface temperatures increased by up to ~3 °C (Haywood and Valdes 2004), and CO₂ concentrations reached values of 400 ppm (Pagani et al., 2009; Bartoli et al., 2011), similar to the modern anthropogenic values. The Italian pollen record is quite remarkable for these last 700 kyr of the Piacenzian but it lacks continuous data for the interval spanning the Zanclean-Piacenzian transition; this is the time when modern European climates begin to develop at ca 3.6 Ma (e.g. Zagwijn & Suc, 1984; Suc et al., 1995) in conjunction with a cooling event, and the Brunsumian-Reuverian transition (Zagwijn, 1960; North West European Stages-NWES, Cohen & Gibbard, 2022).

In central Italy, at Santa Barbara (Upper Valdarno intermountain basin) a rich and diverse vegetal assemblage (e.g. *Taxodium/Glyptostrobus* type, *Nyssa*, *Engelhardia*, *Itea*, *Symplocos*, *Cephalanthus*, *Myrica*, *Carya*, *Quercus*, *Carpinus*, *Ulmus*, *Zelkova*, Clethraceae, Cyrtaceae) is documented during the short-lived ‘warm blip’ centred at 3.0 Ma, after the MG2 and M2 cold culminations. A humid forest vegetation, typical of subtropical to warm-temperate climate, dominated swamps in a lacustrine system, up to about 2.8 Ma when a cooler forest, with *Picea* and *Fagus*, as main components, became widespread. Herbs including steppe taxa formed a very minor component (Napoleone et al., 2003; Bertini, 2010, 2013). The cooling occurred gradually, in agreement with isotopic records (e.g. Raymo et al., 1989) that show an increase in glacial intensity over several cycles, rather than an abrupt increase at 2.6 Ma. A permanent/temporary disappearance and/or the significant reduction of some taxa (e.g. Symplocaceae, *Myrica*, *Nyssa*, *Cephalanthus*, “Taxodiaceae”), points to a progressive floristic impoverishment in many sites of both central (e.g. Lower Valdarno: Valleri et al., 1990, Benvenuti et al., 2007; and Tiberino basin: Pontini & Bertini, 2000, Pontini et al., 2002, Martinetto et al., 2014) and northern (Villafranca: Francavilla et al., 1970, Lona & Bertoldi, 1972, Carraro et al., 1996; Stirone: Bertini, 2001; Val Marecchia: Rio et al., 1997; M. Falcone-Rio Crevalesse: Monegatti et al., 2002) Italy. The decrease in temperature, associated with the forthcoming onset of the North Hemisphere Glaciation, resulted in a gradual increase in relatively more resilient arboreal plants such as *Quercus* and *Carya*, which progressively replaced *Taxodium/Glyptostrobus* type and *Engelhardia* (Bertini, 2001; Fauquette & Bertini, 2003).

In southern Italy, the Piacenzian is only represented by rather short and discontinuous pollen records. At 3.31 Ma (close to the FAD, first appearance datum, of *Globorotalia bononiensis*) on the site of Bianco, a cool, humid climate (with decreased seasonality) has been reconstructed during a short-term forest phase dominated by the *Picea-Abies* group, while Mediterranean evergreen virtually disappeared and non-arboreal cover declined (Bertoldi et al., 1989). Between 3 and 2.92 Ma, Marine Isotope Stage (MIS) 108 to 104 (Combourieu-Nebout et al., 2004), at Punta Piccola, a well-diversified pollen flora suggests an altitudinal zonation of the vegetation and several climate fluctuations during precession cycles illustrated in laminites/carbonates couplets. Climate reconstructions from the high resolution pollen

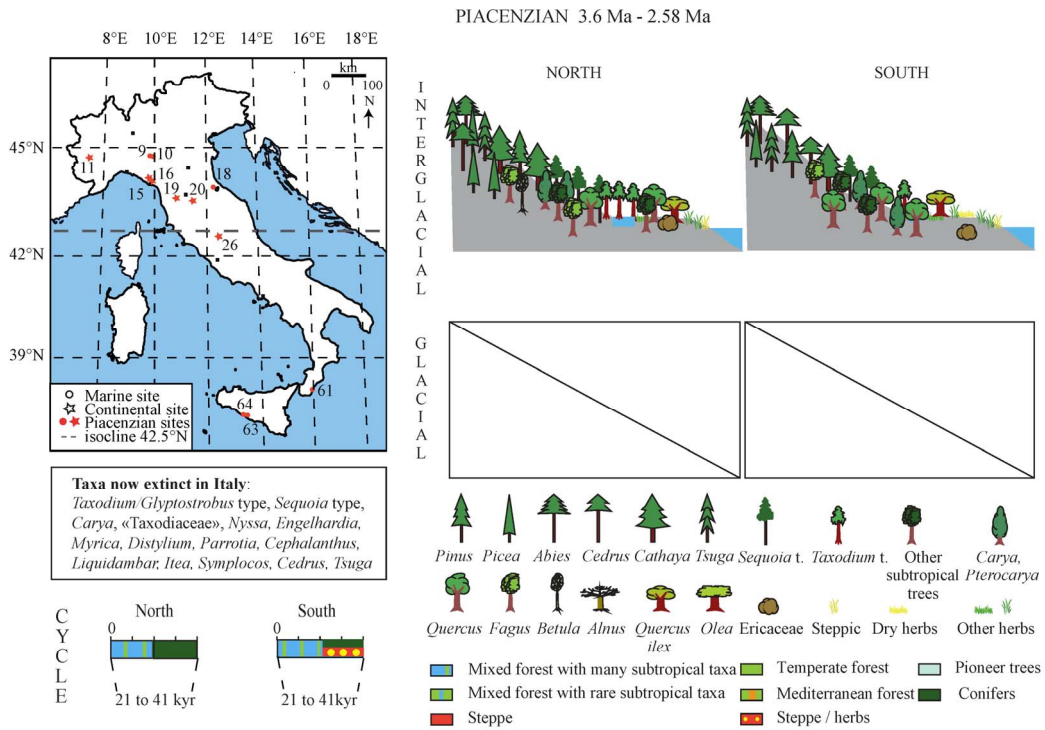


Fig. 3 - The Piacenzian. On the left (top to bottom): location map of the Piacenzian sites (for numbers, see also Tab. 1), list of main taxa now extinct in Italy and main vegetation groups during the 21 to 41 kyr cycles in North and South Italy. On the right the sketchy vegetation profiles for North and South Italy.

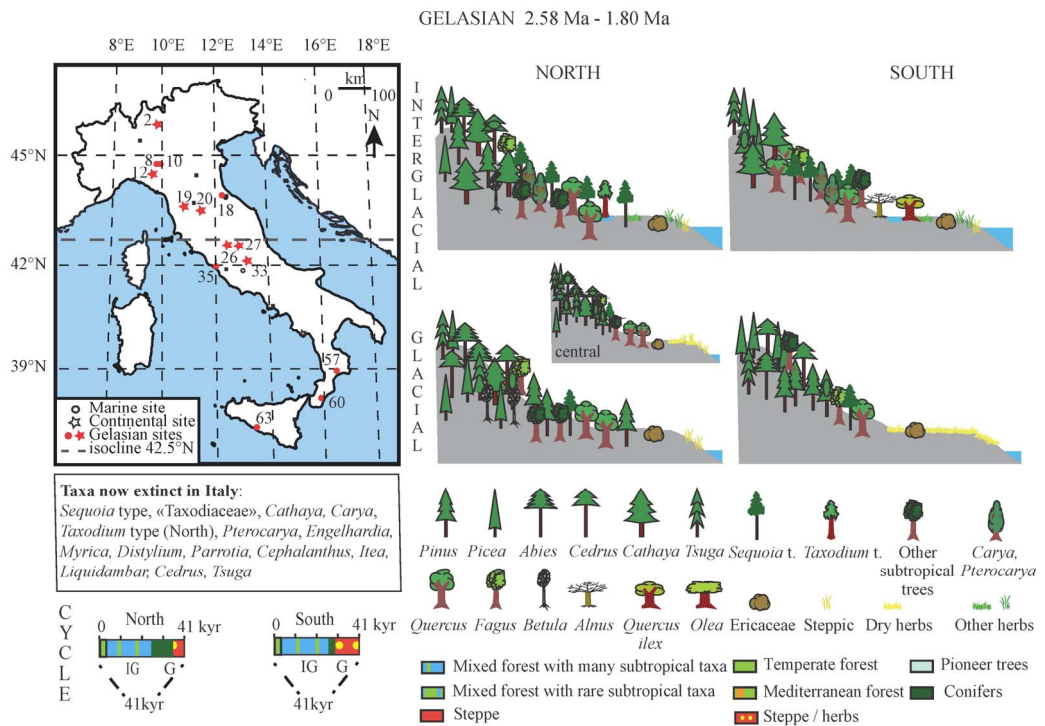


Fig. 4 - The Gelasian. On the left (top to bottom) location map of the Gelasian sites (for numbers, see also Tab. 1), list of main taxa now extinct in Italy and main vegetation groups during the 41 kyr cycles in North and South Italy. On the right the sketchy vegetation profiles for North and South Italy.

