Title

Terrestrial plant microfossils in paleoenvironmental studies, pollen, microcharcoal and phytolith. Towards a comprehensive understanding of vegetation, fire and climate changes over the past one million years.

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Abstract

Earth has experienced large changes in global and regional climates over the past one million years. Understanding processes and feedbacks that control those past environmental changes is of great interest for better understanding the nature, direction and magnitude of current climate change, its effect on life, and on the physical, biological and chemical processes and ecosystem services important for human well-being. Microfossils from terrestrial plants, pollen, microcharcoal and phytolith preserved in terrestrial and marine sedimentary archives are particularly useful tools to document changes in vegetation, fire and land climate. They are well preserved in a variety of depositional environments and provide quantitative reconstructions of past land cover and climate. Those microfossil data are widely available from public archives, and their spatial coverage includes almost all regions on Earth, including both high and low latitudes and altitudes. Here, i) we review the laboratory procedures used to extract those microfossils from the sediment for microscopic observations and the qualitative and quantitative information they provide, ii) we highlight the importance of regional and global databases for large-scale syntheses of environmental changes, and iii)

we review the application of terrestrial plant microfossil records in paleoclimatology and paleoecology using key examples from specific regions and past periods.

1. Introduction

The Intergovernmental Panel on Climate Change (IPCC) was established in 1988 by the World Meteorological Organisation (WMO) and the United Nations Environment Programme (UNEP) to provide an assessment of the understanding of all aspects of any climate change over time, whether driven by natural variability or by human activity (IPCC, 2001). Thirty years later, the scientific consensus is that current climate change, an average global warming, is anthropogenically-driven, rapid and of large magnitude. Population's daily life is already or will be affected and the "climate action" is now targeted as one of the Sustainable Development Goals by the United Nations.

Over the last decades our perception of our environment radically changed. The curiosity of scientists observing and trying to understand past climate variability enabled contextualizing the current climate change within a long-term perspective. Over the geological times, the Earth experienced large changes in global and regional climates. Multi-millennial time scale changes in orbital and greenhouse gas forcings during the Quaternary, for example, have produced several glacial and interglacial periods of different length and magnitudes (Hays et al., 1976; Masson-Delmotte et al., 2010; Milankovitch, 1941; Past Interglacials Working Group of PAGES, 2016; Yin and Berger, 2012). The current interglacial period, the Holocene, is part of the 100-ky world established since the Middle Pleistocene transition (1.25-0.7 Ma) and characterized by large amplitude glacial-interglacial oscillations occurring with a periodicity of 100 kyr (Clark et al., 2006). The Earth climate also experienced decadal to millennial-scale variability (e.g. Fleitmann et al., 2009; Johnsen et al., 1992; Jouzel et al., 2007; Loulergue et al., 2008; McManus et al., 1999; Sánchez Goñi et al., 1999). Observing, modeling, and understanding processes and feedbacks that control those past environmental changes are of critical importance for a better understanding of the nature, direction and magnitude of current climate change, its effect on life, and on the physical, biological, and chemical processes and ecosystem services essential for human well-being.

Climate on Earth is conceptualized as a system where different spheres, i.e. the atmosphere, cryosphere, hydrosphere, lithosphere, biosphere, respond to external forcings, such as astronomical and anthropogenic forcing (Ruddiman, 2001). The anthroposphere is sometimes considered as a sphere of the climate system, and not as an external forcing (Cornell et al., 2012). The different spheres interact and depend on one another as an interconnected Earth system. Paleoclimate studies not only aim at reconstructing the response of the atmosphere, but also of all different spheres as well as their interactions and related feedback mechanisms modulating climate changes. Climate models are necessarily now designed to include interactive coupled components that extend to all of these aspects of the Earth system.

Vegetation, which is a major element of the biosphere, develops in response to climate and soil characteristics and plays an important role in the climate system. It is involved in different vital ecosystem services like nutrient and food production, mitigation of climate change, and soil and fresh water production and conservation (Faucon et al., 2017).

Terrestrial plants act as a carbon sink and can limit the warming of atmospheric and ocean temperature by removing carbon from the atmosphere during the photosynthesis. Through the evapotranspiration process, plants also increase water vapor locally in the atmosphere, enhancing precipitation and cloud cover, which reinforces cooling. Changes in land cover further modify the albedo and act as a positive (warming) or negative (cooling) radiative forcing. Vegetation is therefore an integral part of the biogeochemical- and -physical processes between the land surface and the atmosphere.

All ecosystems experience disturbances at different scales, and fire is one of the most widespread and severe disturbances in ecosystems globally, although it may maintain certain vegetation type, like savanna (Bond et al., 2005). It is commonly found in intermediate environments in terms of climate, vegetation and demography, in all vegetation types (Harrison et al., 2010). Fire dynamics today result from the complex interplay between climate (precipitation and temperature controlling fuel flammability), vegetation (fuel type and load), ignition (lightning and human induced) and human fire suppression (Harrison et al., 2010). Fires have impacts on climate by modifying the carbon cycle and atmospheric chemistry, clouds, and albedo through the release of greenhouse gases and aerosols (Bowman et al., 2009; Lavorel et al., 2007).

Terrestrial plant-derived microfossils, preserved in terrestrial and marine sediments, such as pollen, microcharcoal and phytolith, greatly contributed to the present knowledge of the Quaternary vegetation and fire dynamics, and land-climate changes. (Fig. 1). Pollen grains are part of the reproduction cycle of seed plants (angiosperms and gymnosperms); they are the male gametophyte, allowing for dissemination of the genetic material. Fossil pollen consists only of the external envelope, the so-called exine, which is made of sporopollenin that is very resistant to decay. Microscopic charcoal (microcharcoal) is a carbonaceous material formed by pyrolysis, i.e. during the combustion process of vegetal elements (Jones et al., 1997). Phytoliths are opaline silica particles that precipitate in and/or between the cells of living plant tissues forming particular morphotypes. They are deposited in sediments when the plants die or burn.

Pollen, microcharcoal and phytoliths are studied from both terrestrial and marine archives. Terrestrial and marine sequences of plant-derived microfossils may give different but often complementary information due to the source vegetation area varying from local (peat, pond, small lakes) to regional (large lakes, ocean) and transport processes. Deglacial and Holocene vegetation and fire changes were far more largely studied due to easier recovery of short cores and accessibility to recent sediments. Back in time, terrestrial sequences become rarer and rarer and often suffer from discontinuities, involving chronostratigraphic complications that often hamper reliable reconstruction of past vegetation and climate changes. For instance, fragmentary Pleistocene sedimentary sequences are common in regions that have experienced the repeated expansions and retreats of the large northern North hemisphere ice-sheets such as northern Europe and North America (de Beaulieu et al., 2013; Turner, 1998; Zagwijn, 1996), or glacier advances such as in New Guinea and New Zealand (Kershaw and van der Kaars, 2013), or in arid and semiarid environments of Africa or Australia (Kershaw and van der Kaars, 2013; Meadows and Chase, 2013). The Pleistocene marine sedimentary archives in which terrestrial microfossils are studied, benefit in contrast from a continuous sedimentation. They are mostly located on continental margin from the shelf to the deep-sea, usually on seamounts to be devoid of turbidites, recruiting terrestrial microfossils produced by the vegetation of the nearby continent (Heusser, 1998). Marine records provide information on vegetation and fire changes at regional-scale on a chronology, beyond radiocarbon dating, that derives from stable oxygen isotope measurements on foraminifera enabling a reliable comparison with oceanic records (Heusser, 1998; Sánchez Goñi et al., 2018).

Since the beginning of the 20th century, a large amount of palynological data was produced, revealing the major features of Pleistocene vegetation history and constituting the foundations of many basic concepts in Quaternary paleoecology. For instance, in Europe and North America, where there is a long tradition in palynological research, pollen studies have played an important role for the understanding of Holocene vegetation history (Birks and Berglund, 2018; Davis, 1984) and climate. They have yielded important contributions to diverse biogeographical and paleoecological topics such as continental-scale tree migrations

(Huntley and Birks, 1983; Huntley and Webb, 1989) and the biomes dynamics (e.g. Overpeck et al., 1992; Williams et al., 2004) after the end of the last Ice Age, the rates and magnitudes of species declines (e.g. Peglar, 1993) and vegetation response to interglacial climate changes (e.g. Turner and West, 1968; Zagwijn, 1994). Marine palynology greatly developed since Heusser's seminal works in the seventies (e.g. Heusser and Balsam, 1977; Heusser and Shackleton, 1979) bringing unique information on the phasing of the terrestrial and marine responses to orbital and millennial-scale climatic changes (Dupont, 2011; Sánchez Goñi et al., 2018).

Fossil microcharcoal preserved in terrestrial and lacustrine sediments has been counted classically during pollen analyses as a complementary proxy of vegetation since the eighties (Clark, 1982; Tolonen, 1986). They constitute a powerful approach for reconstructing paleofire histories over time older than few centuries provided by remote sensing and by dendrochronological and historical records (Whitlock and Larsen, 2001). During the last decade, a significant increase in the number of paleofire records and their regional or global syntheses has substantially improved our understanding of key drivers of fire under different climate conditions and of anthropogenic fire regime alteration (Daniau et al., 2012; Marlon et al., 2008; Vannière et al., 2011). Marine microcharcoal studies also developed relatively recently to address regional fire responses to orbital and millennial-scale climatic changes (Beaufort et al., 2003a; Daniau et al., 2009b; Daniau et al., 2013; Daniau et al., 2007). Paleofire science has also led to new perspectives on long-term fire ecology paradigms (Aleman et al., 2018a).

Phytoliths were firstly described at the beginning of the 19th century (Struve, 1835) and well-studied in plant tissues (e.g. Prat, 1932) before being used as paleoecological indicator in the sixties (Twiss et al., 1969). Interpretation of phytolith assemblages is far more complex than that of pollen assemblages due to imprecise correspondence between phytolith shapes and taxonomy. However, phytoliths, unlike pollen, present a high resistance to oxidation and therefore are well-preserved in arid environments. The increasing amount of modern reference collection from fresh terrestrial plants and soil assemblages allowed the development of archeological and paleoenvironmental research after the eighties (see Piperno, 2006). Today, fossil phytolith assemblages are much well-understood. Combined with a multi-proxy approach, they were recently used to discuss the evolution of grassland over the last million years in North America (Strömberg et al., 2013), the origin of the domestication of maize in Mexico (Piperno et al., 2009), or to examine late Quaternary C3 and C4 grasses vegetation history in East Africa (Montade et al., 2018). Phytolith have also been studied from deep-sea cores to document glacial-interglacial variations in aridity in the tropical Africa (Parmenter and Folger, 1974; Pokras and Mix, 1985).

Here we present a review of how terrestrial plant microfossils are extracted from different sedimentary archives during laboratory processing, how they are identified and quantified, and how they can inform us about past environmental changes at different spatial and temporal scales necessary for understanding the Earth system (Fig. 1) focusing on continents from northern and southern hemispheres: Europe, Africa, North and South America.

Figure 1

2. Microfossil concentrates and slide preparation

Sample processing consists of a series of physical and chemical laboratory treatments in order to obtain clean slides of microfossil concentrates, i.e. a sufficient amount of microfossils that are observable under the microscope. The different chemical treatments are determined according to the composition of the sediments, mostly of calcium carbonates, organic matter and siliceous materials. Hydrochloric acid (HCl) is used to remove calcium carbonates. A variety of chemical reagents are suited for organic matter removal, such as the potassium hydroxide (KOH), the acetolysis mixture consisting of acetic anhydride ($(CH_3CO)_2O$) and concentrated sulphuric acid (H_2SO_4), the hydrogen peroxide (H_2O_2), or a mixture of nitric acid (HNO_3) with potassium chlorate ($KClO_3$). Hydrofluoric acid (HF) is used to eliminate siliceous material, although use of this highly dangerous chemical can be substituted by a density separation process using much more benign sodium polytungstate.

2.1 Pollen and spores

Standard procedure for pollen extraction may include short boiling with potassium hydroxide (10 % KOH) for deflocculation and humic acid removal, cold diluted hydrochloric acid treatment (10 % HCl), to remove calcium carbonates ($CaCO_3$) and hydrofluoric acid (30 % to 70 % HF) treatment to retrieve siliceous material (Faegri and Iversen, 1964; Moore et al., 1991). Acetolysis, with concentrated sulphuric acid and acetic anhydride, can also be performed after KOH digestion in particular in cellulose-rich material preparation such as peat deposits. Successive HCl digestions at higher concentrations (25 %, 50 %) may be processed depending on the sample richness in $CaCO_3$. It is recommended to use cold HCl since hot reagent can cause corrosion of the pollen wall (Moore et al., 1991). Traditionally, cold HF treatment for a long time (at least 24 hours) or hot HF for a few minutes has then been performed, followed by another HCl treatment to remove colloidal SiO_2 and silicofluorides formed during the HF digestion. Alternatively, an inert heavy liquid such as sodium polytungstate solution can be used to remove siliceous material, rather than the highly dangerous (and expensive) HF. This process works by preparing a solution of a specific gravity that is sufficiently dense to support the pollen, but allows the denser siliceous material to float to the bottom, allowing the pollen fraction to then be simply decanted off. Through a series of washes and filtering using a 5 µm nylon mesh, it is also possible to reclaim the sodium polytungstate so that it can be reused. In addition, ultrasonic vibration can be used to disperse clays. A final sieving step using a 10 µm nylon mesh screen that is particularly useful for removal of fine particles in clay-rich samples can end the extraction procedure. The use of 5 µm filter is recommended for tropical pollen flora which typically includes grains of size below 10 µm.

To determine the sample pollen concentration, a tablet containing a known amount of exotic marker grains (commonly of *Lycopodium* spores) is added to the sample at the beginning of the preparation. The volumetric and weighting methods are other classical techniques used to establish pollen concentrations (Moore et al., 1991).

Pollen grains may be stained by adding drops of safranin or fuchsin to the residue with KOH during the final wash or directly into the mounting medium. Staining can help observation and identification under the microscope, although it is optional.

Residues obtained after pollen extraction are preferentially mounted in a mobile mounting medium such as glycerol or silicone oil since identification requires turning over the pollen grain for observation of the polar and equatorial views. Both mount types have side effects: glycerol makes the pollen swollen and slides with this media are quite short-lived while silicon oil requires an extra-step for dehydrating the residue before mounting (Andersen, 1960). If silicon oil does not influence pollen size, dehydrating agents such as ter-butanol (TBA) and the formerly used benzene do have an effect (Andersen, 1960; Meltsov et al., 2008). Glycerin jelly that does not allow pollen mobility is preferred for permanent slides such as modern pollen samples for reference collection, although like glycerol it has an influence on pollen size. Before mounting in glycerin jelly, the tube is placed upside down on a filter paper for a couple of hours or even a day to remove extra-water. In contrast to silicon oil, glycerol and glycerin jelly require slide sealing usually done with histolaque LMR, paraffin or nail polish. An advantage of glycerin jelly on normal slides is that because pollen mobility is limited, unknown grains found during the identification process can by recorded by the x-y co-ordinates on the microscope and reviewed later. The disadvantage of jelly in not allowing grains to be rotated for identification can also be somewhat overcome by applying a heated needle to the slide above the grain which temporarily heats and liquefies the jelly.

