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1 Peatlands as an archive of ancient DNA for paleobiodiversity 2 reconstructions

3 Ilaria Fracasso¹, Claudio Zaccone², Nikolay Oskolkov³, Luca Da Ros¹, Anna Dinella¹, Tanja
4 Mimmo¹, Luca Belelli Marchesini⁴, Pietro Buzzini⁵, Ciro Sannino⁵, Benedetta Turchetti⁵, Stefano
5 Cesco¹, Gael Le Roux⁶, Giustino Tonon¹, Cristiano Vernesi⁴, Maurizio Ventura¹ and Luigimaria
6 Borruso¹

7 ¹ Faculty of Agricultural, Environmental and Food Sciences, Free University of Bozen-Bolzano, 39100 Bolzano, Italy

8 ² Department of Biotechnology, University of Verona, 37134 Verona, Italy

9 ³ Department of Biology, National Bioinformatics Infrastructure Sweden, Science for Life Laboratory, Lund University, 221 00 Lund,
10 Sweden

11 ⁴ Forest Ecology Unit, Research and Innovation Centre, Fondazione Edmund Mach, 38098 San Michele all'Adige (TN), Italy

12 ⁵ Department of Agricultural, Food and Environmental Science, University of Perugia, 06123 Perugia, Italy

13 ⁶ Laboratoire Ecologie Fonctionnelle et Environnement (UMR5245 CNRS/UPS/INPT), Université de Toulouse, 31326 Castanet-
14 Tolosan, France

16 Abstract

17 Natural and human-induced environmental changes deeply affected terrestrial ecosystems throughout
18 the Holocene. Paleoenvironmental reconstructions provide information about the past and allow us
19 to predict/model future scenarios. Among potential records, peat bogs are widely used because they
20 present a precise stratigraphy and act as natural archives of highly diverse organic remains. Over the
21 decades, several techniques have been developed to identify organic remains, including their
22 morphological description. However, this is strongly constrained by the researcher's ability to
23 identify residues at the species level, which typically requires many years of experience. In addition,
24 potential contamination hampers the use of these techniques to obtain information from organisms
25 such as fungi or bacteria. Environmental DNA metabarcoding and shotgun sequencing could
26 represent a solution to detect specific groups of organisms without any a priori knowledge of their
27 characteristics and/or to identify organisms that have rarely been considered in previous
28 investigations. Moreover, shotgun metagenomics may allow the identification of bacteria and fungi
29 (including both yeast and filamentous life forms), ensuring discrimination between ancient and
30 modern organisms through the study of deamination/damage patterns. In the present review, we aim
31 to: i) present the state of the art on methodologies in palaeoecological and paleoclimatic studies
32 focusing on peat core analyses, proposing alternative approaches to the classical morphological
33 identification of plant residues, and ii) suggest molecular approaches that will allow the addition of
34 proxies such as invertebrates, fungi, and bacteria, which are rarely used in paleoenvironmental
35 reconstructions.

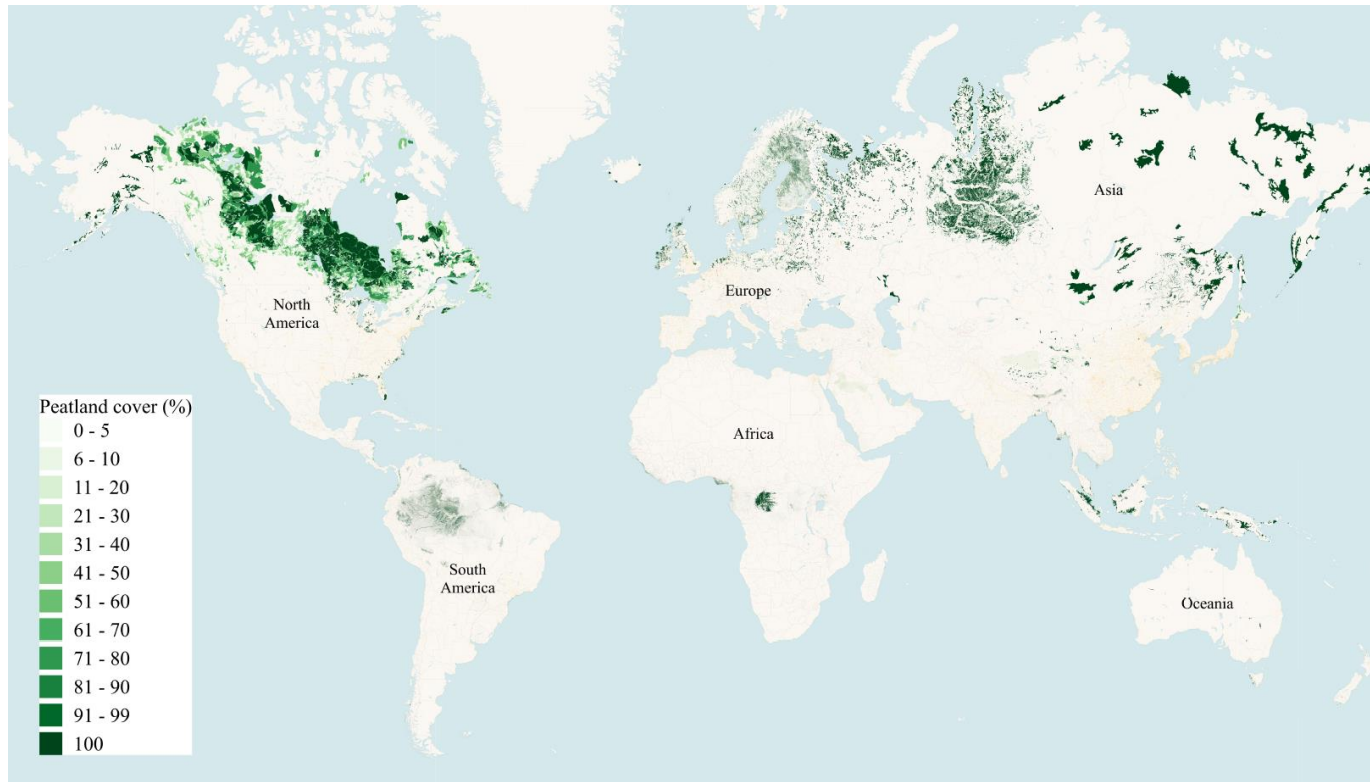
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37 **1. Introduction**