record indicate that high temperatures and relatively intense precipitation prevailed during the deposition of brown laminated sediments; in contrast, arid conditions are associated with light carbonates. Still in Sicily, just before 2.5 Ma, at the site of Capo Rossello, an expansion of Mediterranean formations alongside the presence of open vegetation (including steppe and psammophilous taxa), is documented during a general decrease in humidity and the establishment of drier conditions during the warm season (Guerrera et al., 1984; Bertoldi, 1985a; Bertoldi et al., 1989; Rio et al., 1990).

At Stirone in northern Italy, Climate Amplitude Method (CAM) reconstructions are only available for the last 200 ka of the Piacenzian (Fauquette & Bertini, 2003). They indicate alternating warm/cold phases with temperature and precipitation values very close to those associated with G/I cycles during the following Gelasian (see in 4.2.1).

4.2. The Pleistocene

4.2.1. Gelasian (2.58-1.80 Ma): the decline of subtropical trees and the onset of G/I cycles at the beginning of the Quaternary (Fig. 4)

The intensification of the Mediterranean outflow and the establishment of the Northern Hemisphere ice cap from ~3.0 Ma (e.g., Marlow et al., 2000; Lisiecki & Raymo, 2007) promoted cooler, more seasonal and in some areas dryer conditions in the Mediterranean area (Lourens et al., 1996, 2004). In the Italian pollen records, 40 kyr obliquity-forced G/I cycles are predominantly characterized by the contrast between forest vegetation and steppes (e.g. Bertini, 2010; Combourieu-Nebout et al., 2015 and references therein). This pattern is especially well attested in the Semaforo section (Crotone, Calabria; e.g. Combourieu-Nebout & Vergnaud-Grazzini, 1991; Combourieu-Nebout, 1993, 1995; Lourens et al., 1996) by both pollen and oxygen isotope data, from 2.46 Ma onwards. Nevertheless, in other southern Italian sites, Bertoldi et al. (1989), have highlighted a totally different (opposite) response of the vegetation to G/I cycles, still on the basis of the biostratigraphic and isotopic evidence. In the Gelasian (-Calabrian) Le Castella and Gela (Monte San Nicola) sites, glacials would have been marked by forests (humid conditions), and interglacials by open vegetation (dry conditions). A different scenario emerges from the Northern Italian pollen records (Castell'Arquato: Lona, 1962; Lona & Bertoldi, 1972; Stirone: Lona & Bertoldi, 1972; Bertolani Marchetti et al., 1979; Bertini, 2001; Val Marecchia: Rio et al., 1997; M. Falcone-Rio Crevallese: Monegatti et al., 2002). Here G/I cycles are apparently characterized by contrasts between the subtropical to warm temperate forest and higher-elevation coniferous forest (mainly *Picea*) without any significant extension in space and time of steppe-like vegetation (minimum values of humidity). Herb percentages usually remain low although *Artemisia*, a steppe taxon, can increase but not significantly and according to the specific geographical locations of the above mentioned sites. In the Upper Valdarno (central Italy), the location of the Piacenzian Santa Barbara section, we find evidence for the first substantial spread of herbs, which include a very

large component of *Artemisia* (Bertini, 1994, 2010), within a distinctive aeolian-dominated sandy deposit (Rena Bianca section), 35 m thick. On the other hand, in the Tiberino pollen record, which falls within the Piacenzian-Gelasian transition (Pontini, 1997; Pontini & Bertini, 2000; Pontini et al., 2002; Martinetto et al., 2014), the vegetation response to the G/I cycles is expressed by the competition between coniferous forests dominated by *Picea* and thermophilous arboreal taxa including "Taxodiaceae" (MIS 100 to MIS 82). During the Gelasian the flora suffers a very evident and progressive impoverishment. In northern Italian pollen sites, the first notable reduction in "Taxodiaceae" (with *Taxodium/Glyptostrobus* type as the main component) as well as an increase of *Cathaya* are evident from ca. 2.7 Ma (at Stirone). In the south, at Semaforo, where the record starts at 2.48 Ma, the first significant demise of "Taxodiaceae" forests (with *Sequoia* type as main component) is recorded from about 2.38 Ma whereas the spread of *Cathaya* occurs, especially from ca. 1.92 to 1.74 Ma (Combourieu-Nebout & Vergnaud-Grazzini, 1991; Combourieu-Nebout, 1993; Klotz et al., 2006; Suc et al., 2010).

CAM reconstructions from Stirone (northern Italy) (Fauquette & Bertini, 2003) show that during the Gelasian warm phases, the climate was similar to that of the Zanclean, with high MAT, MAP and available moisture. Annual temperatures were almost equal to the modern value (around 12-13 °C) during glacials whereas precipitation values were between 200 and 500 mm higher than today.

In central Italy, at Poggio Rosso (Upper Valdarno) dating to a G/I cycle just before the Gelasian/Calabrian boundary, the CAM method was used to calculate mean annual temperatures of around 12.5-14 °C and mean annual precipitation of around 800 mm, with a minimum of 400 mm during the glacial phase and 15/16-19 °C and 750 -1200 mm during the interglacial (Bertini et al., 2010). In southern Italy, at Semaforo, the Probability mutual Climatic Spheres (PCS) method reveals mean annual temperatures and winter temperatures from ca. 2.46 Ma to ca. 2.11 Ma (Klotz et al., 2006) that were at least 2.8 °C and 2.2 °C warmer, respectively, than today; it also reveals that annual precipitation during interglacials exceeded today's values by 500 mm. During glacials, temperatures were lower than the present-day, but precipitation was similar. A trend of reduction in annual and winter temperatures (more than 2.3 °C), as well as greater seasonality, were also highlighted over the course of the consecutive interglacials. A significant reduction of at least 1.6 °C in all temperature parameters is also evident during the glacials.

4.2.2. Calabrian (1.80-0.774 Ma): the demise of subtropical ecosystems from the Mediterranean and the beginning of the Early-Middle Pleistocene transition (Fig. 5)

From 1.4 Ma, over the course of the Calabrian, a major global climatic reorganization starts to affect ocean and atmospheric circulation, ice sheets and the distribution and evolution of biota, including the ancestors of modern humans (Head & Gibbard, 2015). During