2.2 Microcharcoal

Charcoal is mostly composed of pure carbon formed at temperature between 200 and 600°C (Conedera et al., 2009). It is divided into two categories based on the size of the particles, the microscopic (length between >10 and <100 µm) and macroscopic (length >100 µm) charcoal particles (Whitlock and Larsen, 2001). It is relatively resistant to chemical decomposition (classified as inertite) (Habib et al., 1994; Hart et al., 1994; Quénéa et al., 2006). Microbial decomposition is minimal (Hockaday et al., 2006; Verardo, 1997) especially if charcoal burial occurs in an environment with high sedimentation rate. Microscopic charcoal particle is commonly counted in the same slides used for pollen analyses in transmitted light. In this case, concentrates of microcharcoal are obtained following the standard procedure described in the pollen section (2.1.1) (Faegri and Iversen, 1964). No ultrasonic baths are used in order to avoid charcoal-particle breakage (Tinner and Hu, 2003). Rhodes (1998) proposed the extraction of microcharcoal of the sediment samples using a dilute solution of hydrogen peroxide (6%) for 48 hours at 50°C to bleach the dark organic component, followed by sieving at 11µm and another bleaching step. Reflected light (or incident light) has been used also during pollen slide analyses (Doyen et al., 2013) to secure the identification of microcharcoal from uncharred organic matter, although polished thin sections are generally more suitable to the analyses using reflected light (Noël, 2001).

The protocol of Daniau et al. (2009b) combines chemical treatments to concentrate microcharcoal and polished slides technique allowing both the particle observations in transmitted and reflected light. It has been developed on marine samples (Daniau et al., 2009b) but has also been recently used for lake sediments (Inoue et al., 2018). It consists of concentrating microcharcoal particles by removing carbonates, silicates, pyrites, humic material, labil or less refractory organic matter (Clark, 1984; Winkler, 1985; Wolbach and Anders, 1989). This procedure bleaches organic matter and does not blacken unburned plant materials (Clark, 1984). The chemical treatment consists of successive chemical attacks by adding hydrochloric acid (HCl), then cold or hot nitric acid ($HNO_{3)}$ and hydrogen peroxide (H_2O_2) on approximately 0.2 g of dried bulk sediment. A hydrofluoric acid (HF) step can be used, followed by rinsing with HCl to remove colloidal SiO_2 and silicofluorides formed during the HF digestion, as in the pollen and spores protocol. A dilution of 0.1 is applied to the residue. The suspension is then filtered onto a membrane of 0.45 mm porosity. A portion of this membrane is mounted onto a slide before gentle polishing for observation under the microscope. The chemical treatment may be slightly modified, depending on the sample sediment composition.

Although this review focuses on microcharcoal, we briefly present laboratory analyses for macrocharcoal because many fire syntheses information were obtained from studies using both macro and microcharcoal records (see section 4.4 and fire discussion section). It is suggested however that the trends between macro and microcharcoal records display similar fire history patterns (Carcaillet et al., 2001). Macro-charcoal is extracted by using a KOH or sodium pyrophosphate solution to removes humic acid and dissagregates, followed by a dilute hydrogen peroxide (4-6% only) step and a wet sieving through a 125 µm sieve (Stevenson and Haberle, 2005).

2.3 Phytolith

Phytolith extraction procedure from soil or lacustrine sediments consists of multiple steps following Aleman et al. (2013b). The sediments are deflocculated using a 5 % weight solution of $NaPO_3$ heated at 70 °C, and shaked for twelve hours. Decarbonatation, using a 1N-solution of HCl at 70 °C during one hour on a hot plate, is performed prior to the organic matter reduction as this step is more efficient in a slightly acid and non-calcareous environment (Pearsall, 2000). This step is also crucial to disperse the mineral fraction and prevent secondary reactions (Madella et al., 1998). Lake sediments are generally rich in organic matter which is removed by using 33 % H_2O_2 (Kelly, 1990; Lentfer and Boyd, 1998) at 70°C to accelerate the reaction to properly obtain cleaned slides for easier identification and counting. Alternatively, a mixture of nitric acid (HNO_3) with potassium chlorate (at a ratio of 1:3) heated for two hours at 90°C using glass material on a hot plate can be used to accelerate the reaction (Strömberg, 2002; Strömberg et al., 2018).

For lateritic sediments, removal of oxidized iron using tri-sodium citrate and sodium dithionite is recommended (Kelly, 1990). Another deflocculation, using $NaPO_3$ at 70 °C (Lentfer and Boyd, 1998) shaken for 12 hours, then is required to remove clay efficiently since high clay concentration may affect data quality (Madella et al., 1998). Clay is removed by gravity sedimentation using ‘low-speed’ centrifugation to speed up the processing. Distilled water is added to the residue to a height of 7 cm and centrifuged for 1 min 30 s at 2000 rpm (Stokes' law for particles < 2 µm, calculated for a Sigma Aldrich 3–16 centrifuge with an RCF.g of 769 at 2000 rpm). The step is repeated until the float is clear. Before performing densimetric separation of phytoliths, the residue is dried using ethanol to avert dilution of the dense liquor by the water contained in the residue.

The density of the heavy liquid is crucial for the densimetric separation step to prevent bias regarding phytolith selection, densities of which range from 1.5 to 2.3. Different heavy liquids can be used: $ZnBr_2$/HCl solution adjusted to a relative density of 2.3–2.35 (Kelly, 1990) or, better, sodium polytungstate (Na 6[H2W12O40]) that is a non-toxic of solution. The density 2.3 of 1 L of dense liquor is obtained by mixing 1662 g of sodium polytungstate powder with 637 ml of distilled water. The residue and the dense liquor are mixed and then centrifuged for two minutes at 3000 rpm. Disposable transfer pipets are used to suck the fine white layer floating on the dense liquor and transfer it to a 5 µm PTFE filter (Kelly, 1990) mounted on a vacuum glass filtration holder. The dense liquor is recycled to reduce the costs of the extraction procedure and the environmental pollution. The floating residue on the filter is rinsed with HCl (1 N) if $ZnBr_2$ is used, and distilled water; otherwise the supernatant is only washed with distilled water. The phytoliths are transferred to a vial and an exotic marker is added (a lycopodium tablet or silica microspheres (Aleman et al., 2013b)). The samples are decanted for twelve hours and then dried in a drying oven if silica microspheres are used; otherwise naturally dried by evaporation. The residue is preserved in ethanol or glycerin.

3. Identification, counting and digital image processing of terrestrial plant microfossils

3.1 Pollen and spores

Microscopic observation of the pollen of flowering plants and gymnosperms and spores of pteridophytes allows identification with a taxonomical resolution rarely reaching the specific level but more often the family or genus levels and sometimes the group of species within a genus (Jackson and Booth, 2007). The identified grains are allocated to a morphotype (or pollen taxa) based on various features related to the size and shape of the grain, to the shape, number and distribution of the apertures/scars and to the structure and ornamentation of the pollen/spore wall (Fig. 2). A large literature describes these features although the associated terminology varies depending on the authors (Erdtman, 1954; Faegri and Iversen, 1964; Hesse et al., 2009; Kapp's, 2000; Moore et al., 1991; Reistma, 1969). We only report hereafter the main characteristics used for identification (see above references for further details), mainly with the terminology used in Moore et al. (1991). The descriptive terminology can be bewildering for the novice but provides an essential basis for accurate description, comparison and identification of morphotypes; a valuable illustrated glossary is provided by Punt et al. (2007).

Pollen size varies mostly between 15 and 100 µm although some grains can be as large as 140 µm such as Malvaceae pollen or slightly less than 10 µm such as pollen from tropical and subtropical trees and shrubs, like *Elaeocarpus* and *Cecropia*. The shape of a pollen grain generally varies from *spherical* to *elliptical*, either *oblate* when the polar axis is shorter than the equatorial axis or *prolate* for the reverse. An *aperture* is a thin area or a missing part of the exine, either circular to elliptical (*pori* or *pores*) or elongated (*colpi* or *furrows*), that allow the germination of the pollen tubes for plant reproduction. The shape, number and arrangement of the apertures constitute a primary criterion for identification of pollen types. Types names include the terms *porate*, *colpate* or *colporate* describing the aperture shape with a prefix (*mono*-, *di*-, *tri*-, *tetra*-, *penta*-, *hexa*- and *poly*-) defining the aperture number. It is possible to find grains without aperture, corresponding to the *inaperturate* pollen type. Another prefix describing the aperture arrangement can also be added: *zono*- and *panto*-, following Erdtman (1954) and Moore et al. (1991) or *stephano*- and *peri*- following Faegri and Iversen (1964) for apertures distributed in the equatorial zone or all over the surface of

the grain, respectively. The structure and sculptures of the pollen wall present a large variability constituting precious criteria for the identification of the pollen grains. The fossil pollen wall of angiosperms, namely the *exine*, is composed of a homogenous inner layer, the *endexine*, and a complex outer layer, the *ectexine*, which may include a *foot layer*, with above radial rods, named *columellae*, supporting a *tectum* with various supratectatal *sculpturing elements* (*bacula, clavae, echinae, pila, gemmae, verrucae, scabrae* or *granules*). All layers may be continuous, discontinuous or absent, may present particular thickening features such as *arcus* or *annuli* (cf. *Alnus* and *Poaceae* pollen grains). When there is no tectum (*intectate* grain as opposed to *tectate* grain), sculpturing elements may be found on the top of the foot layer. Columellae can also be partially joined at their heads; the grain is described in this case as *semitectate*. The arrangement of the columellae or of the supratectal sculpturing elements or their fusion in elongated elements can give rise to a network (*reticulum*) or *striations*. Gymnosperm pollen wall slightly differs: the endexine is lamellate and the ectexine never has columellae but alveoli or granulas (Hesse et al., 2009). Pinaceae and Podocarpaceae pollen grains display a special feature: the air sacs (*sacci*).
Pteridophyte spores have the same size range but depart from pollen for the presence of *monolete* and *trilete* scars and a simpler wall structure, although it can be multilayered and ornamented (Kapp's, 2000).

Figure 2

An exhaustive list of pollen atlases are referenced in Hooghiemstra and van Geel (1998). Pollen atlases published since 1998 are reported in Table 1. In addition, an initiative has been developed to aid the identification of pollen grains, and provide virtual access to reference material at https://globalpollenproject.org/ (Martin and Harvey, 2017).

Region	**Reference**
Europe	Beug (2004)
Africa	Schüler and Hemp (2016) Scott (1982) Gosling et al. (2013)
Asia	For Japan: Demske et al. (2013) For Indonesia: Jones and Pearce (2014) For India: Kailas et al. (2016); Mudavath et al. (2017) For China: Fujiki et al. (2005); (Yang et al., 2015)
North America	Kapp's (2000); (Willard et al., 2004)
Central and South America	For the whole Neotropics, freeware online database: Bush and Weng (2007) For Amazonian taxa: Colinvaux et al. (1999) For Paramo and high elevation Andean taxa: Velasquez (1999) For Brazil: Cassino and Meyer (2011) For Venezuela: Leal et al. (2011) For Atlantic forest: Lorente et al. (2017)

Table 1. List of pollen atlases for different regions of the world available for pollen grains identification (not referenced in Hooghiemstra and van Geel (1998)).

Counting is routinely done with a light microscope at 400x although oil immersion objective allowing a 1000x is required in some cases (Birks and Birks, 1980). The number of pollen grains and spores counted varies depending on the research objectives although it should be enough high to reach constant percentages of the different taxa and at least exceed a minimum count of 100 to calculate the relative proportions (expressed as percentages of the pollen sum). For terrestrial sediments, 300 to 500 grains are usually counted (Birks and Birks, 1980). For marine sediments, counting usually aims at reaching a total of 300 pollen and spore grains with at least 100 pollen grains excluding *Pinus*, a well-known over-represented taxa (Desprat, 2005; Turon, 1984). At least 20 taxa are usually identified to provide a representative image of the composition and diversity of the European or North American vegetation (McAndrew and King, 1976; Rull, 1987). In tropical regions where the taxa diversity is far more important and largely variable, saturation curves can be used to determine the number of grains that have to be counted to reach a plateau in the number of taxa found (Birks and Birks, 1980).

3.2 Microcharcoal

Microcharcoal is identified microscopically in transmitted light as black debris, opaque, with sharp edges according to criteria from Boulter (1994) (Fig. 3). Petrographic criteria in reflected light include visible plant structures characterised by thin cell walls and empty cellular cavities, or particles without plant structure but of similar reflectance than the previous ones (Noël, 2001).

Originally, both the number of microcharcoal and the area of microcharcoal were analysed in pollen slides. The area of microcharcoal was estimated using tedious methods, the square eye-piece grid method (Swain, 1973) or the point-count method (Clark, 1982). Both the concentration of pieces of microcharcoal and the concentration of microcharcoal areas are highly positively correlated (Tinner and Hu, 2003). It was therefore suggested avoiding the quantification of microcharcoal areas because it was time consuming for gaining little additional information compared to a simple counting of microcharcoal fragments. Counting microcharcoal on pollen slides is currently performed at 200x or 500x magnification (Doyen et al., 2013; Morales-Molino et al., 2011) by counting only the number of microcharcoal in pollen slide (Tinner and Hu, 2003) with a minimum of two hundred items (the sum of charcoal and exotic marker grains) (Finsinger and Tinner, 2005).

More recently, some studies indicated that fragmentation of charcoal particle may occur during taphonomical processes (Crawford and Belcher, 2014; Leys et al., 2013). This potential fragmentation may lead to an overrepresentation of microcharcoal, i.e. a virtual increase of the number of fragments per gram, while this increase would not have been seen in the total area concentration (see below for an explanation of the two concentrations). Using the total area helps therefore interpreting charcoal number concentration. Counting and area measurement of individual charcoal particles is recommended further because it provides an opportunity to link both particle counts and particle areas to different metrics of fires, such as burned area, fire number, fire intensity or fire emissions (Adolf et al., 2018b; Hawthorne et al., 2018).

Digital image processing can be used to generate microcharcoal data more efficiently and to conduct morphological particle analyses. Image analysis can be carried out in software such as ImageJ (open source) (Abramoff et al., 2004) which can be used to measure the individual area of each particle, total area of all particles and the number of particles that are observed in each microscopic field (Beaufort et al., 2003a; Daniau et al., 2009b; Doyen et al., 2013; Inoue et al., 2018; Thevenon et al., 2004). The shape is studied using the length, width and the elongation measurements.

Automated image analysis consists of scanning the slides in a controlled light adjustment (transmitted light) to detect and measure microcharcoal using a threshold value in red, green and blue (RGB), or in tint, saturation and lightness (TSL) color space (see for example Daniau et al., 2009a). Automated scanning of the slides requires the microscope to be equipped with a stage motorized in the X, Y and Z axes. Moving on the X and Y axes permits to scan different separate fields of the slide (150 or 200 images with a pixels digitising camera to provide reproducible results, (Beaufort et al., 2003b; Daniau et al., 2007; Doyen et al., 2013). The Z-axis permits to adapt the focus for each field. Observations and automated image analysis is performed in general at 400x (Doyen et al., 2013) or 500x magnification (Daniau et al., 2009b; Inoue et al., 2018). Identification of uncharred organic matter (in reflected light, using oil immersion), characterized by the absence of plant structures and distinct level of reflectance, can be used to set the best-fit threshold level to secure identification of microcharcoal by image analysis.

From these measurements, two types of concentration per gram of dry bulk sediment are calculated, i.e. the number of fragments of microcharcoal (number or fragments #/g) and the total area of microcharcoal (mm^2 or $\mu m^2/g$). When the density or the volume of the treated sediment is known concentrations are expressed per volume (cm^3). The total area corresponds to the sum of the individual areas of microcharcoal. The shape is studied using the elongation ratio (or aspect ratio) expressed as the ratio Length on Width (Umbanhowar and McGrath, 1998) (Crawford and Belcher, 2014); or as the ratio Width on Length (Aleman et al., 2013a).