38 To comprehend the extent of anthropogenic impacts on biogeochemical cycles and predict future
39 global change scenarios, natural archives can be used to open a window to the past to understand
40 natural processes prior to human influence (Shotyk et al., 2004). Natural archives, substrates that
41 grow or accumulate over time, can provide quantitative insight into physical and chemical processes
42 in historic and pre-historic times, thereby preserving a record of environmental changes. Examples
43 of highly reliable archives include lacustrine and marine sediments, tree rings, peat bogs, alpine and
44 polar ice, as well as carbonate formations (Shotyk et al., 2004; Weiss et al., 1999). The use of each
45 has inherent advantages and disadvantages; for example, separating atmospheric from non-
46 atmospheric signals is challenging when using lake sediments. These archives also differ in their time
47 spans, ranging from several millions of years for deep-sea sediments (Christensen et al., 1997; von
48 Blanckenburg et al., 1996), to 15,000 years for peat bogs (Shotyk et al., 1998), to only a few hundred
49 years for coral and tree records (Hagemeyer, 1993; Shen & Boyle, 1987). Ice caps and peat bogs are
50 unique archives because they are directly linked to the atmosphere. Ice cores have provided valuable
51 records of the concentrations and isotopic compositions of gases, soil dust, volcanic ash particles,
52 trace metals, and direct evidence of links between greenhouse gas concentrations/emissions and
53 climate (Andersen et al., 2004; Boutron, 1995; Hong et al., 1996). Peatlands are recognized as
54 excellent archives of palaeoclimate and palaeovegetation changes (Lamentowicz et al., 2008, 2009;
55 Moore et al., 1991; Van Geel, 1978), fire occurrence (Marlon et al., 2016; Sim et al., 2023), and
56 records of historical human activity (Le Roux et al., 2020; Pheiffer-Madsen, 1981; Shotyk et al., 1998,
57 2017; Zaccone et al., 2007).

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60

61 **Figure 1** Global peatland distribution (data from Xu et al., 2018).

62 Compared to glaciers, peatlands have several unique advantages: i) they occur in every climatic zone
63 and continent from lowlands to high mountains, covering roughly 3–5% of the Earth's land surface
64 (Limpens et al., 2008; Roulet et al., 2007; Xu et al., 2018) (Figure 1) and offer the possibility to study
65 changes at a local scale; ii) due to climate change, glaciers are in danger of disappearing almost
66 completely within 60 years (Festi et al., 2021; Marzeion et al., 2014; Zemp et al., 2015); and iii) some
67 glaciers belong to the group of so-called “temperate glaciers”, which implies that their icy bodies are
68 close to the melting pressure point, leading to melting and percolation phenomena (Di Stefano et al.,
69 2019; Eichler et al., 2001; Zhang et al., 2015) that can cause contamination and uncertainties in the
70 dating. At the same time, one limitation of sedimentary records, which include peat bog cores, is that
71 they provide more compact but less detailed inventories. While ice cores from glaciers exhibit rapid
72 accumulation rates, reaching several cm/yr (Boutron, 1995; Haeberli & Wallén, 1992), peat bogs are
73 deposited much more slowly, typically in the range of 0.5–1 mm/yr (Barber et al., 1994; Poto et al.,
74 2013; Shotyk et al., 1998), although a few exceptions of much higher accumulation rates have been
75 reported (Lähteenoja et al., 2012; Zaccone et al., 2017).