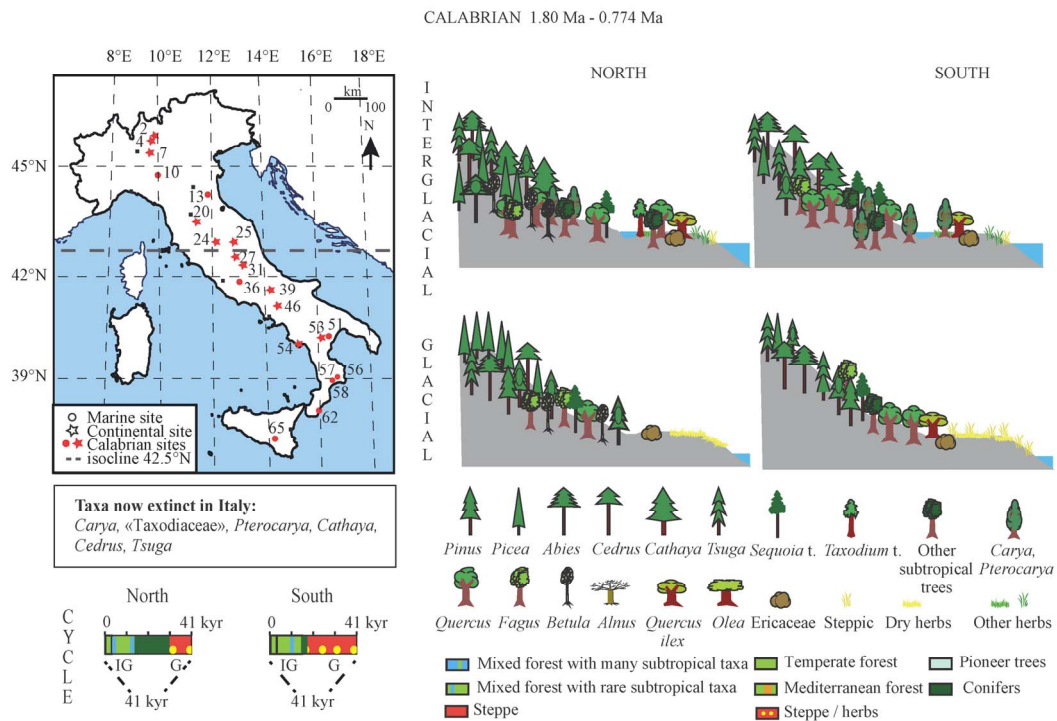


Fig. 5 - The Calabrian. On the left (top to bottom), location map of the Calabrian sites (for numbers, see also Tab. 1), list of main taxa now extinct in Italy and main vegetation groups during the 41 kyr cycles in North and South Italy. On the right the sketchy vegetation profiles for North and South Italy.

this phase, termed the Early-Middle Pleistocene transition (EMPT) which extends up until 0.4 Ma, low-amplitude 41-ka obliquity-driven climatic cycles of the earlier Pleistocene were progressively superseded by 100 kyr fluctuations in the later Pleistocene. A succession of severe glacial episodes (i.e. MIS 36, 24, 22) occurred, particularly in the northern hemisphere. A rich and detailed palynological record, often very well calibrated, is available for southern Italy in particular. In the Crotona basin (Calabria) the most significant pollen sites are: Vrica (ca. 2.2-1.36 Ma; e.g. Combourieu-Nebout et al., 1990), Santa Lucia (1.356-1.24 Ma, MIS 43-40; Joannin et al., 2007), and Valle di Manche (0.87-0.73 Ma, MIS 22-18.3; Capraro et al., 2005, 2015, 2017, 2022). Moreover, in Basilicata some 150 km north of the Crotona basin, the marine Montalbano Jonico (1.24-0.9 Ma and MIS 37-MIS 23; Joannin et al., 2008; 0.82-0.774 Ma and MIS 20-19 p.p.: Bertini et al., 2015; Toti, 2018; Toti & Bertini, 2018; Nomade et al., 2019;) and the neighbouring continental Sant’Arcangelo (San Lorenzo cycle: ca. 1.1-0.8 Ma; Sabato et al., 2005) successions were also studied. In Sicily, data for the 1.23-1.095 Ma interval are available from the Monte San Giorgio section (Caltagirone; Dubois, 2001). In the uppermost part of these sites, G/I fluctuations are well illustrated by open vegetation and forest alternations. The open vegetation assemblages include a large amount of steppe taxa, including *Artemisia* and *Ephedra*, and sometimes also thermophilous taxa, such as *Cistus* and *Phlomis fruticosa*. Warm temperate forest

assemblages include mainly deciduous taxa, such as *Quercus*, *Carya*, *Carpinus*, *Pterocarya*, *Ulmus* and *Zelkova* after the progressive reduction and disappearance of the most thermophilous taxa, e.g. “Taxodiaceae”. However, according to Capraro et al. (e.g. 2005, 2015), in the marine Valle di Manche succession, the glacial interval MIS 20 (as well MIS 18) is characterized by an alpine type forest (*Picea*, *Abies*, *Fagus*), whereas a wooded steppe landscape was established only later (i.e. at the Matuyama-Brunhes boundary), during the Early-Middle Pleistocene climatic transition, at the beginning of the deglaciation from MIS 20 to MIS 19. Another very different scenario is expressed by the pollen records from northern Italy (Lamone, Stirone, Lefte, Pianengo). Here, glacial phases are, as in the Gelasian, often marked by expansions of coniferous forests dominated by *Picea*, although interglacials do not exhibit major expansions of steppe vegetation but rather thermophilous forests as described in the classic schemes of Combourieu-Nebout (1993) and Fusco (2007). In the Lamone marine succession three distinct forest formations, i.e. mixed-deciduous forest (with *Quercus* dominating), Juglandaceae forest (with *Carya* dominating) and mountain coniferous forest (with *Picea* dominating) expanded between MIS 64-46 (Fusco, 2007, 2010). A complete vegetation cycle only developed when forest dynamics were interrupted by the spread of open vegetation, indicating a decrease in humidity (Fusco, 2007). Flora continued to be depleted as documented, in more detail, in

both Bertini (2010) and Magri et al. (2017) papers which also traces the abundance, reduction, and disappearance of certain key taxa (e.g. "Taxodiaceae", *Cathaya*, *Tsuga*, *Carya*, *Pterocarya*) in selected sites (e.g. Vrica, Saticula, Madonna della Strada, Colle Curti, Formaci di Ranica, Pianengo, and Piànico-Sèllere). The disappearance of the subtropical ecosystems and their replacement by deciduous forest taxa was identified in the Mediterranean area at ca. 1.2 Ma (Combourieu-Nebout & Vergnaud-Grazzini, 1991; Combourieu-Nebout, 1993, 1995) i.e. after the appearance of the large *Gephyrocapsa* a coccolith (at about 1.56 Ma), and the foraminifer *Hyalinea baltica* (at about 1.49 Ma).

Climate reconstructions, using the pollen data, indicate an enhanced cooling between 1.4 and 1.3 Ma, with winter temperatures decreasing at both interglacial maxima and glacial minima (Combourieu-Nebout et al., 2015). During the same interval, annual precipitation during both interglacial and glacial stages decreased marking a progressive increase in aridity, especially in glacial times.

4.2.3. The Chibanian (0.774-0.129 Ma): the development of temperate broadleaf and mixed forests in full EMPT (Fig. 6)

In the Mediterranean area, the progressive floristic impoverishment, according to climate gradients, continues during the upper portion of the Early-Middle Pleistocene climate transition, which also includes some severe glacial episodes (i.e. MIS 12 and 6). The 41 kyr G/l cycles were replaced by 100 kyr cycles, with lengthening of glacial stages (Tzedakis, 2005, 2007; Leroy, 2007; Tzedakis et al., 2012). However, from MIS 11 onwards, an abrupt increase in both interglacial temperatures and in reconstructed interglacial CO₂ values (Masson-Delmotte et al., 2010; Lang and Wolff, 2011; McClymont et al., 2013 and references therein) is revealed by marine, terrestrial and ice-core records during the so-called Mid-Brunhes Event (MBE).