Figure 3

3.3 Phytolith

The recovered phytolith fraction from the extraction procedure is mounted on microscope slides using mobile mounting medium, glycerin or immersion oil, to allow the rotation of phytolith for observation. Phytoliths are counted at 400x or 600x magnification. Immersion oil may be preferred as mounting media to facilitate observation because phytolith show a better contrast under the microscope rather than by using glycerin. Phytoliths are amorphous silicate and are distinguishable from quartz grains using a polarizing filter on the microscope. Other siliceous components can be diatoms, freshwater sponge spicules or siliceous protozoans such as testate amoebae (Rhizopoda). Diatoms, or even parts of valves, are easily distinguishable from phytoliths via finer ornamentations compared to phytoliths. Sponge spicules are generally needle-like in form and are either smooth or spined. They are visually distinguishable from phytoliths because their surfaces are generally smooth and the purity of the silicate makes it translucent. Finally, testate amoebas are recognizable when they are entire, but the tests are composed of siliceous plates that may be disarticulated during taphonomic processes or lab treatments. These plates have round to square shapes and measure usually between 5 to 15 µm. Rounded curved plates can be confused with microspheres. In this case rotation of the particle is needed for identification.

During the counting procedure, sufficient items (exotic marker and the most frequent phytolith morphotype with taxonomic significance) should be counted to reach an estimate of the total phytolith concentration with a precision of at least ±15 %, as described in (Aleman et al., 2013b). In general, this consists in counting at least 300 phytolith of morphotypes with taxonomic significance per sample and with size greater than 5 µm.

Description of phytolith morphotypes should be done according to their three-dimensional shape and classification should follow the International Code for Phytolith Nomenclature (ICPN; Madella et al. (2005)). The ICPN was developed in order to use a standard protocol to name and describe new phytoliths, and to use a glossary of descriptors for describing phytoliths. As such, when describing a phytolith type the following information are necessary: 1) description of the shape (3D and 2D), 2) description of the texture and/or ornamentation, and 3) symmetrical features. Other information can also be provided when possible (e.g. morphometric data, illustrations and anatomical origin, Madella et al. (2005)). Because of redundancy and multiplicity in phytolith shape (Fredlund and Tieszen, 1994; Mulholland, 1989; Rovner, 1971), one phytolith type can rarely be related to one plant taxon and therefore in order to use this vegetation proxy, the whole phytolith assemblage must be considered. Past tree cover, aridity/humidity changes and plant water stress can be assessed by grouping morphotypes into specific indices. In addition, phytoliths from the Poaceae family produces peculiar morphotypes that provide information about past grass dynamics and evolution (Strömberg, 2002).

In general, phytolith morphotypes are grouped into five large categories (Fig. 4):

Figure 4

1. Grass silica short cells (GSSC) are produced by Poaceae (Mulholland and Rapp, 1992). Among the GSSCs, the bilobates (a), polylobates and crosses (b) are mainly produced by the Panicoideae subfamily (Fredlund and Tieszen, 1994; Kondo et al., 1994; Mulholland, 1989; Twiss et al., 1969), which are C4 grasses adapted to warm and humid climate. The saddle (c) type occurs dominantly in the Chloridoideae subfamily (Mulholland, 1989; Twiss et al., 1969) (Fredlund and Tieszen, 1994; Kondo et al., 1994), C4 grasses adapted to a warm and dry climate. The rondel type (d), corresponding to the pooid type defined by Twiss et al. (1969) and the conical, keeled and pyramidal types (e) from Fredlund and Tieszen (1994), include conical, conical bilobate (f), conical trilobate and conical quadrilobate morphotypes. The trapeziform short cell type (Fredlund and Tieszen, 1994; Kondo et al., 1994; Mulholland, 1989; Twiss et al., 1969) comprises trapeziform, trapeziform bilobate (g), trapeziform trilobate (h) and trapeziform quadrilobate morphotypes. The rondel and trapeziform short cell types are preferentially produced by the Pooideae subfamily (C3, high elevation grasses), but also by the other subfamilies (Barboni and Bremond, 2009). *Zea mays* produces a particular cross type, and using morphometric analysis it is possible to precisely identify its presence in archeological records (Piperno, 2006). Bambusoideae grasses produce Bilobate and Saddle short-cells and some genus produce distinct phytolith types such as Chusquoid body or collapsed saddles in Chusquea (Piperno and Pearsall, 1998).

2. The bulliform cells category relates to cell morphology trackers that can be identified. For example, epidermal cells have been calibrated to reconstruct leaf area index (LAI) (Dunn et al., 2015). Bulliform cells (i) from the leaves of Poaceae are used as a proxy of aridity (Bremond et al., 2008).

3. The woody dicotyledon category is composed of globular granulate (j) (Alexandre et al., 1997; Bremond et al., 2005a; Kondo et al., 1994; Scurfield et al., 1974), globular decorated (k) (Neumann et al., 2009; Novello et al., 2012; Piperno, 2006; Runge, 1999), sclereid (Mercader et al., 2000; Neumann et al., 2009; Runge, 1999), blocky faceted (l) (Mercader et al., 2009; Neumann et al., 2009; Runge, 1999) and blocky granulate morphotypes (Mercader et al., 2009).

4. The other family-specific morphotypes are composed of morphotypes that can be attributed to specific families. Papillae types (m) (Albert et al., 2006; Gu et al., 2008; Novello et al., 2012; Runge, 1999) are produced by Cyperaceae (Kondo et al., 1994) that mainly grow in wetlands. The globular echinate morphotype (n) is produced by palms (Arecaceae) (Kondo et al., 1994; Runge, 1999). Phytoliths of Musa are volcaniform (o) (Ball et al., 2016) when the ones from Cucurbita are spheroidal or hemispheroidal with deeply scalloped surfaces of contiguous concavities (Piperno et al., 2000). Other specific phytoliths can be attributed to rice, Maize or Marantaceae (see the exhaustive discussion in Piperno (2006)).

5. Non-diagnostic morphotypes (p) such as globular smooth, elongated or tabular and blocky types are sometimes attributed to specific vegetation types, such as closed environments. However, the diversity of shapes behind the generic terms makes it difficult to be exhaustive for this category (see Garnier et al., 2012; Novello et al., 2012; Runge, 1999).

Comprehensive databases and atlases for phytolith identification do not exist yet. The web and scientific papers provide some atlases but the data are diverse, dispersed and not easily comparable. The data are presented generally by taxon (Family, Genus or Species) or by phytolith morphotypes. Modern phytolith assemblages have been extensively studied in Africa (Barboni et al., 2007). The PhytCore DB (http://www.phytcore.org) provides modern phytolith assemblages but it is very oriented for archeological studies. It is therefore important analysing modern soil or recent sediment samples in the surrounding vegetation types of the "fossil" studied area. Here, we provide a non-exhaustive list of different phytolith atlases available on the web (Table 2).

Name	**Website link**
PhytCore (Archeological sites from Spain, East and South Africa)	http://www.archeoscience.com/
The University of Missouri Online Phytolith Database (essentially the flora of Ecuador)	http://phytolith.missouri.edu/
Paleobot (collaborative, open-access web resource for scientists and scholars engaged in paleobotanical research)	http://www.paleobot.org/
Old World reference phytoliths	http://www.homepages.ucl.ac.uk/~tcrndfu/phytoliths.html
The Blinnikov's Phytolith Gallery	http://web.stcloudstate.edu/msblinnikov/phd/phyt.html

Table 2: List of phytolith atlases available online.

4. Terrestrial plant microfossils for qualitative and quantitative environmental reconstructions

4.1 Information from pollen

4.1.1 Environmental information

Fossil pollen assemblages are widely used for reconstructing past vegetation composition and distribution, and thereby climate and land-use changes. Pollen analysis is based on a set of principles that allow relating the pollen assemblage found in sedimentary archives with the surrounding vegetation (e.g. Birks and Birks, 1980; Prentice, 1988). Information on the pollen-vegetation relationship in particular is issued from the extensive study of surface (modern) pollen samples, taken in defined vegetation units characterizing an ecosystem or a bioclimate, as well as in various sedimentary contexts. Modern pollen rain-vegetation relationship was therefore investigated in a wide variety of landscape worldwide, although some regions are still under-studied, such as arid and semiarid environments. From these studies arose several regional modern pollen databases for Europe (Davis et al., 2013; Fyfe et al., 2009), North America (Whitmore et al., 2005), East Asia (Zheng et al., 2014), Africa (Gajewski et al., 2002) and South America (Flantua et al., 2015).

Surface sample studies have shown there is no linear relationship between pollen proportions and plants abundances. Pollen proportions from a sedimentary archive give qualitative information on changes in vegetation composition through time and over a spatial area. Many studies demonstrated that pollen assemblages clearly discriminate between vegetation formations or forest-types and that pollen proportions of the major taxa reflect their relative importance in the vegetation (Prentice, 1988). Individual calibration studies prior to the analysis of a sedimentary archive are recommended to provide the characterization of the relationship between the pollen rain and local and regional vegetation essential to interpret the fossil pollen records in terms of vegetation changes. For example, in Southern Africa, Poaceae percentages were demonstrated to be critical to distinguish the pollen signal of the major biomes and associated climatic zones (Urrego et al., 2015). In the Mediterranean region, pollen assemblages within degraded maquis, for instance, appear largely influenced by adjacent land-covers such as conifer woodland and open vegetation (Gaceur et al., 2017).

A large literature aims at understanding and estimating the factors that determine the source vegetation and modifies the pollen representativeness in terms of vegetation composition and abundance (e.g. Broström et al., 2008; Bunting et al., 2013; Gaillard et al., 2008; Havinga, 1984; Prentice, 1985; Sugita, 1994; Traverse, 2007). The differential pollen production, dispersal and preservation between pollen taxa lead to the over- or under-representation of some morphotypes. The long-transport of anemophilous taxa is a common factor biasing the representation of the local vegetation by pollen assemblages (e.g. Traverse, 2007). This is particularly true in mountain regions where wind drives uphill transport of tree pollen (Ortu et al., 2006). The most widely known example is the pollen over-representation of *Pinus* that produces a large quantity of highly buoyant saccate pollen.

The structure and composition of the surrounding vegetation affect the source area of pollen. For instance, pollen rain in open landscape is prone to increased contribution of pollen originating from far-distant vegetation (Bunting et al., 2004). The size (i.e. few meters to kilometers) and type (e.g. bogs, mires, lakes and ocean) of the sampling site also influence the pollen source area from local to regional inputs (e.g. Prentice, 1985; Sugita, 1994; Traverse, 2007). Ponds and small lakes mostly receive pollen from the vegetation surrounding the sampling site and therefore represent more local estimates of vegetation than large lakes (in their centers) that collect predominantly wind-transported pollen from the regional vegetation background (e.g. Sugita, 1994, 2007a, b). Note that without using specific pollen-based modelling approaches (see section 4.1.2) the dissociation between local and regional pollen signals cannot be assessed. Pollen studies on modern marine surface sediments showed that pollen assemblages reflect an integrated image of the regional vegetation of the adjacent continent (e.g. Heusser, 1983; Naughton et al., 2007). Such studies revealed that pollen grains are mainly transported to the ocean realm by wind and rivers but the role of these transport agents depends essentially on the environmental conditions of each area (e.g. Dupont et al., 2000; Groot and Groot, 1966). Pollen is predominantly supplied to the ocean by fluvial transport, in regions where hydrographic systems are well-developed such as in the western Iberian margin, northern Angola basin, western North Atlantic margin and in the Adriatic Sea (e.g. Bottema and van Straaten, 1966; Dupont and Wyputta, 2003; Heusser, 1983; Naughton et al., 2007). In arid zones, like in northwest (NW) of Africa, with weak hydrological systems and strong winds, pollen are mainly wind-blown (e.g. Hooghiemstra et al., 2006; Rossignol-Strick and Duzer, 1979). A mixture of fluvial and wind pollen transport may also occur as shown in the Gulf of Guinea (Lézine and Vergnaud-Grazzini, 1993) and the Alboran Sea (Moreno et al., 2002). Once in the ocean, pollen grains sink rapidly through the water column thanks to processes decreasing its floatability such as agglomeration (taking part to the marine snow), flocculation and incorporation in fecal pellets (Mudie and McCarthy, 2006) and thereby preventing from long-distance marine current transport (Hooghiemstra et al., 1992).

4.1.2 Pollen-based land cover reconstruction

Pollen assemblages extracted from terrestrial sedimentary cores reflect a mix of both local and regional vegetation, and this makes difficult the assessment of quantitative vegetation reconstruction based on pollen proportions. Correction factors were proposed as early as the fifties to minimize biases in the representativeness of pollen assemblages (see Birks and Berglund (2018) and references therein). From the eighties, important methodological improvements took place with the development of models taking into account the differential production and dispersal of pollen, and the size and type of the sedimentary basin (e.g.

Prentice and Parsons, 1983; Sugita, 1993, 1994, 2007a, b). These models have resulted in the development of the Landscape Reconstruction Algorithm (LRA; Sugita (2007b)) for quantitative reconstruction of past vegetation composition.

The LRA approach corresponds to two sub-models, REVEALS (Regional Estimates of Vegetation Abundance for Large Sites; (Sugita, 2007a) and LOVE (Local Vegetation Estimate; Sugita (2007b)). REVEALS reconstructs the regional vegetation composition in a radius of ca. 50 km using pollen counts from large lakes (>50 ha). REVEALS can also be used for a combination of small and large lakes and bogs, although the standard errors would be greater than when using for a large lake only (Marquer et al., 2017; Trondman et al., 2016). LOVE reconstructs the local vegetation composition in a radius of few meters to kilometers that corresponds to the relevant source area of pollen (RSAP). LOVE uses pollen counts from small sites (lakes and bogs <50 ha) and REVEALS estimates as the regional background of pollen (i.e. pollen coming from beyond the RSAP) to subtract the regional background of pollen and calculate quantitative estimates of local vegetation composition. LOVE estimates represent the local vegetation composition within the RSAP. The LRA models incorporate critical parameters to correct the non-linear relationships between pollen percentages and plant abundances, e.g. pollen productivity estimates of specific plant taxa, fall speed of pollen and basin size, and several assumptions, e.g. specific wind speed and characteristics of atmospheric conditions. Current model improvements correspond to the implementation of an alternative pollen dispersal model in the LRA approach (e.g. Theuerkauf et al., 2016; Sugita, unpublished).

The REVEALS and LOVE models are now increasingly applied to provide quantitative reconstructions of the Holocene vegetation composition from local, regional to sub-continental spatial scales (e.g. Cui et al., 2014; Fyfe et al., 2013; Hellman et al., 2008a; Hellman et al., 2008b; Marquer et al., 2017; Marquer et al., 2014; Mazier et al., 2015; Nielsen et al., 2012; Nielsen and Odgaard, 2010; Overballe-Petersen et al., 2013; Soepboer et al., 2010; Sugita et al., 2010; Trondman et al., 2015; Trondman et al., 2016). The REVEALS model has largely been used for pollen-based land cover reconstruction in Europe and it is now applied to other regions (essentially in the Northern Hemisphere) via the support of the PAGES LandCover6k initiative (Gaillard et al., 2018). Evaluation of the LRA models reliability in the Southern Hemisphere and tropics (Southern Asia, Central Africa and South America) is in progress.

The REVEALS approach requires some a priori information on pollen productivity estimates, which are difficult to collect and highly variable, lake size and assumptions on wind speed. This constitutes one disadvantage of the approach since all these parameters may vary through time, increasing the uncertainties of the REVEALS land-cover reconstructions. In addition, the physical size of taxa in the landscape which can be important in reconstructing past forest cover is not reconstructed (Zanon et al., 2018).

An alternative and less resource intense approach has been developed by Williams (2003), based on the popular modern analogue technique (MAT) applied in pollen-climate reconstructions, whereby analogues of fossil pollen samples are found in a modern pollen database. In the land-cover reconstruction method, the fossil sample is assigned the remote-sensing derived forest cover of the closest matching modern pollen sample site.

This method is particularly useful to reconstruct past forest cover at continental scales. It was used to reconstruct Holocene forest cover in North America (Williams, 2003), Europe (Zanon et al., 2018), Northern Eurasia (Tarasov et al., 2007), and time slices for the whole of the Northern Hemisphere mid and high latitudes (Williams et al., 2011). Zanon et al. (2018) showed that both methods generally provide comparable results. However, the MAT systematically estimates lower forest cover than REVEALS although this offset reduces in some pioneer vegetation landscapes. This discrepancy may be due to different definitions of ‘forest cover’ between the two methods, with trees greater than 5 m in the case of MAT, whereas forest is simply defined as the proportion of forest forming taxa irrespective of their size in REVEALS.

Other semi-quantitative methods for reconstructing land-cover are based on the ‘biomisation’ method (Prentice et al., 1996). This essentially compensates for differing pollen productivity and dispersion by transforming pollen percentages data using the square-root method. This has the effect of de-emphasising the taxa which represent the larger proportions (often the trees) and emphasizing more the taxa with the smaller proportions (often the herbaceous taxa). Taxa are then grouped into common plant functional groups (pft’s) grouped in turn into biomes. The sum of the square rooted percentages of each group of taxa represents its ‘score’. The highest ‘score’ represents the vegetation biome of the pollen sample assemblage. Biomisation classification schemes have been developed for almost all regions of the world (Prentice and Jolly, 2000). The original motivation for this work was the evaluation of climate model simulations through forward modelling. This side-steps the problems associated with pollen-climate based data-model comparisons (see section 4.1.3) because the vegetation represented by the pollen record is directly compared with the vegetation generated by a process based vegetation model fed with output from the climate model simulation (Prentice et al., 1998). This approach has many advantages, not least the ability to take into account the complex response of vegetation to many different aspects of climate, such as temperature, precipitation, seasonality, cloudiness and frost frequency. Unfortunately, one of the main disadvantages is the difficulty in aligning the vegetation generated by the vegetation model with that represented by the pollen record. For instance, the link between the original biome vegetation model and pollen biomisation classification schemes (Prentice et al., 1996) is based on the unproven assumption that modelled Net Primary Productivity (NPP) is directly linked to pollen percentages. Similarly, because the model generates potential natural vegetation, and the pollen data reflects actual vegetation, it becomes difficult to judge the accuracy of a pollen biomisation scheme with for instance over 8 different schemes available in Europe alone (Allen et al., 2010; Allen et al., 2000; Bigelow et al., 2003; Binney et al., 2017; Marinova et al., 2018; Peyron et al., 1998; Prentice et al., 1996; Tarasov et al., 1998)).

However, considering the simplicity of the approach, the biomisation procedure nevertheless proved to work remarkably well in many regions at continental scales. While the original procedure was developed specifically to reconstruct the natural potential vegetation, the procedure has also been adapted to reconstruct human impacted landscapes, the pseudo-biomisation approach (Fyfe et al., 2010). It was used to reconstruct the land-use and forest cover of Europe throughout the Holocene (Fyfe et al., 2015). Roberts et al. (2018) showed that the three methods, pseudo-biomisation, REVEALS and biomisation approaches, captured the basic trend in forest cover change over Europe during the Holocene.

Biomisation, pseudo-biomisation and modern analog technique can be used at continental and global scales and provide semi-quantitative estimates for biomes, plant functional types, land cover classes and tree covers, when LRA provides quantitative estimates of the cover of plant taxa at specific spatial scales, i.e. from local, regional to continental scales. Those quantitative estimates of vegetation are critical to i) evaluate climate and human-induced changes in vegetation composition and diversity, ii) answer archaeological questions about land use, iii) inform strategies related to conservation of natural resources and iv) be used as inputs for climate and dynamic vegetation modelling (e.g. Cui et al., 2014; Gaillard et al., 2010; Marquer et al., 2018; Marquer et al., 2017; Mazier et al., 2015).

4.1.3 Pollen-based climate reconstruction

Fossil pollen data have been used for quantitative reconstructions of past climate for over 70 years (Iversen, 1944). Pollen remains the main terrestrial proxy used for continental-scale evaluation of climate model simulations as part of the Paleo-climate Model Intercomparison Project (PMIP) for key time periods of the last climatic cycle (126, 21 and 6 ka) (Otto-Bliesner et al., 2017), and as far back as the mid-Pliocene (3.0-3.3 Ma) under the Pliocene Model Intercomparison Project (PlioMIP) (Haywood et al., 2013). Those models are used to simulate future climate and their paleo-climate evaluations provide the only real test of reliability outside of our modern climatic experience. Paleo-climate reconstructions have been based on widely spaced time-slices. It becomes possible now to produce spatially explicit continuous reconstructions through time in data rich regions such as Europe (Davis et al., 2003a; Mauri et al., 2015) and North America (Viau and Gajewski, 2009). Spatially explicit reconstructions allow us to view the spatial structure of climate change, much of which is driven by change in atmospheric circulation which appears to be under-estimated in climate models (Mauri et al., 2014). The high spatial variability indicated by pollen synthesis studies (and others; (see de Vernal and Hillaire-Marcel, 2006; Kaufman et al., 2004)) suggests strong sampling bias in regional or even global interpretations from one or very few sites (Hansen et al., 2006; Marcott et al., 2013). Large networks of pollen sites allow area-average estimates that reflect more accurately climate system energy-balances. They are also more comparable with climate models with their large grid box resolutions (Bartlein et al., 2011).

The main advantage of pollen data is its almost unrivalled spatial coverage from almost all terrestrial regions of the Earth, together with the wide range of seasonal and annual climate parameters that can be commonly reconstructed. Disadvantages include relatively low centennial-scale temporal resolution (especially when multiple records are combined at large spatial scales), and the possibility that non-climatic environmental factors may also influence the vegetation record through disease, succession, migration lag, soils and human action (Mauri et al., 2015). Another issue is the no-analogue-vegetation problem (Jackson and Overpeck, 2000; Williams et al., 2001), i.e. unique associations of taxa in the past that do not occur today, such as during the rapid post-glacial re-colonisation of higher mid-latitudes following the retreat of LGM ice sheets. This problem is also related to the no-analogue-climate problem, when there is no modern analogue for a climate in the past, such as the particular combination of seasonal insolation during the last Interglacial, or the low CO_2 concentration during the LGM. It should be noted that the problem of human action on vegetation is often the inverse of how it is popularly conceived, since most transfer functions are assessed and calibrated for the present day when human action has probably been at its highest. It is in fact a lack of human action in the past that can create a no-modern-analogue problem for the transfer function.

Since the first pollen-climate transfer function over 70 years ago, there have been a large number of different methods developed, largely motivated by the problems that we have already outlined. These methods can be grouped into 4 main groups.

1) The first and generally the most popular group of methods is based on matching an assemblage of taxa present in a fossil pollen sample with unknown climate, with the same assemblage in a modern pollen sample whose climate is known. This includes the classic modern analogue technique (MAT), but also variants such as response surfaces (Brewer et al., 2007). Advantages include simplicity and an ability to incorporate non-linear responses to climate, while disadvantages include the need for a large calibration dataset of modern pollen samples and poor statistical treatment of uncertainties.

2) The second group of methods builds a regression model for each taxa based on the relationship between modern pollen samples and known modern climate, which is then used to deduct the past climate from the taxa in a fossil pollen sample assemblage. This includes

the popular Weighted Averaging – Partial Least Squares (WA-PLS) method (Birks et al. 2010). The advantage of this method includes better statistical treatment of uncertainties and elimination of problems such as spatial auto-correlation that are common to MAT. However disadvantages include heavy reliance on capturing the correct climate response within the calibration dataset and poor performance at the edges of the response envelope.

3) Both the previous two groups of methods require an extensive and representative modern pollen surface sample dataset for calibration of the transfer function, and also rely on the relative proportions of the taxa in the pollen assemblage. The third group of methods instead uses modern vegetation distribution rather than modern pollen samples as the basis for calibrating the transfer function, and generally uses presence and absence of taxa rather than its proportional occurrence in the assemblage. This includes classic methods such as mutual climatic range, as well as the more recent probability density function approach (Chevalier et al., 2014). These methods work by establishing the climate envelope for each taxa based on its modern vegetation distribution, and then combining the envelopes of the taxa found in the fossil pollen assemblage to deduce the most likely climate where all the taxa are able to exist together. This group of methods does not require a calibration dataset of modern pollen samples. They are especially good in areas where these datasets are limited such as in Africa (Chevalier et al., 2014), as well as being able to perform in no-analogue situations where taxa are found combined in assemblages that are not found today. The disadvantages of this type of model is that pollen may be found in areas beyond the geographical range of its source vegetation, while the use of geographical range alone to define the optimum climate for a taxa (rather than abundance) leads to large envelopes and consequently large uncertainties in reconstructions.

4) The final fourth group of methods uses a process based vegetation model to determine the climate of a fossil pollen assemblage. Normally vegetation models use climate data as input

to arrive at a vegetation, but in this ‘inverse’ method, the vegetation model is used in inverse mode where the vegetation is already known (the fossil pollen assemblage) and the most likely climate to result in that vegetation is the output. This method does not require any modern calibration data (although in reality vegetation models are largely parameterized based on what we know of modern vegetation), and since it is process based, it can provide reconstructions in no-analogue situations such as low CO_2 climates (Wu et al., 2007). The importance of pollen-based climate reconstructions are likely to increase in future as more climate models simulations are made in transient mode and at increasing spatial resolutions. At the same time, more fossil and modern calibration pollen data becomes available in public relational databases. Improvements in transfer function performance can also be expected, particularly through the application of Bayesian approaches that include multi-sample and multi-site analysis.

4.2 Information from microcharcoal

Vegetation fires produce different sizes of particles of which the smallest, classified as fine particles, are deposited far from the source (Patterson et al., 1987). Aeolian and fluvial processes are the main agent responsible for the transport of microcharcoal from the combustion site to the sedimentation basin where they are preserved. These microcharcoal particles remain in the atmosphere and are transported over long distances (Clark, 1988) by low atmospheric winds (<10 km) and deposited a few days or weeks after their formation (Clark and Hussey, 1996; Palmer and Northcutt, 1975). In water, after a short period of bedload transport, charred fragments break down into relatively resistant, somewhat rounded pieces, and thereafter remain stable. They exhibit the same behaviour as fragments of highly vesiculated pumice, which initially floats and sinks as it becomes waterlogged (Nichols et al., 2000). (Whitlock and Millspaugh, 1996) have reported charcoal introduced into deep lake sedimentary record within a few years after a fire event. Suspended fine material (including microcharcoal) fluvially supplied to the ocean can be transported to the deep ocean through canyons (Jouanneau et al., 1998). Microcharcoal sedimentation, which may be comparable to pollen sedimentation behaviour, can be deposited in several weeks on the ocean floor as a part of the marine snow (Chmura et al., 1999; Hooghiemstra et al., 1992). It is assumed that microcharcoal mostly reflect regional fire history.

Microcharcoal accumulations (concentrations and influx) are used therefore to reconstruct changes in biomass burning at regional scale. The chronology of the record, through the development of age models, is used to calculate the sediment accumulation rate (sediment accumulation thickness per unit time, cm/yr). Microcharcoal influx (also called microcharcoal accumulation rate) is expressed as number of fragments per unit area per unit time (#/cm2/yr) or total areas of microcharcoal per unit area per unit time ($\mu m^2/cm^2/yr$). It is calculated by multiplying the concentration of microcharcoal per volume by the sediment accumulation rates, or by multiplying the concentration of microcharcoal per weight by the density of the sediment samples and by the sediment accumulation rates.

Influx accounts for variations in the sedimentation rate over time which can vary widely (Adolf et al., 2018b; Marlon et al., 2016). When the sediments are varved, it is possible to obtain an accurate estimation of the sediment accumulation rate and to calculate microcharcoal influx for each sample (Maher, 1981). In this case, assuming that the full production of microcharcoal is transported to the sediment deposition site, microcharcoal influx may be interpreted directly in terms of charcoal production.

However, varved-sediments are rare and the age-depth model of sedimentary sequence commonly derives from discrete dated levels (radiometric dating, use of “tie-points” based on events stratigraphy). Several studies then present calculated values of microcharcoal influx for each sample of the dated sequence. However, an average sedimentation rate over several meters of core lacks information about the rate in a sample taken from a centimeter interval within the dated sequence (Maher, 1981). Because of this uncertainty in the sedimentation rate, a rigorous solution is not possible for a single sample: interpreting long term trend in microcharcoal influx is preferred rather than interpreting single microcharcoal influx variation. Maher (1981) suggested using in this case an averaged influx between two dates, calculated by the average concentration multiplied by the average sedimentation rate. More recently, the ^{230}Th normalization method provides a means of achieving more accurate interpretations of sedimentary fluxes (Francois et al., 2004).

In addition, calculation of microcharcoal influxes for some marine sediment sequences obtained by piston coring may be prevented. The piston coring process sometimes elongate parts of the core, and this elongation is not constant over the sequence. It can increase virtually the sedimentation rate and so the derived influx. The coring artefacts should be corrected before influx calculation, if physical parameters of the coring are recorded during the core collection (Toucanne et al., 2009). For some cores collected in the past decades, some missing parameters avoid this correction. The equipment of the upgraded R/V Marion Dufresne for example now prevents or minimizes elastic stretching of the sediment and allow physical parameters to be recorded (http://www.insu.cnrs.fr/en/node/5762).

In a few cases, some “apparent” sediment hiatuses of tens of centimeters in the core are observed. In the absence of changes in lithology, those apparent sediment hiatuses may happen because of the split of the sediment due to stretching strength during core collection. The original depths therefore need to be corrected before the calculation of the depth-age model and of the influx (see for example core MD04-2845 in Sánchez Goñi et al. (2017)). In addition, the lack of information about the density of the sediment may also prevent influx calculation from microcharcoal concentration per weight. However, it is possible to use an estimated marine sediment density (Tenzer and Gladkikh, 2014).

The deep ocean (in the absence of turbidite deposits) receives plant microfossils and terrigenous sediments coming from the adjacent continent and material derived from in situ biological surface productivity. Those materials are part of the hemipelagic sedimentation. Quick events of high sediment accumulation of material produced outside of the adjacent continent or outside of the depositional basin may happen, such as the Ice Rafted Debris deposits (due to the melting of icebergs during ice sheet abrupt calving) in the marine realm, or such as volcanic ash deposits. The sedimentation rate increases sharply and so the calculated microfossil influx. However, this influx increase informs that the sediment source is modified rather than that more microfossils attain the depositional basin. For example, core MD04-2845, located on a seamount, receives hemipelagic sediment including allochthonous terrigenous material, i.e. eolian and fluvial particles coming from the adjacent continent, including plant microfossils (Daniau et al., 2009b). During the last glacial period, several events of high sedimentation rate are associated with the Heinrich layers, i.e. a huge amount of IRD released during the melting of icebergs in the North Atlantic. To estimate plant microfossils influx, biogenic and glacial terrigenous influx (IRD) should be removed from the total sediment influx. Caution is therefore needed in interpreting influx when the source area of the sediments is modified.

Rare calibration studies, performed in some varved sediment lakes and one in an oceanic basin, suggest that microcharcoal accumulation is strongly linked to “burnt area” (Mensing et al., 1999; Tinner et al., 1998) but further investigations are required (Adolf et al., 2018b).

In addition to microcharcoal concentration or influx, the morphology of charcoal including the elongation ratio may provide information about the type of burnt vegetation in paleoecological and paleoenvironmental studies (Aleman et al., 2013a; Courtney Mustaphi and Pisaric, 2014; Daniau et al., 2013; Daniau et al., 2007)). Charcoal fragmentation occurs along axes derived from the anatomical structure of plant species and the elongation degree is preserved even when the particle is broken (Clark, 1984; Umbanhowar and McGrath, 1998). Experimental studies show that the dominance of elongated particles (high elongation ratio) in a sample characterizes the burning of herbaceous vegetation while a near-squared morphology (low ratio) indicates the burning of forest (Crawford and Belcher, 2014; Umbanhowar and McGrath, 1998).