Early Chibanian pollen records from southern sites attest to widespread alternations between *Artemisia* (plus *Ephedra*) steppes and temperate to warm-temperate deciduous forests, during the still dominant 41 kyr G/l cycles. At Montalbano Jonico, clear expansions of steppe taxa are documented, during both glaci-als and stadials from MIS 19 and the base of MIS 16 (e.g. Bertini et al., 2015; Toti, 2018; Toti & Bertini, 2018; Nomade et al., 2019). At Valle di Manche, MIS 18 is again (as well MIS 20) characterized by an alpine type forest (*Picea*, *Abies*, *Fagus*) according to Capraro et al. (2005, 2015). At Piànico Sèllere in northern Italy (Prealps, Lombardy) pollen data document a long interglacial phase within MIS 19, dated by the K/Ar age of a tephra level (779±13 ka; Pinti et al., 2001) and palaeomagnetic data (Scardia & Muttoni, 2009) within biogenic varved sediments. Here the onset of the interglacial is marked by the expansion of broad-leaved deciduous thermophilous forests with *Quercus*, *Ulmus*, *Tilia* and *Fraxinus*, followed by the expansion of *Abies* and *Carpinus betulus*. The interglacial succession is interrupted by a short phase characterized by the almost complete disappearance of thermophilous trees and the

expansion of conifer forests (*Picea*, *Pinus*, *Larix*) and herbaceous steppe communities (Ravazzi, 2003; Pini et al., 2014). A generalized drop in temperature in both steppe and forest phases is indicated by changes in the floristic assemblages; for example, *Hippophaë rhamnoides* expanded during the steppe phases ("cold steppes"), whereas thermophilous taxa, such as *Cistus* and *Phlomis fruticosa*, disappeared. The best calibrated pollen sites permitted the tracing of the chronological distribution of some taxa, notably of "Taxodiaceae", *Carya*, *Pterocarya* and *Tsuga*, including their LO (last occurrence) or LCO (last common occurrence). In northern Italy, *Tsuga* is virtually absent at Pianengo, from the late Early Pleistocene, and only sporadic pollen grains (0.2-0.8%) were recovered during the early Middle Pleistocene (Muttoni et al., 2003). In central Italy *Tsuga* declined during the lower part of the Brunhes (Bertini, 2000); here, both *Carya* and *Pterocarya* are absent. At Torre Mucchia (Abruzzi) *Tsuga* is still present (at >3%) during MIS 17 according to Pieruccini et al. (2016). At Rignano Flaminio (Latium) in a diatomite deposit attributed to MIS 13, *Tsuga* is absent whereas *Carya* and *Pterocarya* are sporadic (Di Rita & Sottili, 2019). At the archaeological site of Ceprano, just below the stratum including hominin remains, pollen analyses permitted a detailed picture of interglacial vegetation development during MIS 13 (Margari et al., 2018). Here *Tsuga* is absent and *Cedrus* sporadic, whereas *Carya* exhibits a continuous presence. Moving further south, *Tsuga* is present at Valle di Manche until MIS 18 (ca. 0.73 Ma) but with values that never exceed 5%; *Taxodium*, *Carya*, *Pterocarya*, *Liquidambar* and *Cedrus* are also present in low percentages; the LO of *Carya*, specifically, has been recorded between MIS 18 and the successive wooded steppe expansion. At Vallo di Diano, between 0.65-0.45 Ma (MIS 16 to 13) *Tsuga* is virtually absent (as well as at Isernia la Pineta; Lebreton, 2002) whereas *Carya* is constantly present, and *Pterocarya* is sporadic (Russo Ermolli, 1994). At Sessano, in contrast, *Tsuga*, along with *Cedrus*, *Zelkova* as well as a few grains of *Pterocarya* and *Taxodium* type have been recorded between ca. 0.58 and 0.44 Ma (MIS 15-12) (Russo Ermolli et al., 2010a). Both *Tsuga* and *Carya* are absent in the Mercure Basin (MIS 13; Petrosino et al., 2014b) as well as in the lacustrine succession of Acerno, where pollen analyses documented an interglacial/glacial cycle correlated with MIS 14 and 12 (Petrosino et al., 2014a). At Boiano, *Tsuga* is absent whereas *Carya* is present until the MIS 9 which, at present, represents its latest occurrence in Western Europe (Orain et al., 2013, 2015). According to previous data, *Tsuga* apparently disappeared from southern Italy later than in the north. However, in the southern assemblages its presence is usually subordinate, at least since the Messinian (Suc & Bes-sais, 1990; Bertini et al., 1998). Bertini (2000), on the one hand, related the disappearance of *Tsuga* to the shift in global aridity as well as the progressive decrease in temperature associated with the Middle Pleistocene shift from the 41 to 100 ka cyclicity in the Milankovitch orbital record (Bertini, 2000). Ravazzi et al. (2005), on the other hand, linked the *Tsuga* decline (at Fornaci di Ranica) to catastrophic fires triggered by summer

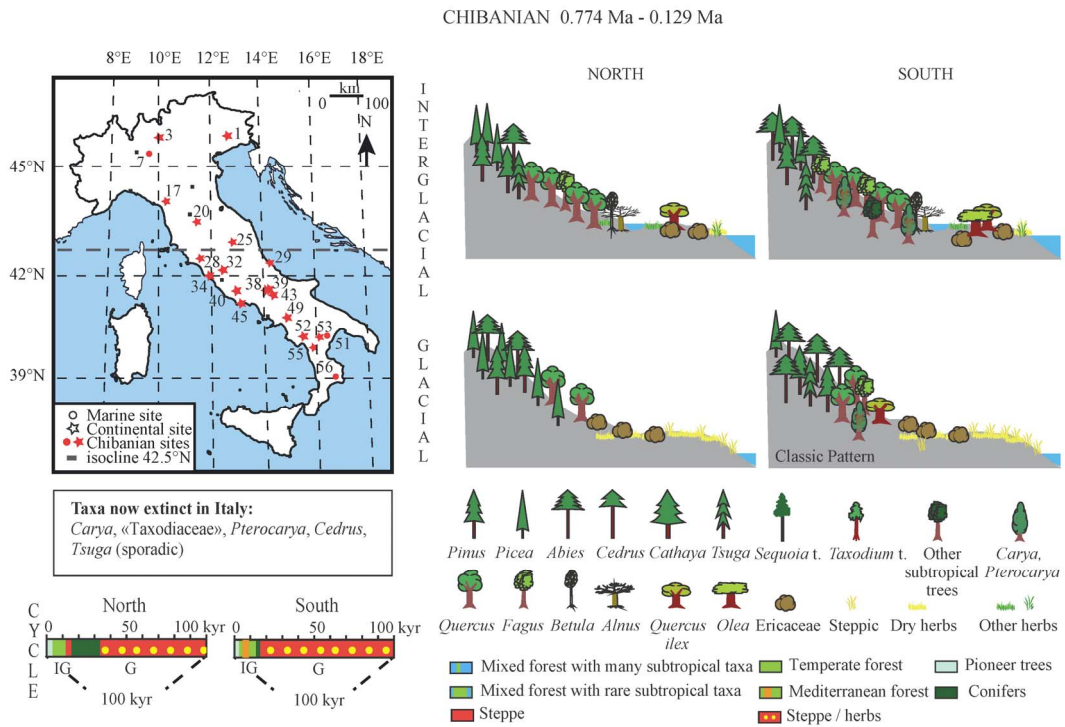


Fig. 6 - The Chibanian. On the left (top to bottom), location map of the Chibanian sites (for numbers, see also Tab. 1), list of main taxa now extinct in Italy and main vegetation groups during the 41 to 100 kyr cycles in North and South Italy. On the right the sketchy vegetation profiles for North and South Italy.

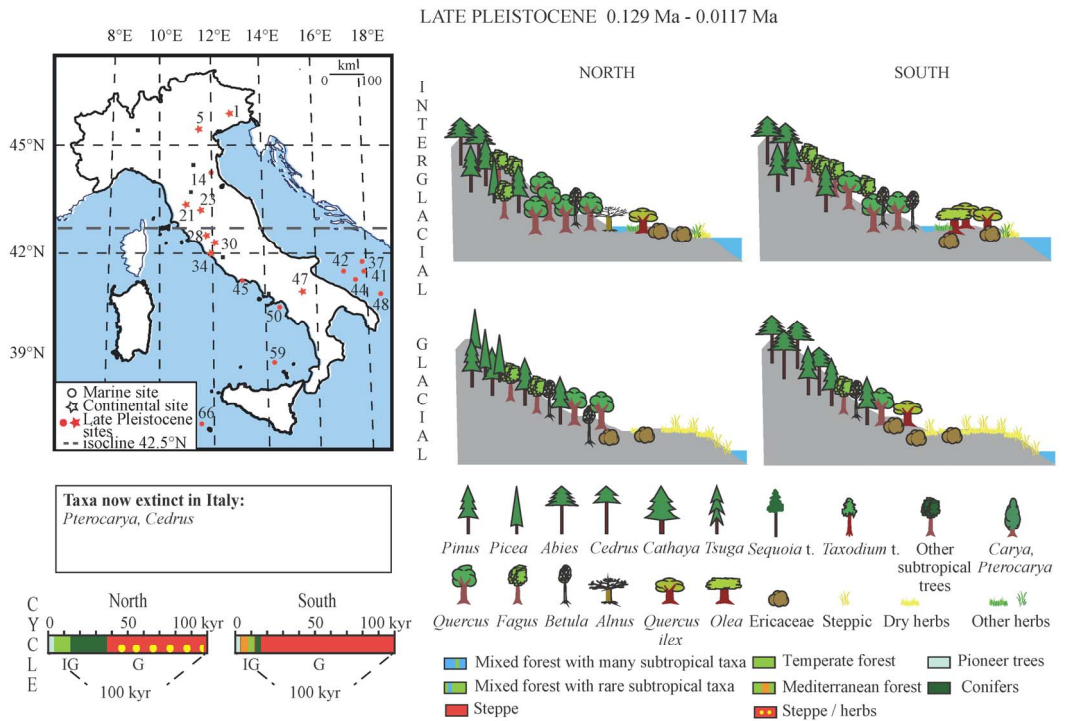


Fig. 7 - The Late Pleistocene. On the left (top to bottom), location map of the Late Pleistocene sites (for numbers, see also Tab. 1), list of main taxa now extinct in Italy and main vegetation groups during the 100 kyr cycles in North and South Italy. On the right the sketchy vegetation profiles for North and South Italy.