4.3 Information from phytolith

Phytolith deposition and accumulation are associated with the decomposition of local vegetation (Piperno, 2006), thus phytolith studies can provide valuable complementary information to pollen analysis that have a larger source area. However, since grasses produce much more phytoliths than any other plant types, the direct environment of the sedimentary archive needs to be carefully described and studied. For example, it has been shown in some African studies that a lake surrounded by a grass-marsh will record a ‘super’ local signal, i.e. the signal from the marsh overrides the signal from the surrounding landscape (Aleman et al., 2014). In this case, the source area is very local and the main transportation mode is by run-off. Conversely, a lake surrounded by a riparian forest perfectly records the landscape surrounding the lake (Aleman et al., 2014). The source area is wider and the main transportation mode is wind-blown (Aleman et al., 2014; Alexandre et al., 1997; Bremond et al., 2005b). Knowing the taphonomic processes therefore is of particular importance when interpreting a micro-proxy assemblage and the derived indices (see Strömberg et al., 2018).

4.3.1 Land cover reconstructions from phytoliths

The phytolith tree cover index or D/P, is the ratio of woody dicotyledons to Poaceae phytoliths and is commonly used to characterize the openness of an environment (Alexandre et al., 1997). It has been quantitatively calibrated against the Leaf Area Index (LAI) in two studies from Africa (Aleman et al., 2012; Bremond et al., 2005a). Recently, the D/P index was slightly changed from the original calibration publication (Bremond et al., 2017) to avoid infinite values of ratio. The ratio used is D/(D+P), with D corresponding only to the globular granulate and P only to the GSSC (Aleman et al., 2014; Bremond et al., 2017). This new index is thus bounded between 0 and 1 making it easier to interpret (Bremond et al., 2017). This proxy, however, can only be used in tropical environment where D phytoliths are produced. As such, other studies have calibrated LAI against phytoliths derived from leaf epidermal cells for which morphology is light-dependent (Dunn et al., 2015). Indeed, there are large differences between sun leaves and shade leaves: shade leaves have larger and more undulated epidermal cells than sun leaves. Using this proxy, the authors were able to reconstruct LAI for the Cenozoic (49 to 11 Ma) in middle-latitudes of Patagonia (Dunn et al., 2015).

4.3.2 Characteristics and phytolith indices

Several GSSC indices exist and enable to characterize the grassland or grass-dominated type of ecosystem. First, the Iph or humidity-aridity index compares the number of saddle short cell phytoliths against the number of lobate short cell phytoliths observed in a soil/sediment assemblage [Iph (%)= saddle vs. cross + dumbbell + saddle]. Calibrated for western Africa, the Iph index accurately characterizes the grass cover, allowing the discrimination of Sahelian grass communities from Sudanian ones (Bremond et al., 2005b) and the dominance of short-grass or tall-grass savannas (using a boundary of ~20%). The Fs or water stress index is computed as the ratio of bulliform phytoliths over the sum of characteristic phytoliths [fan-shaped index (Fs) (%) = fan-shaped vs. sum of characteristic phytoliths]. It was calibrated over the same area as the Iph index by using modern soil assemblages and climate data (Bremond et al., 2005a) and was proven successful to record the water stress and transpiration experienced by the grass cover. While the calibration is relevant for this part of Africa, care must be used when applied in other bio-climatic zones.

The Iaq index refers to the percentage of grass short cell morphotypes present in a soil/sediment assemblage that are mostly produced by hydro-/helophytic (=aquatic) grass species (Novello et al., 2012). It was calibrated for Chad (central Africa), where the Iaq index was shown to display high values for samples from the vegetated marshes of the current Lake Chad where aquatic grass communities are largely represented (Novello et al., 2012; Novello et al., 2015; Novello et al., 2016). Additionally, recent studies (Novello et al., 2015; Novello et al., 2016) have demonstrated that an Iaq value of 34.5% or more is estimated to represent the signal of aquatic grass communities in a fossil assemblage.

Combining indices can improve the interpretation of past grass-dominated communities (Strömberg, 2004). For example, the combination of the Iaq and Iph indices, calculated for each of the fossil assemblages, may allow distinguishing the signal of the dry-loving grass communities (mostly observed in arid domain), from the signal of the humidity-loving grass communities associated with regional high precipitation (mostly observed in wetter domain) or else with local aquatic conditions (Novello et al., 2012).

4.4. Online data sharing for regional and global environmental data syntheses using plant microfossil data

Plant microfossil data from a sedimentary archive are long to generate but rich in information on past local to sub-regional paleoenvironments. It is important therefore to study, and to continue the training of the next generation of scientists on plant microfossils that inform us about past changes in vegetation and fire dynamics, paleoclimates and paleoecology. Data needs careful archiving and long-term storage. Data of a specific site or a dataset can be archived easily (for instance, the NOAA, http://www.noaa.gov/ and Pangaea, https://www.pangaea.de/, offer this service to the paleo scientific community).

Over the past 15 years, the increasing amount of plant microfossils paleodata and the establishment of data sharing in the scientific culture (although some barriers still exist in hampering data sharing and good management practice, Neylon, 2017), and the development of large dataset analysis skills opened the possibility to tackle new questions at regional and global scale. Databases including plant microfossils are useful tools for comparing different records, for reconstructing past regional dynamics of vegetation, fire and climate, and for examining their feedbacks to climate. Those databases are also key for evaluating modeling results of past climate, vegetation and fire. For example, recently the analysis of the European Pollen Database allowed to re-examine the mean annual temperature trend over the Holocene (Marsicek et al., 2018). They would make possible also to tackle questions arising from global environmental change such as acclimation, adaptation, migration, risk and safe-operating space ecosystems.

Some databases can be focused on one proxy, on one continent or on a specific time period of interest. The structure of the existing paleo databases is generally similar and includes key metadata as geospatial and dating (chronological) information as well as data in the form of pollen and charcoal counts. The main structure includes sites, samples, pollen or charcoal data, and dating tables.

The Global Pollen Database (GPD) has now been replaced by the new Neotoma multi-proxy paleoecological database. The North American Pollen Database is already included in Neotoma and the other regional constituent databases of the GPD are in the process of being absorbed into the new structure as quickly as resources permit it (largely through voluntary efforts). This includes the European Pollen Database, the Latin American Pollen Database and the African Pollen Database. It is hoped that other regional pollen databases that presently remain outside the public domain such as the Chinese and Indo-Pacific Pollen Databases will ultimately be made available through Neotoma over the next few years. It should be noted that all of these databases are relational databases composed of interlinked tables, together with a harmonized and standardized taxonomy, and including additional information on related aspects such as chronologies. In this way, they differ markedly from simple data archives such as NOAA paleoclimate and Pangaea, which only provide file storage. By creating a global interlinked database, Neotoma is providing the scientific community with a powerful new analysis tool, and one that will allow analysis of not just pollen data but all kinds of paleocological information.

The Global Charcoal Database holds hundreds of fire history records from six continents mostly based on macro and micro-charcoal particles and on few black carbon accumulations in diverse terrestrial and marine sediments. Successive global syntheses based on increasing number of quantitative data demonstrated a strong relationship between fire and climate over the past 21,000 years (Daniau et al., 2012; Marlon et al., 2016; Power et al., 2008). As charcoal values vary by orders of magnitude between and within sites the data have to be standardised to facilitate comparisons between sites and through time. A full description of the procedure and details about the contents of the database can be found in Marlon et al. (2008) and Power et al. (2010b). The current version of the database is now stored under the MySQL environment at gpwg.paleofire.org. The paleofire R package (Blarquez et al., 2014) allows easy access to the GCD data and manipulation of its contents to produce biomass burning reconstructions for subsets of records.

The ACER (Abrupt Climate Changes and Environmental Responses) project is an international Focus Group of INQUA. ACER aims to understand the timing, frequency and amplitude of the rapid climate variability, the so-called Dansgaard–Oeschger (D–O) cycles, which occurred during the last glacial period (73–15 ka) and the feedback mechanisms involved. Those rapid changes are similar in velocity and magnitude to those expected in the 21st-century. The global pollen and charcoal database released in 2017 (Sánchez Goñi et al., 2017) aims specifically at examining the nature of the vegetation and fire responses. The database includes 93 pollen records with a temporal resolution better than 1000 years, 32 of these sites also provide charcoal records. In order to compare patterns of change from different regions, harmonized and consistent chronology based mostly on radiometric dating and additional tie points based on event stratigraphy below ^{14}C dating limit or below ^{14}C levels has been constructed for ninety six of these records.

The ACER synthesis emphasized the scarcity of paleoclimatic records from the tropical regions with enough resolution to investigate millennial-scale climate events (Harrison and Goñi, 2010; Sánchez Goñi et al., 2017). The Latin American ACER (LaACER) project was conceived to fill this gap by compiling and synthesizing data from the American tropics and subtropics. Paleorecords of these regions may help understanding globally-important oceanic and atmospheric systems in the climate variability since these regions are influenced by the Pacific and Atlantic oceans, and by large-scale atmospheric features including the Intertropical convergence Zone (ITCZ), El Niño-Southern Oscillation (ENSO), the North American Monsoon (NAM) and the South American Summer Monsoon (SASM) (Garreaud et al., 2009). LaACER sits within the Paleoclimate commission of INQUA, and was co-sponsored by PAGES (Urrego et al., 2014).

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Acronym	**Full name**	**Status**	**Website link**	**proxy**	**Key references**
APD	African Pollen Database	archive		pollen	Vincens et al. (2007)
EPD	European Pollen Database	Active	http://www.europeanpollendatabase.net/data/	pollen	Giesecke et al. (2014)
GCD	Global Charcoal Database	Active, MySQL	https://paleofire.org/	charcoal	V1: Power et al. (2008) V2: Daniau et al. (2012) V3: Marlon et al. (2016) V4: in progress
ACER and LaACER		archived in Microsoft AccessTM at https://doi.org/10.1594/PANGAEA.8		Pollen and charcoal - focus on the last glacial period	Sánchez Goñi et al. (2017)

		70867.			
Neotoma	Neotoma Paleoecology Database	Active	http://www.neotomadb.org	Various paleoecological data including pollen	(Williams et al., 2018)

Table 3: List of databases including pollen and microcharcoal sedimentary records

5. Glacial-interglacials cycles of the 100-ky world and the climatic shift of the Mid-Bruhnes event during the Middle Pleistocene

5.1 Vegetation

For the last climatic cycle, vegetation reconstructions and simulations suggest that temperate forests dominated the mid-latitude landscape during the last interglacial while steppe and tundra largely expanded, south of a large area covered by ice-sheets, during the last glacial period (e.g.Harrison et al., 1995; Harrison and Prentice, 2003; Hoogakker et al., 2016). The interglacial-glacial cooling generated a fragmentation of the boreal and temperate forests. Their area of extent during the LGM was greatly reduced in Eurasia while they migrated southward in eastern North America. Temperature variations as well as the low CO_2 concentrations, which have a direct physiological effect on plants, strongly influenced the vegetation worldwide during the last glacial period (e.g. Bennett and Willis, 2000; Harrison and Prentice, 2003). For further details, the reader is directed to a set of review papers making a state of the art knowledge on vegetation changes on each continent based on Late Pleistocene pollen records (Bigelow, 2013; de Beaulieu et al., 2013; Hooghiemstra and Berrio, 2013; Kershaw and van der Kaars, 2013; Lozhkin and Anderson, 2013; Meadows and Chase, 2013; Thompson, 2013; Urrego et al., 2016). Hereafter, we will focus on vegetation changes during the Middle Pleistocene, from 781 to 126 kyr ago.

Several terrestrial and marine continuous pollen records covering only part of the Middle Pleistocene exist. Here we review the long pollen sequences covering continuously the full Middle Pleistocene. The most well-known terrestrial long pollen sequences were recovered in the sixties and seventies in southern Europe and South America: Tenaghi Philippon and Funza (Fig. 5 and 6). They yields a 1.35 Ma continuous history of the vegetation and climate in the Philippi plain from Greece (Tzedakis et al., 2006; Van Der Wiel and Wijmstra, 1987a, b; Wijmstra, 1969; Wijmstra and Smit, 1976) and a 2.25 Ma history of the tropical Andean vegetation in the Bogotá high plain from Colombia (Hooghiemstra, 1989; Torres et al., 2013), respectively. Over the past two decades, a huge effort was done in the frame of the ICDP (International Continental scientific Drilling Program) to drill ancient lakes and recover long terrestrial sedimentary archives. In particular, the Heqing lake drilling allowed producing an outstanding pollen sequence recording the vegetation and Asian monsoon variability in southwestern China over the last 2.6 Ma (Xiao et al., 2007; Xiao et al., 2010; Zhisheng et al., 2011). Sedimentary archives going back to 1.8 and 1.2 Ma were also collected from the tropical African lakes Bosumtwi and Malawi and pollen records were generated for the last 540 and 600 kyr, respectively (Ivory et al., 2016; Ivory et al., 2018; Miller and Gosling, 2014). In Brazil, a 50 m deep borehole drilled in 2017 at Lake Colônia will allow studying the response of the Atlantic rainforest and fire to the South American subtropical monsoon variability during the last 1.6 Myr (Ledru et al., 2015; Ledru, pers.comm.). At higher latitudes, pollen data from the famous Siberian drill sites Lake El’gygytgyn, Lake Baikal and Lake Hovsgol are also available. However, pollen data from Lake El’ El’gygytgyn are so far available for selected periods only, mostly interglacial periods (Melles et al., 2012; Wenwei et al., 2018)). In the Baikal region, although both sedimentary archives are continuous, pollen records are not because of low pollen concentrations in glacial sediments (Prokopenko et al., 2010; Prokopenko et al., 2009). A global synthesis of the available marine pollen records (Sánchez Goñi et al., 2018) reveals that among the 129 sites listed, 19 cover several climatic cycles, 8 go beyond the Mid-Brunhes event with only 3 sites covering entirely the Middle Pleistocene. These sites are the ODP site 1144 from the South China Sea (Sun et al., 2003), the ODP Site 646 off Greenland (de Vernal and Hillaire-Marcel, 2008) and the IODP site U1385 from the SW Iberian margin although pollen data are mostly available for interglacial periods, so far (Sánchez Goñi et al., 2018). One additional site, the ODP site 1075 from the Congo fan, contains pollen data for the interval 600-1050 kyr (Dupont et al., 2001). The Middle Pleistocene sequences reveal that like the last climatic cycle, the past glacial-interglacial cycles forced repeated large biome shifts.

In southern Europe, the 100-kyr cycles are marked by the alternation of interglacial temperate forest and glacial open vegetation as shown by the Tenaghi Philippon and the IODP site U1385 pollen sequences but also in other southern European pollen sequences covering several climatic cycles such as Ioannina and Kopais in Greece (Okuda et al., 2001; Tzedakis, 1993; Tzedakis et al., 1997; Tzedakis et al., 2006), Praclaux in France (de Beaulieu et al., 2001; Reille et al., 2000), Lake Ohrid in Albania (Sadori et al., 2016), Valle di Castiglione in Italy (Follieri et al., 1988) and cores MD99-2331/MD03-2697/MD01-2447 from the NW Iberian margin and MD95-2042/MD01-2443 from the SW Iberian margin (e.g. Desprat et al., 2017; Sánchez Goñi et al., 2018). During all interglacial Marine Isotopic Stage (MIS), two or even three major phases of forest expansion occurred, related with low ice volume (warm MIS substages) and boreal summer insolation peaks. Despite small ice volume fluctuations during the interglacial MIS, the temperate tree variations in the Mediterranean region are of high amplitude due to the strong influence of precession on the Mediterranean vegetation (Sánchez Goñi et al., 2018; Tzedakis, 2007). However, the most important forest phase often occurs at the beginning of the MIS during the substage with the largest ice volume minimum, corresponding to the interglacial *sensu stricto* (e.g. Desprat et al., 2017; Tzedakis, 2005). In addition, emblematic constituents of ancient European forests, the so-called “Tertiary relicts”, such as *Eucomia*, *Carya*, *Pterocarya*, *Cedrus* and *Tsuga*, became extirpated over Europe during the Middle Pleistocene. Most of them disappeared from the Philippi plain during the MIS 16 glacial period, setting the point from which less diverse interglacial forests, similar to the modern one, established in southern Europe (Tzedakis et al., 2006).

In south America, glacial-interglacial temperature changes forced cyclical altitudinal migration of the montane forest and páramo, the open equatorial alpine vegetation, as shown by the Funza sequence and the 280 kyr-long pollen record Fuquene (Groot et al., 2011; Hooghiemstra and Sarmiento, 2001). However, the composition of interglacial Andean forest changed over the last one million years. *Quercus* immigrated in the Bogota area at ~430 kyr ago, during MIS 12, becoming a major constituent of the Andean forest since MIS 7, competing at high altitudes with *Weinmannia* and *Podocarpus* and replacing *Polylepis* near the upper forest limit (Torres et al., 2013).

In Africa, marine pollen records such as the IODP site 1075 and the 700 kyr-long records M16415-2 and GIK16867-3 located off tropical Africa, indicate that the extent of the major vegetation formations also varies with the 100 kyr glacial-interglacial cycles although migrations of the southern Saharan desert limit appear paced by obliquity. In addition, in the tropics the rain forest fluctuated with summer insolation and precession, likely related with the orbital forcing of the monsoon variability (Dupont, 2011; Dupont and Agwu, 1992; Dupont et al., 2001). At the orbital-scale, tropical lowland ecosystems drastically shifted from woodland to savannah in the western Africa and from tropical forest to desert, steppe and grassland vegetation in the eastern Africa in response to strong regional hydroclimatic changes (Ivory et al., 2018; Miller et al., 2016b).

While the MBE is clearly recorded by marine and ice archives, this event is not a clear feature of pollen records. The amplitude of forest expansion does not appear higher during the post-MBE interglacials in southern Europe pollen sequences (i.e. Tenaghi Philippon, Tzedakis et al. (2006); IODP site U1385, Sánchez Goñi et al. (2018); Lake Ohrid, Sadori et al. (2016)) nor in northern high latitudes (ODP 646, de Vernal and Hillaire-Marcel (2008)) and tropical Africa and South America (Dupont (2011); Funza, Torres et al. (2013)) records (Fig. 6). In the Heqing basin, *Tsuga* percentages, an indicator of winter temperature and annual temperature range, also do not display the MBE, although the XRF data show reduced strength of the summer monsoon rainfall during the interglacial peaks of the last 400 kyr likely related to strong inter-hemispheric interaction (Zhisheng et al., 2011). Simulations with the LOVECLIM model showed that in comparison with pre-MBE interglacials, the post-MBE interglacials are globally warmer mainly during boreal winter in response to both higher atmospheric greenhouse-gas concentrations and increased insolation during this season, in particular in the Southern Hemisphere (Yin and Berger, 2010). However, this simulated warming differences exhibit a strong regional and seasonal pattern supporting that some regions such as western Europe or tropical South America, were likely not affected by the MBE or as strongly as the southern high latitudes where the largest difference is displayed.

Long pollen sequences also contribute to show that past interglacial periods of the past one million years are diverse in terms of intensity, temporal trend, duration as well as spatial variability (Past Interglacials Working Group of PAGES, 2016; Tzedakis et al., 2017). For instance, records from northern high latitudes clearly display this diversity in warming strength, suggesting that some interglacial periods were particularly warm, such as the "super-interglacial" MIS 11 (Melles et al., 2012). During this stage, the southern Greenland ice-sheet collapsed (Reyes et al., 2014) allowing the expansion of the boreal conifer *Picea* in that region usually devoid of trees (de Vernal and Hillaire-Marcel, 2008). In contrast, in the mid-latitudes, the difference in warming intensity between interglacials appears tenuous as shown by weak differences in temperate tree percentages in the European pollen records from the NW Iberian margin and the Massif Central (de Beaulieu et al., 2001; Desprat et al., 2017) Pollen records from the southern Iberian margin show that the magnitude of Mediterranean forest development in the Iberian Peninsula substantially differed from one interglacial to another suggesting that the amount of winter precipitation was quite variable (Desprat et al., 2017; Sánchez Goñi et al., 2018). The interglacial hydroclimate variations observed in SW Iberia do not, however, parallel with the high latitude warming strength. The regional variability of the magnitude of temperature and hydroclimate change on land is a strong feature given by the few available Pleistocene sequences. However, an accurate view and understanding of the regional impact of climate changes during warm periods require suitable sedimentary archives to be recovered and analysed in the future.

Figure 5

Figure 6

5.2 Fire

The different syntheses of the Global Charcoal Database (Daniau et al., 2012; Marlon et al., 2016; Power et al., 2008) showed that biomass burning varies closely with climate changes. For example, biomass burning increased globally from the Last Glacial Maximum to the Holocene (Fig 6d). Daniau et al. (2012) demonstrated this global increase in biomass burning is controlled by rising mean annual temperature and moisture, temperature being the primary control.

Few biomass burning records document older glacial/interglacial transition. The synthesis of twenty long records of charcoal, registering not only the Holocene but also the Eemian and part of the last glacial period, suggested that biomass burning is generally high during interglacials and low during glacials (Daniau et al., 2010). Similar results based on microcharcoal analyses were observed more recently in Anatolia (Pickarski et al., 2015) and Greece (Lawson et al., 2013), and in the Andes from a macroscopic charcoal record covering the last ca. 370 kyr (Gosling William et al., 2009; Hanselman et al., 2011). Increases of biomass burning during interglacials in the Andes appeared to be associated with increased fuel load from the Polylepis woodlands expansion.

However, other regions in the tropics and the subtropics illustrate the opposite trend in biomass burning, i.e. high level of biomass burning during glacials or during the LGM (Daniau et al., 2013; Inoue et al., 2018; Nelson et al., 2012). A clear cyclic pattern is observed in southern Africa by a marine long microcharcoal record covering several glacial/interglacial cycles over the last 180,000 - 30,000 years (Fig. 7c). Peaks in biomass burning occur during each precession and local summer insolation maxima (Fig. 7b) (Daniau et al., 2013). Under reduced monsoonal activity, dry and fuel-limited interglacials would have reduced fire activity compared to glacials characterized by enhanced precipitation supporting grass-fueled fires. This hypothesis was confirmed by modeling (Woillez et al., 2014) and by vegetation observation (Urrego et al., 2015). Grass-fueled fires were also suggested to be higher under colder climates in China based on the analysis of the black carbon content, another fire proxy, from loess sequences (Wang et al., 2005).

Two long terrestrial charcoal records older than the MBE exist yet. One is from tropical woodland (lake Malawi, eastern Africa) and covers the last 1.2 million years (Ivory et al., 2016). Charcoal record was only interpreted for the last 600,000 years and the study suggested that fire activity was a component of the ecosystem since the beginning of MIS7 and a driver of the decline in species richness at 80,000 years (Ivory et al., 2018). Presence of charcoal is also reported in the lake Bosumtwi sequence covering the last 540,000 years, located in the tropical rainforest region of West Africa (Miller et al., 2016a) but no charcoal time series were presented in this paper.

The longest published record of fire covering the last one million years is from Bird and Cali (1998) but is a measure of organic resistant elemental carbon (OREC). Originally, they reported peaks in fire activity at the transitions from interglacial to glacial modes since MIS 13. The only peak during a full interglacial occurred at MIS 1 and was interpreted as of anthropogenic origin because no peak in fire was observed during other past interglacials. They later published a revised chronology of the record (Bird and Cali, 2002) showing that fire also peaked during the interglacial MIS7; their anthropogenic influence hypothesis from their original paper being then challenged. The microcharcoal analyses (Daniau A-L, work in progress) on the IODP site U1385 from the SW Iberian margin (Sánchez Goñi et al., 2018) covering the last one million years will allow exploration of patterns of fire at orbital-scale in relation to changes in vegetation and hydrology in a region considered highly vulnerable to future fires (Settele et al., 2014).

6. Millennial-scale changes during the last glacial period

6.1 Vegetation

About 200 pollen records cover the last glacial period worldwide, but only half have sufficient resolution and dating control to show millennial-scale variability (Harrison and Goñi, 2010). Here we illustrate patterns of vegetation in response to Dansgaard-Oeschger events (D-O) focusing on Europe, North America, Africa and South America obtained from the synthesis of the ACER International Focus group in 2010 (Fletcher et al., 2010; Hessler et al., 2010b; Jimenez-Moreno et al., 2010; Sanchez Goñi and Harrison, 2010). Those patterns are based on changes in biomes, defined by original authors as pollen percentages of certain taxa. The recent published harmonised chronology (Sánchez Goñi et al., 2017) and the application of biomisation on those records (Harrison S, pers. com) will allow a deeper analysis of the impact of rapid climate change on the land biosphere.

In Europe, high temporal resolution terrestrial, such as Lago Grande di Monticchio in Italy (Allen et al., 1999) or Tenaghi Philippon in Greece (Müller et al., 2011), and marine pollen records (for instance MD95-2042, Fig 6h, (Sánchez Goñi et al., 2000b)) reveal changes in vegetation cover and composition on millennial timescales during the last glacial period. Continuous records spanning the entire last glacial are concentrated in the Mediterranean region and southern Europe, while records from central and northern Europe tend to be fragmentary (Feurdean et al., 2014; Fletcher et al., 2010). Greenland Interstadials (GI) were associated with relatively warm and humid conditions over Europe, promoting the establishment of grassland and shrub tundra in northwestern Europe, shrub-and forest-tundra in northeastern Europe, open boreal forest in central western Europe and the Alpine region, and open temperate forest in southern Europe (Fletcher et al., 2010). Greenland Stadials (GS) or Heinrich Stadials (HS) were marked by cool and dry stadials over Europe and by the expansion of xerophytic and steppe taxa (Fletcher et al., 2010). Marine pollen records from the Atlantic and Mediterranean furthermore play a vital role in demonstrating the effective synchrony of atmospheric and oceanic signals of D-O variability (Naughton et al., 2009; Roucoux et al., 2005; Sánchez Goñi et al., 2002; Sánchez Goñi et al., 2000b), since vegetation changes typically display a one-to-one match with millennial-scale changes in marine paleoclimate tracers such as foraminiferal assemblages, organic biomarkers or ice-rafted detritus (in the Atlantic) (Sánchez Goñi et al., 2018). In addition, high temporal resolution records from the Iberian margin show that vegetation/climate response to Heinrich Stadials (HS) is even more complex, marked by two or three phases (Fletcher and Sanchez Goñi, 2008; Naughton et al., 2007; Naughton et al., 2009; Naughton et al., 2016). In particular the last HS (HS1) (Oldest Dryas on the continent; Naughton et al. (2007)) is marked by three synchronous main phases in regions directly influenced by the North Atlantic: a first phase with extremely cold/relatively wet conditions, a second phase characterized by cool/dry conditions, and a last phase with relatively warmer/increasing moisture availability. Both the Atlantic Meridional Oceanic Circulation slowdown and changes in the strength and position of North Atlantic westerlies could explain the temperature and moisture variability within HS 1 in western Iberia (Naughton et al., 2009; Naughton et al., 2016).

In North America, vegetation responded rapidly also to millennial-scale variability but the absolute phasing of this response to Greenland atmospheric surface temperatures is uncertain. Altitudinal movements of climate-sensitive plant species occurred in the western part characterised by more mountainous regions while the southeast showed latitudinal shifts in vegetation (Jimenez-Moreno et al., 2010). The YD signature is spatially variable. It is clearly marked by a cold reversal in pollen records from the northwest and northeastern North America(Peteet, 1995; Shuman et al., 2002b; Whitlock and Brunelle, 2007). Toward the continental interior, in the Midwest, pollen records do not display vegetation reversal during the YD but distinct plant associations from earlier and later time periods suggesting with warmer than before summers and colder than before winters. This vegetation patterns is likely related to the unique combination of forcings (Shuman et al., 2002a). In contrast, warmer and wetter conditions during the YD and the HS are recorded in Florida at Lake Tulane (Grimm, 2006). The YD atypical warming is even detected up to the Virginia Appalachians, at Browns Pond, although at the same latitude, the Chesapeake Bay pollen record indicates cooler and drier conditions close to the coast (Kneller and Peteet, 1999; Willard, 2013).

Tropical Africa and South America present few high resolution records covering the full glacial period. The compilation of Hessler et al. (2010a) based on about 16 pollen records showed that the vegetation signature of HS and GI can be opposite between the northern and southern parts of the region influenced by the ITCZ. The influence of the ITCZ is particularly well evidenced in northeastern Brazil where a rain forest development during the HS 1 is related to an ITCZ southward shift (Ledru et al., 2006). Furthermore, concomitant lowland vegetation changes between this region and western Patagonia reveal that the ITCZ and the southern westerlies shift together through an atmospheric teleconnection regulated by the Atlantic Meridional Oceanic Circulation variations (Montade et al., 2015). The recent study of Urrego et al. (2016) identified rapid responses of the tropical vegetation to millennial-scale climate variability in the Andean tropics. They found that Andean forest migrations as far as 16.5° south of the Equator displayed millennial-scale climate oscillations closely linked to the Greenland ice core (Wolff et al., 2010) and North-Atlantic records (Martrat et al., 2007). The signature of HS and the Younger Dryas were generally recorded as downslope migrations of Andean forest and likely linked to air temperature cooling. The GI 1 signal is overall comparable between northern and southern records and indicates upslope Andean forest migrations and warming in the tropical Andes. Cooling during Northern-hemisphere stadials and warming during interstadials recorded by Andean vegetation was consistent with millennial-scale fluctuations of $\delta^{18}O$ in the Sajama ice cap and uk'37-derived sea surface temperature (SST) changes in the western tropical Atlantic. However, differences in amplitude between the SST and forest migrations suggested a potential difference between the magnitude of temperature change in the ocean and the atmosphere that could be related to the thermal inertia of the oceans. Together these findings suggest that the precipitation signature of millennial-scale events follows the predicted migration of major atmospheric systems and circulation cells, but the temperature signature is driven by Northern-Hemisphere fluctuations.

6.2 Fire

Sixty seven sedimentary charcoal records (30 sites with better than millennial resolution) which have records for some part of the last glacial period were compiled to examine changes in global biomass burning to rapid climate changes associated with Dansgaard–Oeschger (D-O) cycles (Daniau et al., 2010). This synthesis indicated that biomass burning increased during D-O warming events and decreased during intervals of cooling, including the Heinrich stadials. In addition, this analysis showed that biomass burning responded extremely quickly to rapid climate changes, within a few hundred years. At global scale, a vegetation productivity forcing was speculated to explain increases (decreases) in fire during D-O warming (cooling) because vegetation itself responds to rapid millennial-scale changes (Daniau et al., 2010). At regional scales, this vegetation productivity hypothesis is clearly illustrated by a marine record documenting south-western Iberian Peninsula vegetation (Fig. 7h, Sánchez Goñi et al. (2000b)) and fire (Fig. 7g, Daniau et al. (2007)). Variations in fire dynamics are related to changes in fuel type and quantity due to shifts between semi-desert vegetation during D-O stadials and Heinrich stadials and Mediterranean forest during D-O interstadial (Daniau et al., 2007).

Other proxies like ammonium from Greenland ice cores also exhibit D-O cycles, with increases in fire in North America during GI (Fig 7e, Fischer et al. (2015)). A pattern of D-O cycles is also observed in the Australasian region (Mooney et al., 2011).