drought. However, both hypotheses confirm the global shift toward aridity of the Early Middle Pleistocene climate transition at ca. 0.9 Ma (Ruddiman et al., 1989; Raymo et al., 2004).

Rare climate data from pollen records provide evidence for increasing drought during increasingly and longer glacials, while the shorter interglacial began to become cooler (Combourieu-Nebout et al., 2015).

4.2.4. The Late Pleistocene (~0.129-0.0117 Ma): towards the present under the effects of the sub-Milankovitch-scale climate variability (Fig. 7)

The reconstruction of millennial and sub-millennial fluctuations during the last G/I cycles and the associated floristic and vegetational changes before the main anthropic interferences have mainly been based on the pollen records, especially lacustrine ones, from northern (Azzano Decimo and Fimon; Pini et al., 2009a,b; 2010, 2022; Badino et al., 2020a,b; Venice pro parte: Mullenanders et al., 1996, Massari et al., 2004, Canali et al., 2007), central (Valle di Castiglione: Follieri et al., 1988; Lagaccione: Magri, 1999; Vico: Leroy et al., 1996, Magri & Sadori, 1999) and southern (Laghi di Monticchio: e.g. Brauer et al., 2007a) Italy. However, a number of marine sedimentary successions were also retrieved from cores in the Mediterranean area (Figs. 1, 7; Tab. 1).

Recurrent forest and open vegetation developments as well as vegetation dynamics, together with repetitive changes in the vegetation structure, flora composition and plant biomass, are documented by the mainly continuous high resolution pollen records. Forest phases developed during the Eemian according to a dominant vegetation pattern and with the presence of a small number of taxa now extinct in Italy (e.g. *Pterocarya* and *Cedrus*; Magri et al., 2017). In fact, most of the changes in floral composition occurred in earlier times. In contrast, steppe phases, usually characterized by the same flora (e.g. *Artemisia*, Poaceae, Amaranthaceae), are generally less typical with respect to the interglacial ones.

At Azzano Decimo (north-eastern Italy), during the last 0.215 Ma the mixed temperate forests persisted during MIS 7a-7c, whereas they were replaced by the conifer forests after the local glacio-eustatic regression, during early MIS 6 (Pini et al., 2009a). The Azzano Decimo Eemian forest record, though incomplete, indicates the absence of Mediterranean evergreen trees, in accordance with the Lake Fimon sequence. Here, mixed oak forests characterized the first part of the Last Interglacial; these were then replaced by oceanic mixed forests that persisted for a further 7 ka until the end of the Eemian succession (Pini et al., 2010). At Azzano Decimo, repeated stadial-interstadials are evident since ca 0.115 Ma. A correlation has been proposed between major xerophyte peaks and IRD (Ice Rafted Debris) maxima during Heinrich events in deep-sea cores off-shore Iberia and in the North Atlantic. As a consequence, the interstadial phases, marked by *Picea* peaks, were interpreted as being linked to Dansgaard-Oeschger warm events (Pini et al., 2009a). The disappearance of broad-leaved thermophilous forests from the north-eastern plain of Italy was placed at the end of

the Early Würm with cool-temperate mixed forests persisting in the southern Alpine foothills up until the onset of Heinrich stadial 4 as documented in the Lake Fimon record (Pini et al., 2010). This high-resolution multiproxy record (including pollen and dust flux) from Lake Fimon (Pini et al., 2022) provided climate evidence of the MIS 3-2 interval with a focus on the dynamics of the Alpine Last Glacial Maximum and the early Alpine Lateglacial, including the expression of Heinrich stadial 2 and 1, on land. The onset of the Last Glacial Maximum at 27.3 ka was associated with a 4 °C drop in July temperatures, likely responsible for the onset of glacial build-up in the Southern Alpine piedmont (Pini et al., 2022).

In central Italy, the integrated pollen records from the crater lakes of Valle di Castiglione, Lagaccione and Lago di Vico document the history of vegetation covering the last two interglacials (last 0.3 Ma, from MIS 7e). The evidence for floral and vegetation changes allows the most important events e.g. Eemian, Saint Germain I and II and the Pleniglacial Interstadials (Lazio complex) (Follieri et al., 1998) to be recognized. At Valle di Castiglione, the Eemian is characterized by the large scale expansion of thermophilous and Mediterranean vegetation (Follieri et al., 1988, 1998). The Saint Germain I forest phase at both Valle di Castiglione and Lagaccione is expressed by the expansion of *Fagus* and *Abies*. The subsequent steppe period is characterized by the almost total absence of trees with the exception of *Pinus*. Due to a core gap, the Saint Germain II Forest phase, is not recorded at Valle di Castiglione, whereas it is well characterized at Lagaccione and Lago di Vico by the consistent spread of *Abies*. During the following Glacial and Lateglacial phases, *Artemisia*, Poaceae, and Amaranthaceae alternately dominated. These steppe and grassland formations were interrupted during the pleniglacial (roughly corresponding to MIS 3) by a number of slight expansions of tree cover, in particular of mesophilous and thermophilous taxa; this is termed the "Lazio complex" by Follieri et al. (1998) and probably corresponds to the Heinrich events found in oceanic cores. At Monticchio (southern Italy), varve chronology indicates the onset of the sedimentation at about 0.133 Ma (MIS 6 to present, Allen & Huntley, 2009 and references therein). Regional vegetation was dominated by herbs with steppe taxa as the main components during MIS 6, 4, and 2. During Melisay 1 only, the decrease of steppe taxa together with an increase in *Betula* probably suggest that, although cold, this period had greater moisture availability than other cold periods. Mesic woody taxa reached moderate abundance during a large number of MIS 3 interstadials, but dominated during the Saint Germain I and II and Eemian. Palaeoclimatic reconstructions as well as comparisons with the main European sites reveal significant complexity in the geographical and altitudinal environmental patterns (Allen & Huntley, 2000, 2009).

Pollen-based climate reconstructions for Southern Italian sites (Combourieu-Nebout et al., 2015) show that the Mean Temperature of the Coldest Month (MTCO) during marine isotope sub-Stage 5e was nearly as warm as during the Early Pleistocene interglacials. Nevertheless, annual precipitation remained low compared

to the earlier interglacials. During glacials, both temperature and precipitation values were very low. This is probably linked to recurrent Mediterranean cooling, along with increased aridity on the continent induced by the global climate effects of Heinrich event discharges in the North Atlantic, as is also attested by palynological studies on the Spanish and Portuguese margins (e.g. Combourieu-Nebout et al., 2002; Sánchez Góni et al., 2002).

5. DISCUSSION

The present overview of Italian Pleistocene pollen records includes a total of 66 selected pollen sites (with 12 also providing information for the Piacenzian) studied since 1950 (i.e. Lona, 1950) (Fig. 8). A large number of continental (including freshwater terrestrial carbonates such as travertine, calcareous tufas and flowstone) (38) and marine (28) sedimentary successions (sites) are presented, as well as a few sedimentary successions from depositional transitional environments (Tab. 1). Pollen records are especially abundant for the Calabrian and Chibanian. The majority of marine pollen records refer to the Gelasian when we exclude the offshore sites from the Late Pleistocene; most sites are located on the south. Continental records refer especially to Chibanian; again, southern sites are the most abundant. Different vegetational belts, at different altitudes between sea level and 850 m a.s.l. (Colfiorito basin: Colle Curti - Cesi composite section; Bertini, 2000) and between the latitudes 45 and 36 °N, have been documented.