The Younger Dryas (~12.9 – 11.6 thousand years ago) was the last of a series of abrupt deglacial climate events and its end marks the beginning of the Holocene. It is sometimes considered the most recent D-O event, but it is not thought to be caused by ice-rafted debris and so is different. Charcoal records across North America were synthesized for the YD interval in part to address a hypothesis that a large comet impact caused the climate change and set of continent-wide wildfires. The fire synthesis (Marlon et al., 2009) provided no evidence for this, but did indicate widespread fire activity at both the beginning and end of the YD interval, suggesting that fire increases when large and rapid climate changes and associated ecosystem reorganizations occur.

In the central American lowlands, fire activity increased during Greenland stadials and decreased during interstadials (Correa-Metrio et al., 2012) although the direction of this relationship is heavily dependent on the chronology.

Figure 7

7. Post-glacial vegetation and fire changes

7.1 Europe

At the beginning of the Holocene, the higher summer insolation, rising greenhouse gas levels and retreating residual LGM ice-sheets caused a general warming of the climate that encouraged the spread of early-successional trees such as birch and pine across Europe and the arrival of other arboreal taxa from their glacial refugia. This post glacial development led to a rapid change in the abundance and composition of plant taxa (Birks and Birks, 2008; Marquer et al., 2014). The mid-Holocene represented the warmest period of the Holocene over higher latitudes of the Northern Hemisphere, and in Europe was characterized by the spread northward of temperate deciduous trees (e.g. hazel, elm, lime, oak and Alder; Birks, 1986). Over southern Europe, temperate deciduous vegetation also expanded during the mid-Holocene (Brewer et al., 2017; Collins et al., 2012; Davis et al., 2015; Prentice et al., 1996), indicative of cooler and wetter summers at this time over most (Davis and Brewer, 2009; Davis et al., 2003b; Hessler et al., 2014; Huntley and Prentice, 1988; Mauri et al., 2015; Wu et al., 2007), but not all of the region (Samartin et al., 2017). From the mid-Holocene, the climate cooled over northern Europe and generally warmed over southern Europe, following a decline in summer insolation (Imbrie et al., 1992) and weakening of the Earths latitudinal temperature and insolation gradient (Davis and Brewer, 2009). In the circum-Mediterranean lands, forest expansion was not limited by distance to glacial refugia and where moisture levels permitted, forests developed rapidly in the early Holocene, or indeed had already developed during the Late Glacial (e.g. Allen et al., 2002; Fletcher and Sanchez Goñi, 2008). In drier settings, including Mediterranean North Africa, steppic, scrub and open woodland landscapes often persisted into the Early Holocene (Campbell et al., 2017), delaying the maximum development of mixed Mediterranean and temperate forest cover until the later Early Holocene and Mid-Holocene. From the Mid-Holocene (ca. 5 ka), forests declined in the Western Mediterranean associated with a gradual aridification trend (Carrión et al., 2010; Chabaud et al., 2014; Fletcher and Sanchez Goñi, 2008), while in the central Mediterranean compositional changes including increase in Mediterranean elements is recorded (Allen et al., 2002; Desprat et al., 2013).

The development of pollen records at high sampling resolution, with strong dating control and often in a multiproxy investigative framework has also yielded a major contribution to the understanding of Holocene vegetation responses to climate on short timescales. Pollen records have played an important role in evaluating the speed of ecosystem response to global climate change at the onset of the Holocene. They reveal that vegetation responses to major climatic perturbation initiated within a few decades, on timescales similar to those observed in fast-reacting tracers such as the Greenland ice cores (Birks and Ammann, 2000). High-resolution pollen records also reveal vegetation responses to rapid climate changes during the Holocene. The 8.2 ka abrupt cooling event has been widely detected, for example (Ghilardi and O’Connell, 2013; Pross et al., 2009; Tinner and Lotter, 2001). Numerous pollen records also reveal that the 8.2 ka event is not unique, but rather one of several recurrent Holocene cooling events which impacted on vegetation development. For example, in the Western Mediterranean pollen records reveal multiple early Holocene climatic perturbations, as well as pervasive variability associated with the North Atlantic Bond Events (Burjachs et al., 2016; Pèlachs et al., 2011; Pérez-Sanz et al., 2013; Ramos-Román et al., 2018). More widely, especially sensitive dynamics can be observed at ecological margins, and pollen records are valuable for reconstructing climate impacts at mountain timberlines (Feurdean et al., 2016; Haas et al., 1998). At the sub-continental spatial scale, pollen records furthermore support the identification of oscillating behaviour in atmospheric circulation systems, thus contributing to the understanding of past dynamics of important modes of variability such as the North Atlantic Oscillation (Di Rita et al., 2018; Fletcher et al., 2013). Against the wealth of pollen evidence for sensitive and rapid vegetation response to Holocene climate variability can also be set important examples of resilience and inertia (Aranbarri et al., 2014) which can ultimately help to refine the understanding of the vegetation-climate interactions at the regional to global scale.

Pollen-based land cover reconstructions (REVEALS approach) show a decline in forest cover from ca. 6 cal kyr BP in temperate and northern Europe, while arable land indicators (such as cereals) become recurrent through time (e.g. Fyfe et al., 2015; Marquer et al., 2017; Marquer et al., 2014; Roberts et al., 2018) (Fig. 8). This landscape openness at a sub-continental scale is caused by intense Neolithic land clearance for agriculture practices. The impact of land-use is gradually increasing from the early farming (ca. 7.4 cal ka BP in Central Germany; (Shennan et al., 2013) to the last century. During the second half of the Holocene, human pressure increases and results in a spread of arable land, pastures and intensification of deforestation in most of Europe (e.g. Fyfe et al., 2015; Marquer et al., 2017; Ruddiman et al., 2016; Zanon et al., 2018). Land use is then regarded as the primary driver of this decline in forest cover although the role of climate should not be dismissed (Marquer et al., 2017). Identifying the relative role of climatic and anthropogenic forcing of vegetation changes on different temporal and spatial scales is actually a great challenge based on pollen data (Kuosmanen et al., 2018; Marquer et al., 2018; Marquer et al., 2017; Reitalu et al., 2013). The major anthropogenic impacts occur during the last century, although vegetation still remains climatically sensitive (Marquer et al., 2017). In addition, pollen-based REVEALS modelling (Marquer et al., 2014) indicates an underestimation of grassland cover and later timing of landscape openness during the Bronze Age in temperate and northern Europe compared to the use of untransformed pollen data (pollen proportion). Deforestation was therefore more important and started earlier than previously thought. The use of the REVEALS model also provides a deeper understanding of the vegetation rate of changes and the changes in vegetation composition and diversity over time and space.

Figure 8

Over the past 30 years, charcoal-based paleofire studies have largely developed in Europe because of raising awareness about the importance of fire as both a tool for human-driven landscape transformation and a major ecological factor closely linked to climate and vegetation. This research provided crucial methodological advances like the calibration of the sedimentary charcoal records (Adolf et al., 2018a; Tinner et al., 1998; Tinner et al., 2006), but above all a more comprehensive understanding of human-driven fires imprints on forested ecosystems (Tinner et al., 2005), of the mechanisms causing the decline of certain key species (Morales-Molino et al., 2017b; Tinner et al., 1999), and of the connections between climate variability and fire regimes in previously assumed low flammability temperate areas (Clark et al., 1989).

Charcoal-based studies made a major contribution to the assessment of the chronology and relevance of fire use as a landscape management tool. The first evidence of forest clearance by fire is usually related to the timing of agriculture arrival to the different European regions: e.g. ca. 8 cal kyr BP at the Mesolithic-Neolithic transition in Italy (Vannière et al., 2008), 6.5 cal kyr BP in south-western France (Rius et al., 2009), 5.7 cal kyr BP in southern Germany (Clark et al., 1989) and ca 4 cal kyr BP in southern Sweden (Olsson et al., 2010). Significant vegetation changes such as the decline of several keystone tree species like holm oak (*Quercus ilex)* (Colombaroli et al 2009) and silver fir (*Abies alba*) in the southern Alps and Tuscany were attributed to the early human use of fire (Colombaroli et al., 2007; Henne et al., 2013; Tinner et al., 1999). Climate remains however the main driver of fire regimes at regional to continental scales until the last millennia (Marlon et al., 2013). For instance, increased fire activity between 11.7 and 6 cal kyr BP was related to stronger boreal summer insolation and/or summer drought (Power et al., 2008) while the decreasing fire activity/frequency recorded since the mid-Holocene is attributed to decreasing seasonality and/or wetter summers (Vannière et al., 2011) (Rius et al., 2011). The role of fire, of either anthropogenic or natural origin, in the expansion of some emblematic tree species such as *Fagus sylvatica* (e.g. Giesecke et al., 2007; Tinner and Lotter, 2006; Valsecchi et al., 2008), on forest composition (Carrión, 2002; Carrión et al., 2003; Gil-Romera et al., 2010), and on the historical vegetation dynamics of currently protected areas (Morales-Molino et al., 2017a) (Morales-Molino et al., 2017b) remains matter of debate.

The paleofire research has eventually made available a large dataset of individual charcoal and fire frequency records that has enabled a more comprehensive assessment of fire-vegetation-climate-human activities linkages at the continental scale. Recently, a synthesis of around 20 high-resolution charcoal records from Portugal to Romania (Vannière et al., 2016) highlighted that European fire regimes strongly depend on elevation, which underlines the crucial role of vegetation productivity (biomass availability) of temperate and Mediterranean biomes on fire activity at millennial timescales. This work also showed that fire frequency peaked at *ca* 7-6 cal kyr BP at the European scale, and remained stable at high level from 4 kyr BP onwards, while burned biomass followed an inverse pattern. The decrease in southern European biomass burning since 7 ka is in line with both orbitally-induced climate cooling and reduction in biomass availability because of land use.

7.2 North America

Due to a long history in palynological research in North America, more than 1 300 pollen sequences are included in the Neotoma paleoecology database (Williams et al., 2018) covering entirely or part of the last 20 kyr, although most of them only contain the Holocene period. Several state of the art papers aim at retracing the North American postglacial vegetation history, such as Gavin and Hu (2013), Wigand (2013), Whitlock and Brunelle (2007) and Whitlock (1992) for the western part of the sub-continent, Williams and Shuman (2013), Willard (2013), Grimm and Jacobson Jr (2004), Webb et al. (2003), Davis (2015), Davis (1984), Naughton et al. (2015) and Blarquez and Aleman (2016) for the eastern part and Bigelow (2013) for regions above 60°N. In North America, the deglacial warming (19-11 ka) along with the retreat North American ice-sheets resulted in large range shifts of terrestrial ecosystems. Pollen records reveal a northward and east-west expansion of arboreal taxa in NE North America. For instance, northern pines and spruce began their northward migration while mesic and cool-temperate deciduous tree taxa expanded in the southeastern United States after 17 cal ka BP (Willard, 2013). These cold-tolerant conifers expanded with Betula and Alnus in regions formerly occupied by the Laurentide ice-sheet in the NE North America while Pinus, Artemisia and Ambrosia migrated eastward. In the northwestern, high-elevation mesophytic forest taxa expanded to the west of the Cascade Range and Sub-Alpine parkland to the east when warmth and humidity increased and the Cordilleran ice-sheet retreated (at ~16 cal ka BP), while temperate arboreal taxa only appeared at ~14.5 cal ka BP associated with Sub-Alpine species (Whitlock and Brunelle, 2007). This plant association no longer exists today in North America. No-analog pollen assemblages characterized by high abundances of the conifers Picea and Larix, the hardwoods Ulmus, Ostrya/ Carpinus, Fraxinus and Quercus, and sedges are widely recorded in the Midwest during the late glacial (17-12 ka BP). This unusual taxa combination is known as mixed parkland or spruce parkland resulting from the individualistic plant response to the no-analog climate conditions characterizing the last deglaciation and helped, at least in some areas, by megafaunal population decline (Jackson and Overpeck, 2000; Williams and Shuman, 2013; Williams et al., 2001).

In the eastern North America, the pollen records reveal vegetation shifts in response to the Younger Dryas-Holocene transition warming. *Quercus* became the dominant forest element in the oak-pine association developing in the southeast due to warmer but persistent dry conditions while in the northeast, white pine, oak and hemlock expanded in areas formerly occupied by cold-tolerant taxa in response to increased warmth and moisture availability (e.g. Naughton et al., 2015; Willard, 2013). In the northeast, temperature and humidity continues to increase in the northern areas to reach a maximum during the Mid-Holocene as suggested by the expansion of pine in New England and oak with some mesic tree taxa toward the south during the Early Holocene followed by hemlock and beech during the Mid-Holocene (Naughton et al., 2015; Williams and Shuman, 2013). In the southeast, the increase in humidity only occurred in the Mid-Holocene as indicated by the widespread oak-dominated forest decline and pine expansion. Pollen based reconstructions support stronger than present annual precipitation at 6 ka for most of the eastern North America (Bartlein et al., 2011). The Mid-Holocene wet conditions were interrupted a few millennia later, which resulted in the replacement of pine by oak in the south and likely the well-known hemlock sudden decline widely recorded at 5.5 ka in the northeastern US, although a pest outbreak cannot be discarded (Williams and Shuman, 2013 and references therein). Eastern North American pollen records indicate that dry conditions persisted into the Late Holocene. The Late Holocene increased humidity suggested by vegetation changes in Northeast (NE) US (e.g. Naughton et al., 2015) is supported by tree ring, varve thickness and lake level data (Marlon et al., 2017). A cooling trend in this region over the last 2.5 millennia is also shown by pollen-based summer and annual temperature reconstructions (Marlon et al., 2017 and reference therein). Noticeable human impact on vegetation began with the European colonization 500 years ago, through land clearance practices as shown the large reduction in tree cover and expansion of *Ambrosia* recorded in eastern North America.

In the western North America, the Holocene vegetation changes present a complex pattern due to the heterogeneity of landscape and climatic influences. A main feature revealed by pollen records is that Early Holocene contrasting hydrological changes between the northern and southern regions. Drier (and warmer) than present summers are recorded in the Pacific Northwest to southeastern Alaska and over much of the Northern Rocky Mountains and wetter than present conditions in the American Southwest and the summer-wet regions of the Rocky Mountains in response to stronger summer monsoons (Whitlock and Brunelle, 2007). In the Great Basin, drought-tolerant shrub communities established in the Early Holocene associated to drier conditions than today (Jimenez-Moreno et al., 2010; Wigand, 2013). Pollen-based quantitative reconstructions show lower temperatures at 6 ka than at present and the anomaly also appears stronger in the southwest likely related to the cloud cover generated by the monsoonal circulation (Bartlein et al., 2011). From the middle to late Holocene, western North American pollen records indicate cooler conditions along with increased humidity in the north and dryness in the south likely related to a weakening of the summer monsoon (Whitlock and Brunelle, 2007).

The North American vegetation also responded to higher frequency climatic changes during the Holocene. For instance, the 8.2 ka abrupt cooling event is clearly detected in NE pollen North America (Shuman et al., 2002a). Pollen based temperatures reconstructions show warmer conditions during the Medieval Climate Anomaly than during the Little Ice Age across North America (Viau et al., 2012). Even though differences are subtle, both events are also detected in other proxy-derived reconstructions (Marlon et al., 2017).

Reconstructions of biomass burning from charcoal-based syntheses in four broad regions of North America are generally marked by a gradual, persistent increase in biomass burning during the Holocene except for the north eastern boreal forest (Blarquez et al., 2015). There were large deviations from this general trend in the early Holocene, however, with millennial-scale intervals of high fire activity that often started and ended very abruptly (Marlon et al., 2013). For example, in the northwestern boreal forests, there was relatively high fire activity from 12-10 ka, and in the northeast, there was widespread, intensive fire activity from about 10-8 ka as compared with later intervals. In contrast, fire activity was very low in the west at that same time as compared with late-Holocene fire activity. All regions showed gradual increases during the middle Holocene, and only the continent's interior grass and woodlands show maximum Holocene burning prior to 2 ka – here fire was highest at 4 ka and has subsequently declined. Anthropogenic effects on fire are obvious in the biomass burning records during the past century, but the 4-ka peak in burning in the central region likely reflects anthropogenic activity as well.