5.1. Flora and vegetation

The Piacenzian and Pleistocene pollen floras include six main “formation classes”, informal biome/vegetation units (Bertini, 2001), i.e. Tropical forest (only some rare, scarce taxa, especially present in southern sites), Subtropical humid forest, Temperate broad-leaved deciduous forest, Sclerophyll forest, Mid- to high

-elevation forest, Open vegetation. In Tab. 2 these have been organized in 13 informal pollen groups. Their main components as well as their associated climatic and ecological features, are also summarized in Bertini & Martinetto (2008). Over the last 3.6 Ma, the composition of such “formation classes” has changed due to the gradual disappearance of some of their main components. The analysis of the stratigraphical distribution of taxa has highlighted frequent asynchronous disappearance events determined by the occurrence of climate gradients across the Mediterranean (e.g. Bertini, 2010; Combourieu-Nebout et al., 2015; Magri et al., 2017). Some taxa (e.g. *Engelhardia*, “Taxodiaceae”, *Cathaya*, *Tsuga*, *Carya*, *Cedrus*, *Liquidambar*, *Symplocos*, *Nyssa*, *Pterocarya*, *Embolanthera*, *Distylium*, *Parrotiaopsis*, *Parrotia persica*) attained the status of relict under particular microclimatic and (or) edaphic conditions before their definitive extinction under the effects of the progressive decrease of temperature and changes in the amount and distribution of precipitation. The floristic and vegetation changes, affecting the late Pliocene and Pleistocene Italian terrestrial ecosystems, in particular the first significant spread of steppe formation class close to 2.6 Ma and the disappearance of the “subtropical humid forest” formation class close to 1.2 Ma, contributed to the establishment of the present complex mosaic of different climates/biomes in the Mediterranean area (Tab. 3).

5.2. Pleistocene Glacial/Interglacial cycles: an overview of the main vegetation patterns at the Milankovitch-scale climate variability

Four (1-4) main vegetal patterns associated with G/I cycles have been identified on the basis of the available Italian Pleistocene pollen record (Bertini, 2010) (Fig. 9, Tab. 3).

Pattern 1 is expressed by fluctuations between open vegetation and thermophilous forests. It is usually considered as the most typical and representative pattern for the Mediterranean littoral (e.g. Combourieu-Nebout & Vergnaud-Grazzini, 1991; Suc et al., 1995a). During the first Quaternary cycles, it embraces four main subzones (a-d in Combourieu-Nebout, 1993): (a) mixed temperate forest (transitional phase following a glacial, with increasing temperatures but still dry conditions), (b) sub-tropical humid forest (interglacial with maximum temperature and precipitation), (c) high-altitude coniferous forest (transitional phase with cooler but still humid conditions), and finally (d) expansion of open vegetation, including steppe taxa (full glacial phase with cooler and dry conditions). Sometimes the first (a) or the last (d) one can be absent, as described by Combourieu-Nebout (1993) at Semaforo. During the late Pleistocene the pattern shows the following four main subzones: (a) pioneer forest, (b) mixed temperate forest (interglacial with maximum temperature and precipitation), (c) high-altitude coniferous forest (transitional phase with cooler but still humid conditions), and finally (d) expansion of open vegetation.

Pattern 2 is expressed by fluctuations between altitudinal coniferous forests and thermophilous forests; it was observed in many records from the Northern Ap-

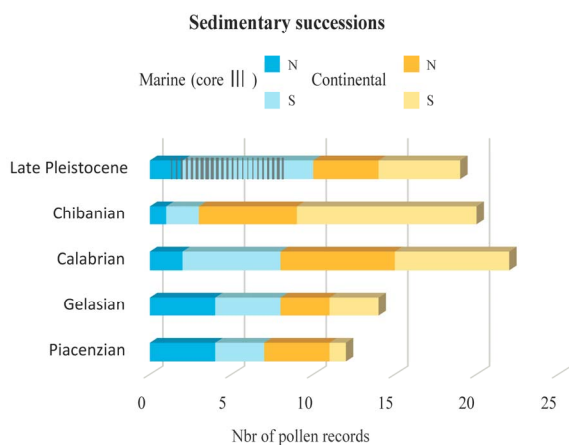













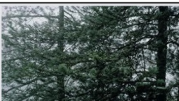































Fig. 8 - The selected Piacenzian and Pleistocene pollen records summarized according to chronology, geographical location (North and South) and type of sedimentary succession (marine vs terrestrial).

VEGETATION GROUPS	FLORAL ELEMENTS	MODERN CLIMATE AND ECOLOGY	VEGETATION IMAGES	SELECTED POLLEN (Optical microscope)
Tropical forest	<i>Nolina, Sindora, Prosopis, Croton, ...</i>	Megathermic taxa. Homogeneous climate regime with moist or dry conditions.		
Subtropical humid forest	<i>Taxodium/Glyptostrobus (1), Sciadopitys, Sequoia type (2), Engelhardia, Distylium, Nyssa, Myrica, Arecaceae, Clethraceae, Cyrillaceae, Sapotaceae</i>	Mega-Mesothermic trees. Low variations in temperature and high and homogenous precipitation throughout the year.		 
Temperate broad-leaved deciduous forest	<i>Quercus (1), Carya (2), Carpinus, Ulmus, Zelkova, Tilia (3), Acer, Pterocarya (4), Juglans, Buxus, Fraxinus, Liquidambar, Parrotia, Castanea, Celtis,...</i>	Mesothermic trees. Seasonal thermic regime (warm summers and cool to cold winters), adequate precipitation throughout the year.		   
Sclerophyll forest	<i>Olea (1), Quercus ilex type (2), Phillyrea, Pistacia, Cistus,...</i>	Xerophilous trees and shrubs. Strong seasonal contrast with wet winters and dry summers (Mediterranean climate).		 
<i>Cathaya + Pinus haploxyton</i> type	Single components	Mesothermic trees. Humid and warm to cool temperate conditions.		
<i>Pinus + Pinaceae saccatae</i> undeterminable	Single components	Not defined. Numerous species with different climate and ecologic requirements.		
<i>Tsuga (1) + Cedrus (2)</i>	Single components	Mesothermic to microthermic coniferous trees. Cool and moist conditions.		 
<i>Abies (1) and Picea (2) + Fagus (3) and Betula (4)</i>	Single components	Microthermic trees dominant in boreal and altitudinal forests (in the south). Cool summers and long cold winters.		   
Other arboreal	<i>Alnus (1), Salix (2), Platanus, Populus, indeterminate and indeterminable grains</i>	Trees without climate significance, often associated to local edaphic conditions (ripisylve).		 
Heath	Ericaceae	Shrubs. Cool and humid conditions.		 
Grassland, meadows, coastline open vegetation	Asteraceae (1) (<i>Artemisia</i> excluded), Poaceae (2) , Amaranthaceae (3) , Caryophyllaceae, Brassicaceae, Apiaceae,...	Cosmopolitan herbs and low shrubs. Dry to local edaphic (coastline) conditions.		  
Steppe and semidesert	<i>Artemisia (1), Ephedra (2)</i>	Grasses or low shrubs. Semi-arid, dry and cold/warm climate.		 
Other non arboreal taxa	Cannabaceae (1) , <i>Knautia (2)</i> , Convolvulaceae, Ranunculaceae (3) , Fabaceae (4) , ...	Cosmopolitan taxa. No climate significance.		   

Tab. 2 - Summary information on Piacenzian and Pleistocene pollen flora and vegetation. From the left: informal vegetation groups, main floristic taxa, their modern and climate and ecology, vegetation images, optical microscope images of selected fossil pollen grains (not to scale).