7.3 South America

Evidence of Holocene environmental change from tropical South America showed that the continent was impacted by significant changes in precipitation and intensified human occupation (Prado et al., 2013; Smith and Mayle, 2018; Urrego et al., 2009). A mid-Holocene drought (MHD) is recorded in the Andes, the savannas and Amazonia (Baker et al., 2001; Berrío et al., 2002; Bush et al., 2007; Mayle et al., 2000; Paduano et al., 2003; Rowe et al., 2002; Urrego et al., 2013b) and had a significant impact in the climate and fire regimes of the region. Multiple records indicate lowering of lake levels and reductions in sediment accumulation or sedimentary hiatuses (Bush et al., 2007). However, mesic forest prevailed around sites located in the core of Amazonia and the eastern flank of the Andes (e.g. Bush et al., 2007; Urrego et al., 2010; Urrego et al., 2013a) while savanna vegetation and dry forest expanded in seasonal parts of South America or nearby ecotones, (e.g. Berrio et al., 2002; Berrío et al., 2002; Mayle et al., 2000). The MHD is also reported in subtropical South

America by paleo-data syntheses predominantly based on pollen records (Prado et al., 2013; Smith and Mayle, 2018). In particular, the replacement of wet forests by shrubs and grasslands are frequently observed in southeastern Brazil during the mid-Holocene (e.g. Behling and Safford, 2010). Only in Northeast Brazil is evidenced an opposite trend, with more humid conditions during the mid-Holocene than during the late Holocene (Smith and Mayle, 2018). Precipitation generally increased during the late Holocene and multiple studies have revealed the interplay between changing climate conditions and human occupation. Southward, in temperate regions, records of past vegetation mainly from western Patagonia generally start after the retreat of the Patagonian Ice Sheet fully extended over the lands during the Last Glacial Maximum (Bennett et al., 2000; Heusser, 1995; Moreno et al., 1999) (Abarzúa et al., 2004; Fontana and Bennett, 2012; Haberle and Bennett, 2004; Markgraf and Huber, 2010; Villa-Martínez and Moreno, 2007). At these southern latitudes, vegetation changes followed the same climate trends evidenced by Antarctic ice core records. In particular, the development of *Nothofagus* forest during the warming of the last deglaciation is interrupted by a cold and wet event contemporaneous with the Atlantic Cold Reversal before to reach Holocene climate conditions (Montade, 2011; Moreno and Videla, 2016). Starting from ca. 11.5 ka, the early Holocene is marked by a development of thermophilous tree taxa characterizing a warm and dry phase in northwest Patagonia (Montade et al., 2012; Moreno, 2004). A subsequent expansion of the cold-resistant conifers from 7.5 ka indicate more variable climate conditions superimposed on a cooling trend associated with an increase in precipitation during the mid-Holocene that has persisted until the present (Henríquez et al., 2015). Further south, in southwest Patagonia (>50°S), the forest-steppe ecotone shifts in lowlands show also a precipitation decrease during the early Holocene followed by a precipitation increase (Fletcher and Moreno, 2011; Moreno et al., 2010). This pattern suggests a co-variability of moisture changes through western Patagonia related to reduced intensity of the southern westerlies during the early Holocene and a sustained increase afterward. However several paleoenvironmental records from southwestern Patagonia indicate a different pattern characterized by wetter/windier conditions at the beginning of the Holocene followed by intermediate conditions to reduced precipitation from the mid- to late Holocene (Kilian and Lamy, 2012; Lamy et al., 2010). Resolving these inconsistencies in southwest Patagonia still needs more high-resolution records of past vegetation and climate dynamics.

Synthesis of fire records in South America since the LGM (Power et al., 2010a) show that fire regimes increased during the late glacial and towards the Holocene. Such an increase in continental-scale fire activity was linked to precipitation seasonality and suggests that fires were mostly likely natural (Power et al., 2010a). However, precipitation seasonality explains only part of the observed variability highlighting the importance of taking fuel availability into account.

The mid-Holocene dry event also had a significant impact in fire regimes in tropical South America. Urrego et al. (2013a) compiled fire records from forest, savanna and ecotone sites in western Amazonia. This regional synthesis showed increased fire activity in forest sites at around 9, 6 and 3 ka (Urrego et al., 2013a). The 6-ka fire peak seems the most consistent amongst sites and largely coincides with the MHD. Regional drought during mid-Holocene resulted in increased fire activity in sites where fuel was available. Increased fire activity was also observed in savanna sites during the late Holocene and was probably associated with human occupation (Maezumi et al., 2018; Urrego et al., 2013a; Watling et al., 2017). Finally, multiple fire records in lowland Amazonia consistently show a signal of fire suppression around 1500 AD when pre-columbian populations decreased due to the arrival of European colonizers (Burbridge et al., 2004; Bush et al., 2000; Bush et al., 2007; Mourguiart and Ledru, 2003; Urrego et al., 2013a).

7.3 Central and West Africa

The distribution of current forests and savannas in West and Central Africa is thought to be the legacy of the long-term history of climate and human impacts. Indeed, paleo-environmental reconstructions suggest that West and Central African forests have experienced a succession of contraction and extension (Maley, 1991; Vincens et al., 1999) in response to dry and humid periods since the Last Glacial Maximum (LGM, ~21 cal ka BP). The LGM was a period of very low precipitation; temperatures and paleodata (Maley, 1991; Shanahan et al., 2016) suggest that during this period tropical forests were even reduced to only few refugees in Central Africa (Maley, 1996). After the Younger Dryas (from ~12.9 to ~11.7 ka BP), which was a short but intensely dry period (Shanahan et al., 2016), rainfall started to increase at the beginning of the Holocene. During this period, also known as the African Humid Period (deMenocal et al., 2000; Shanahan et al., 2015), rainfall was apparently higher than present-day. The tropical forest was more widespread across West and Central Africa than it currently is. Pollen data suggest that tropical forest was present in the Adamawa Plateau of Cameroon (Lézine et al., 2013; Vincens et al., 2010) and the Niari Valley of the Republic of Congo (Vincens et al., 1994; Vincens et al., 1998). The African Humid Period ended abruptly ~4 ka BP, but sequentially in latitude (Shanahan et al., 2015), with a period of reduced precipitation and major droughts that lasted until 1.2 ka BP (Vincens et al., 1999). This period, called the ‘third millennium rainforest crisis’, is divided into two major phases (Maley, 2002; Maley et al., 2018; Vincens et al., 1999). The first phase (~4 ka BP), is associated with an abrupt decrease in rainfall (Maley et al., 2018), that impacted areas in periphery of the Congo Basin and was responsible for the opening of coastal savannas in Central Africa (Elenga et al., 1994; Ngomanda et al., 2005) and of the Dahomey Gap in West

Africa (Salzmann and Hoelzmann, 2005). During the same period, savanna vegetation was also heavily modified, with a gradual (during AHP termination) and abrupt (3 ka BP crisis) floristic shifts from Guinean to Sudan-Guinean savanna (Salzmann et al., 2002).

The second phase was short and abrupt, between 2.5 and 2 ka BP, and showed strong climate seasonality as suggested by sea surface temperature reconstructions and geological limestone zones (Maley et al., 2018). Vegetation reconstructions from pollen data showed increasing abundance of pioneer and secondary forest trees, and grasses (Vincens et al., 1999) suggesting that during this period, forests were highly disturbed. Some authors suggested the opening of a north-south savanna corridor in the Sangha River Interval (Maley and Willis, 2010) that would have permitted the migration of Bantu-speaking people, but the existence of this corridor is not supported by recent phytolith records in the region (Bremond et al., 2017). Interestingly, the relative role of climate and people in the third millennium crisis has been a matter of some debate in the literature. Some authors tend to affirm that the Bantu migrations actively participated to the large-scale forest disturbance (Bayon et al., 2012; Garcin et al., 2018) while others favor the climate hypothesis (Giresse et al., 2018; Lézine et al., 2013; Maley et al., 2012; Neumann et al., 2012b). This debate is not yet resolved, but it seems that the migration of Bantu people from the border of Cameroon and Nigeria, where they originated, was concomitant to this abrupt climate change (Maley et al., 2018). Moreover, Bantu people were agriculturalists and metallurgists (Bostoen et al., 2015), able to use slash-and-burn and needing large quantities of wood for metallurgy. They were farming pearl millet (Neumann et al., 2012a) and cattle (Grollemund et al., 2015) within the present-day tropical rainforest of western and central Africa. Even if they were not responsible for this large scale event, they may have caused more localized perturbations, through canopy opening and wood collection, in the forest (Neumann et al., 2012a; van Gemerden et al., 2003). Additionally, with or without the presence of people, even in the deepest part of the forest, charcoal were found in lakes, wetlands and soils, suggesting extended forest burning (Biwolé et al., 2015; Hubau et al., 2015; Morin-Rivat et al., 2016; Tovar et al., 2014). An increase in the occurrence of charcoal is registered when seasonality increased drastically ~2.5 ka BP (Hubau et al., 2015), with a possible role of people in maintaining newly formed savannas in peripheral areas of the Congo forest (Neumann et al., 2012a). After 1.2 ka BP, rainfall started to increase again, and forest expanded. This trend of forest transgression is still observed today in some areas (Aleman et al., 2018b; Guillet et al., 2001; Youta Happi, 1998).

6. Conclusion and perspectives

Terrestrial plant-derived microfossils -- pollen, microcharcoal and phytoliths -- have been analysed in both terrestrial and marine sedimentary archives for several decades and contributed to the current knowledge of past changes in vegetation and fire dynamics, Quaternary paleoclimates and paleoecology. While the study of pollen is considered to be a “classic” tool in this respect, interest in microcharcoal and phytolith represents a more recent area of growth.

Several different techniques are employed to extract microfossils because of the diversity of Quaternary sedimentary contexts, but the main objective is to concentrate microfossils for microscopic observations. Identification and counting of pollen, microcharcoal and phytolith require specialist expertise. Terrestrial plant microfossil data from sedimentary archives are time-consuming to generate but are rich in information on past local to sub-regional paleoenvironments. It is important therefore to continue improving the identification and interpretation of these microfossils and to keep training the next generation of scientists.

The datasets generated also need to be carefully archived and should benefit from long term storage. Over the past 15 years, the growing wealth of plant microfossil paleodata, the establishment of data sharing protocols in the scientific community and the development of large (continental to global) datasets, and the development of new analytical approaches have provided the opportunity to tackle new scientific questions. Key topics at regional and global scales include the response of vegetation and fire to climate change, as well as feedback mechanisms related to both vegetation, such as the vegetation-(snow)-albedo feedback, and fire, such as fire feedback on the carbon cycle and on albedo. Those databases are also key for developing data-model comparison exercises and evaluating modeling results of past climate, vegetation and fire. Finally, they are also essential for applying lessons from the past to respond to current biodiversity, conservation and management issues.

This review highlights strong regional variability in the response of past vegetation and fire to Pleistocene climate changes. The different studies synthesized here nevertheless suggest similar patterns: vegetation and fire respond to orbital, millennial and sub-millennial climate changes; and their response may be rapid, within a few hundred years. This review also highlights that climate is the major driver of vegetation and fire regimes since at least the Middle Pleistocene. Human activities impacted on vegetation and fire at local scales mainly since the mid-Holocene and most significantly during recent millennia.

Although terrestrial plant microfossils are well-established tools in Quaternary science, the full extent of the information they contain remains to be exploited. Further calibration studies are needed, i.e. coupling microfossil accumulation in sediments with remotely sensed vegetation and fire. In addition, it is important to keep improving the taxonomic resolution of these plant microfossils. For instance, morphometric analyses of pollen grains coupled with statistical classification methods can in some cases provide greater taxonomic detail within visually similar groups, e.g. *Pinus* (Desprat et al., 2015; Lindbladh et al., 2002).

Morphological analyses of microcharcoal may bring also important new information for the determination of burnt vegetation type although is not yet a widely used technique (Hawthorne et al., 2018). Recent studies employing techniques from organic geochemistry also highlight how the chemical composition of the preserved pollen wall may yield valuable insights into taxonomy and/or environmental conditions during pollen formation such as past solar radiation (e.g. Bell et al., 2017; Julier et al., 2016; Willis et al., 2011). In sum, the prospects are great for exciting new insights from the study of terrestrial plant microfossils to the understanding of Quaternary environmental and climatic change.

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Figure captions

Figure 1: Reconstructing vegetation and fire using plant microfossils (pollen, phytolith and microcharcoal) (modified from Patterson et al. (1987)).

Figure 2 : Examples of classical fossil pollen grains and spores presented by grain arrangement and pollen apertural type: a. Pinus, b. Ericaceae, c. Cereal type, d. Poaceae, e. *Carpinus betulus*, f. *Betula*, g. Amaranthaceae, h. Cyperaceae, i. *Aspodelus*, j. *Scabiosa*, k. *Acer*, l. *Quercus* deciduous type, m. *Erodium*, n. *Olea*, o. Brassicaceae, p. *Aster* type, q. *Centaurea scabiosa* type, r. *Fagus*, s. *Cichorioideae*, t. *Ephedra distachya* type, u. *Ephedra fragilis* type, Spores: v. *Isoetes*, w. *Polypodium vulgare* type.

Figure 3: Examples of microcharcoal preserved in marine deep-sea core sediments. a) core MD95-2042 (Daniau et al., 2007); b) core IOPD Site U1385 (Daniau, work in progress); c) core MD04-2845 (Daniau et al., 2009b); d) core MD96-2098 (Daniau et al., 2013).

Figure 4: Examples of classical phytoliths grouped into five large categories. Grass silica short cells (a-i); Bulliform cells (i); woody dicotyledon (j-l); Family-specific families morphotypes (m-o); Non-diagnostic morphotypes (p).

Figure 5: Location of the terrestrial and marine pollen and microcharcoal records presented in Fig. 6 and 7. 1- Funza, 2-Heqing lake, 3-MD96-2098 , 4- Tenaghi Philippon, 5-MD95-2042. The background map represents the present-day potential vegetation after (Levavasseur et al., 2012).

Figure 6: Response of vegetation to orbital variability. (a) summer insolation at 65°N from (Laskar et al., 2004), (b) atmospheric CO_2 EPICA Dome C (Bereiter et al., 2015; Monnin et al., 2001; Petit et al., 1999; Siegenthaler et al., 2005), (c) Antarctic air temperature from EPICA-Dome C (Jouzel et al., 2007), (d) LR04 benthic $\delta^{18}O$ (Lisiecki and Raymo, 2005), (e) arboreal pollen percentages data from Tenaghi Philippon record (Tzedakis et al., 2006), (f) arboreal pollen from Funza sequence (Torres et al., 2013), (g) *Tsuga* pollen percentages from

Heqing lake record (Zhisheng et al., 2011). The grey dashed bar indicates the position of the Mid-Brunhes Event (MBE).

Figure 7: Response of fire and vegetation to orbital and millennial variability. (a) Antarctic air temperature (Jouzel et al., 2007), (b) summer insolation at 25°S (Berger, 1978), (c) biomass burning from southern Africa (microcharcoal record from core MD96-2098) (Daniau et al., 2013), (d) biomass burning (z-score of transformed charcoal, about 700 sites) (Daniau et al., 2012), (e) fire peak frequency from Greenland ice core (Fischer et al., 2015), (f) Greenland air temperature from NGRIP ice record (Landais et al., 2004); data compiled in Sánchez Goñi et al. (2008), (g) biomass burning from southwestern Iberia (microcharcoal MD95-2042 record) (Daniau et al., 2007), (h) Mediterranean forest (pollen percentages from core MD95-2042) from southwestern Iberia (Chabaud et al., 2014; Sánchez Goñi et al., 2000a; Sánchez Goñi et al., 2008).

Figure 8: Example of pollen-based modelling land cover reconstruction for Central Europe (Marquer et al., 2014).

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