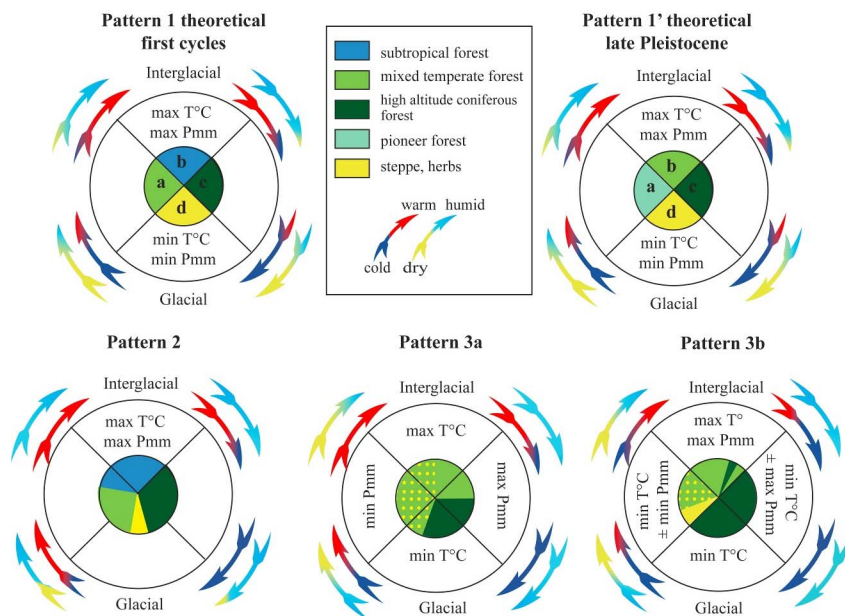


Fig. 9 - Glacial/Interglacial cycles: summary of vegetation and climate evidence. Pattern 1: Gelasian-Calabrian theoretical cycle. Pattern 1': end of Chibanian and Late Pleistocene theoretical cycle. Pattern 2: Northern Apennines (e.g. Lona & Bertoldi, 1972; Bertini, 2001). Pattern 3a (e.g. Bertoldi et al., 1989) and Pattern 3b (e.g. Capraro et al., 2005) both described for the southern Italian sites. See text for detail.

VEGETATION AND FLORA	NORTH		SOUTH	
	Glacial/ cool	Interglacial	Glacial	Interglacial
LATE PLEISTOCENE	Vegetation	Steppe	Deciduous to altitudinal coniferous forest	Steppe or semi desert
	Composition (main representatives)	<i>Artemisia</i> , <i>Poaceae</i> , <i>Amaranthaceae</i>	<i>Quercus</i> , <i>Fagus</i> , <i>Carpinus</i> , <i>Tilia</i>	<i>Artemisia</i>
	Climate	Cold and dry	Temperate and humid with colder temperature in altitude	Cold and dry
CHIBANIAN	Vegetation	Steppe (1) or coniferous forest (2)	Prevalent temperate forest	Steppe (1) or coniferous forest (2)
	Composition (main representatives)	<i>Artemisia</i> (1), <i>Picea</i> (2)	<i>Quercus</i> , <i>Fagus</i> , <i>Carpinus</i>	<i>Artemisia</i> (1), <i>Picea</i> (2)
	Climate	Cool/cold, wet or dry	Warm temperate and humid	Cool/cold, wet or dry
CALABRIAN	Vegetation	Steppe (1) or coniferous forest (2)	Mixed forest	Steppe (1) or coniferous forest (2)
	Composition (main representatives)	<i>Artemisia</i> (1), <i>Picea</i> (2)	<i>Quercus</i> , <i>Carya</i> , "Taxodiaceae"	<i>Artemisia</i> , <i>Ephedra</i> , other herbaceous
	Climate	Cool to cold, wet or dry	Warm and humid	cool to cold and relatively dry
GELASIAN	Vegetation	Steppe (1) or coniferous forest (2)	Subtropical to mixed forest	Steppe
	Composition (main representatives)	<i>Artemisia</i> (1), <i>Picea</i> (2)	<i>Quercus</i> , <i>Carya</i> , "Taxodiaceae"	<i>Artemisia</i> , <i>Ephedra</i> , herbaceous taxa
	Climate	Cool, wet or dry	Warm and humid	Cool and relatively dry
PIACENZIAN	Vegetation	Cool to temperate forest	Subtropical forest	Open vegetation with <i>Artemisia</i> (1) /altitudinal coniferous forest (2)
	Composition (main representatives)	<i>Picea</i> , <i>Fagus</i> , <i>Quercus</i> , <i>Carya</i>	<i>Taxodium</i> , <i>Nyssa</i> , <i>Symplocos</i> , <i>Engelhardia</i>	<i>Artemisia</i> , Asteraceae, <i>Amaranthaceae</i> , (1) <i>Picea</i> , <i>Abies</i> , <i>Fagus</i> , (2)
	Climate	Cool to temperate, moist	Subtropical with year-round humidity	Cool and dry or still rather humid

Tab. 3 - Main floristic, vegetal and climate evidence according to Glacial/Interglacial phases between the late Piacenzian and the Late Pleistocene.

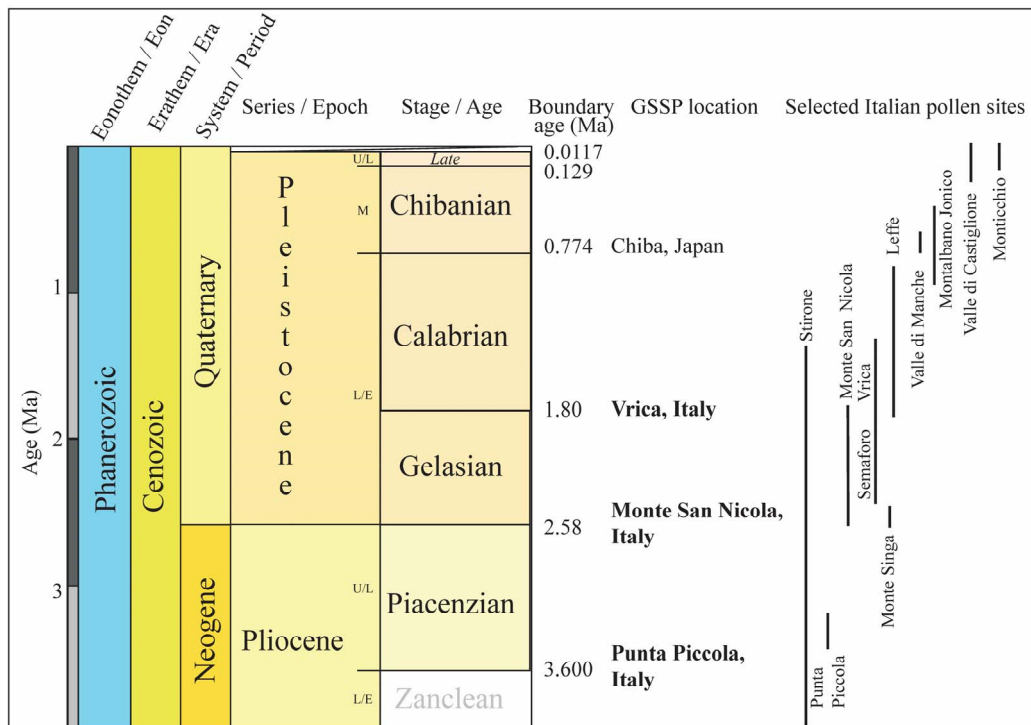


Fig. 10 - Piacenzian and Pleistocene GSSP. On the right, the stratigraphical distribution of selected pollen sites corresponding or relative to the GSSP locations. (Modified from Cohen et al., 2013; updated). The ICS International Chronostratigraphic Chart. Episodes 36, 199-204 (online version 2022/10).

enines (e.g. Stirone, Castell'Arquato, Monte Falcone-Rio Crevaiese, Val Marecchia). When comparing the theoretical cycle of Semaforo with those described for Stirone (Bertini, 2001) and for Lamone (Fusco, 2007), pattern 2 seems to correspond to pattern 1 when its subzone (d) is lacking or extremely reduced.

Patterns 3a and 3b are both expressed by fluctuations between thermophilous forest and open vegetation describing humid glacials and dry interglacials according to the pollen records from some southern sites (e.g. Bertoldi et al., 1989; Capraro et al., 2005), as already addressed in 4.2.1-4.2.3. According to this evidence, steppe (i.e. arid conditions) should not be connected to glacial maxima without independent supporting data. Consequently, the role of orbital signatures on long-term vegetation patterns in the Mediterranean needs to be attentively evaluated before proposing terrestrial chronologies through astronomical tuning of vegetational phases. An explanation for patterns 3a and 3b may lie in the interplay between local factors and the effects of obliquity related warm/humid-cold/dry "interglacial"- "glacial" cycles superimposed by precession related warm/dry-cold/humid cycles, as proposed by Klotz et al. (2006) and Joannin et al. (2007).

5.3. Pollen and Quaternary stratigraphy

Italy is very rich in late Neogene and Quaternary sites with many of them having a significant role in Chronostratigraphy. Fig. 10 shows the GSSP from 3.6 Ma to 0.0117 ka and the main coeval Italian pollen

sites; the locations of some of them correspond exactly with a type-locality (in bold in the figure, e.g. Vrica). Palynology is a powerful tool not only in the area of palaeoclimatic and palaeoenvironmental reconstructions but also with respect to the stratigraphic issues. However, this requires appropriate application of the stratigraphic principles in the interpretation of the significance of pollen zones. The fact that it is almost impossible to identify first appearance events, as well as to exactly trace the time-transgressive extinction of pollen taxa, complicates the use of the pollen content in describing biozones (except for assemblage and acme zones) or climatostratigraphic units, especially when they lack a solid chronostratigraphic framework. The eciostratigraphic events associated with the Pliocene and Pleistocene pollen zones need to be integrated with time-diagnostic (e.g. magnetostratigraphy and tephrostratigraphy) and/or other biological marine or continental evidence in order to render them chronologically significant. In the past, palynostratigraphic correlations were often established according to the idea that the same or similar pollen (assemblage) zones in different sites can identify synchronous pollen signals, e.g. those based on the disappearance of "Taxodiaceae" (i.e. Tiberian phase and boundary; Lona et al., 1969; Lona & Bertoldi, 1972), or those based on the Northern European pollen stratigraphy (e.g. Zagwijn, 1957, 1959, 1960, 1963, de Jong, 1988). Such interpretations, which assigned chronostratigraphic significance to eciostratigraphic events, produced a clear misunderstanding between biostrati-

graphic and chronostratigraphic principles and consequent mistakes in the establishment of correlations, also at regional scale, between different sites. For example, the “Tiberian boundary (and phase)” was identified in the lacustrine Pietrafitta succession with the sudden disappearance of *Taxodium* pollen type directly after an acme phase according to Lona et al. (1969) and Lona (1971). Previous authors also postulated the coincidence of the Tiberian boundary with the former Plio-Pleistocene boundary (1.8 Ma). Later, the Tiberian boundary was also recognized in the marine section of Stirone (Lona et al., 1969, Lona & Bertoldi, 1972) and at the marker bed, in the controversial marine section of Le Castella (Bertoldi, 1977). In the Upper Valdarno, a marked decrease in *Taxodium* type pollen, after an acme phase, was also observed close to 1.8 Ma (Napoleone et al., 2003). However, further evidence demonstrates: 1. recurrent sudden falls in the pollen percentages of “Taxodiaceae” throughout the Gelasian; and 2. the persistence of “Taxodiaceae” after 1.8 Ma in many Italian sites (e.g. Becker-Platen et al., 1977; Bertolani Marchetti et al., 1979; Combourieu-Nebout, 1993, 1995; Ravazzi & Rossignol-Strick, 1995; Fusco, 1996, 2007, 2010; Bertini, 2001). The “Taxodiaceae” stratigraphical range demonstrates that their disappearance cannot be considered as a synchronous and sudden event matching exactly the former Plio-Pleistocene boundary at 1.8 Ma. It is therefore impossible to use the Tiberian boundary to cross-correlate Italian successions. The establishment of wide-scale correlations is even more difficult, on this basis: see, for instance, the correlation of the Tiberian boundary with the Reuverian/Pretiglian transition of The Netherlands (Zagwijn, 1975) proposed by Lona (1971). The Reuverian/Pretiglian transition corresponds on the basis of chronostratigraphical evidence, to the Piacenzian/Gelasian boundary (at ca. 2.6 Ma) and not to the Gelasian/Calabrian transition (at 1.8 Ma). North-western European continental “stages” (e.g. Zagwijn, 1957, 1959, 1960, 1963; de Jong, 1988) summarized in Zagwijn & Hager (1987) and Zagwijn (1992) have represented a significant standard in continental Neogene stratigraphy. However, their validity, and their use by many authors, e.g. for long-distance chronostratigraphic correlations or to establish chronostratigraphical frameworks, have been criticized conceptually and methodologically (e.g. Bertini, 2003; Leroy, 2007). Substantial revisions were carried out by Drees (2005), Donders et al. (2007), and Kemna & Westerhoff (2007). All previous reflections do not reduce the stratigraphical potential of palynology for the study of the Late Neogene and Quaternary. On the contrary, palynology, when correctly applied, is a very powerful tool for stratigraphic and palaeoenvironmental reconstructions, all the more so because, in contrast to other fossils, palynomorphs, being contained in both marine and non-marine sediments, permit direct correlation of onshore and offshore successions (e.g. Combourieu-Nebout & Vergnaud-Grazzini, 1991; Capraro et al., 2005; Joannin et al., 2007; Joannin et al., 2008; Bertini et al., 2010).

5.4. Palaeoclimate change, palaeoenvironments and human migration

The great abundance of pollen records allows for a coherent spatial and temporal framework of the palaeoenvironmental scenarios during successive Pleistocene G/I cycles. This information is also fundamental to understanding the role of climate in the migration and subsequent colonization of the genus *Homo* (e.g. Dennell et al., 2011; Manzi et al., 2011; Messager et al., 2011 and references therein). Chronologically well-constrained pollen records have been included in databases and have often contributed to climate quantification too, contributing to the compilation of regional to continental-scale palaeogeographic maps and the identification of the most likely migration routes for hominin expansion and settlement (e.g. Muttoni et al., 2010, 2018; Moncel et al., 2018; Sánchez Goñi, 2022 and references therein). The beginning of the EMPT which follows several migration attempts can be taken to represent the first undisputed and well-dated phases of human colonization in Europe (e.g. Head & Gibbard, 2005; Head et al., 2008; Muttoni et al., 2010, 2018; O’Regan et al., 2011; Abbate and Sagri, 2012). It includes the last obliquity-forced climate cycles, when hominins spread from Africa to the Eurasian continent (e.g. Dennell et al., 2011 and references therein). According to some authors (e.g. Leroy et al., 2011), the Early Pleistocene interval could provide the latest best narrow windows of opportunity for hominins to disperse into Europe during the transition from glacial to interglacial periods, the full glacials being too cold for them and the interglacial to glacial transition too forested, although this has not yet been demonstrated.

What is more evident is the increasing imprint of Human populations after the Late Pleistocene and up to the present-day. The opportunity to better understand the behaviour of the natural vegetation and its adaptation to climate changes in earlier periods may help to develop strategies for sustainable conservation of vegetation in the future.

6. CONCLUSIONS

The overall pollen record allows us to trace the main vegetational features linked to the complex mosaic of different physiographic and climatic conditions of the Italian peninsula between ca 3.6 Ma and 0.117 ka i.e. preceding the main Holocene human impact on the landscape.

Pollen evidence is chronologically well constrained because it is found on sites that are well calibrated through the use of time-diagnostic tools e.g. magnetostratigraphy, micropalaeontology, biochronology, radiometric dating methods (U/Th, ^{14}C , ...) and varve chronology. This approach allows palynologists to address the main scientific stratigraphic and biological issues for the Quaternary. Particularly relevant is the documentation of the flora and vegetation response to both Milankovitch cycles and sub-millennial events. Moreover, this set of evidence provides indispensable information for a better comprehension of topics which become crucial during the Holocene, i.e. human versus natural climate

factors, location and extent of the glacial refugia for temperate and Mediterranean species, modern floristic richness and genetic diversity.

This summary illustrates the behaviour of Italian vegetation in the face of natural climatic changes through ancient times and in the absence of any human influence; the aim is to contribute to predictions regarding the future of Mediterranean vegetation under ongoing climate changes.

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