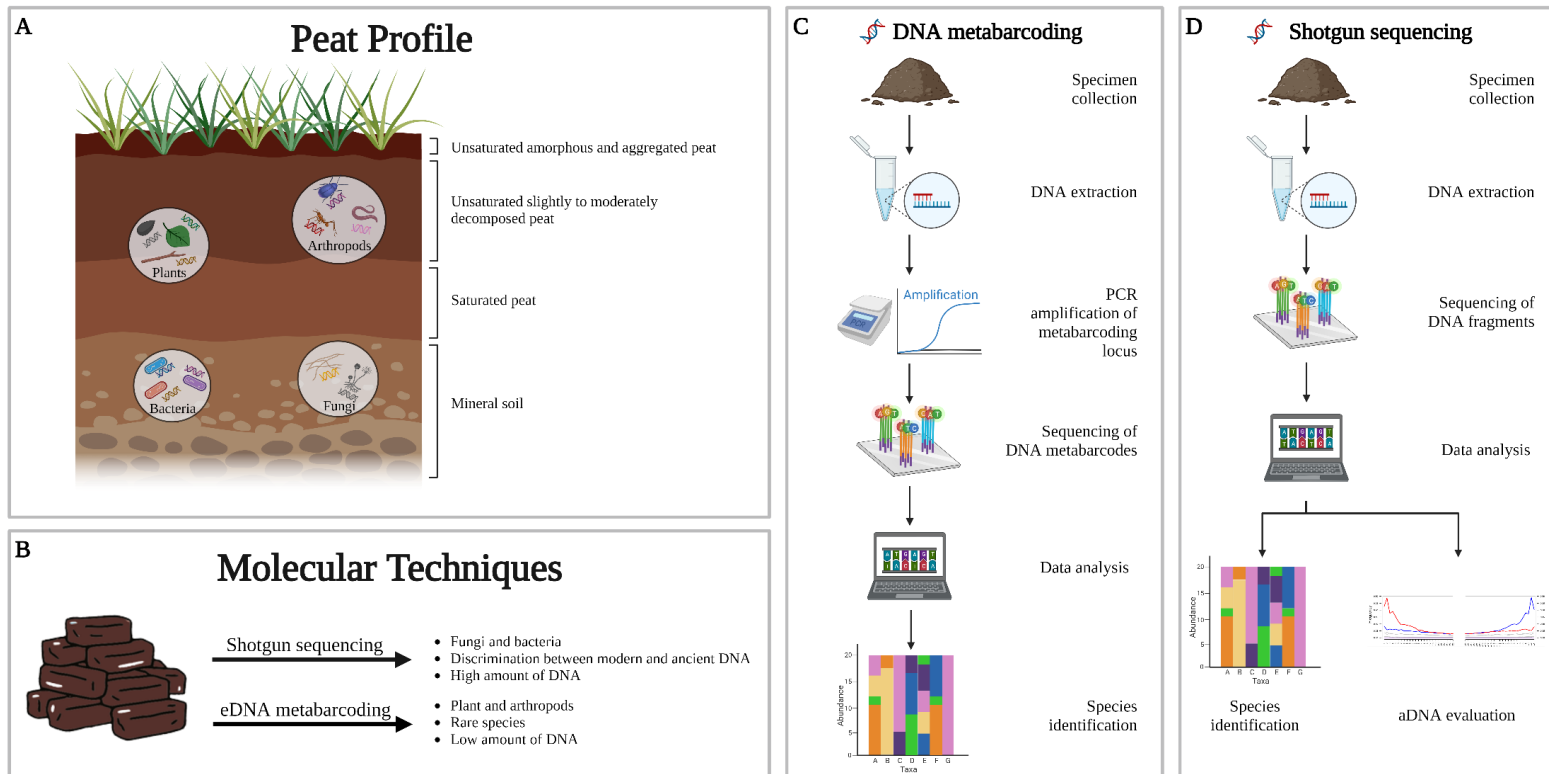
76 Peatlands are defined as areas with or without vegetation with a naturally accumulated surface peat
77 layer (Joosten et al., 2017). They include landscapes still actively accumulating peat (mires),
78 landscapes that are no longer accumulating and do not support the principal peat-forming plants, and
79 peatlands used for economic uses.

80 Peatlands where peat is currently being formed (mires; Sjörs, 1948) are terrestrial wetland ecosystems
81 in which the production of organic matter exceeds its decomposition, because the waterlogged
82 conditions prevent plant material from fully decomposing which leads to the sedentary accumulation
83 of peat (Clymo, 1983). The very slow decomposition processes are driven mainly by temperature,
84 oxygen availability, water saturation, litter quality and pH (Clymo, 1991).

85 Peat is a complex, blond to black material that consists of partially fossilized plants of varied botanical
86 composition (*e.g.*, mosses and other bryophytes, sedges, grasses, shrubs, or trees) and degree of

87 decomposition and humification, along with a small component of amorphous and crystalline
88 inorganic compounds (Shotyk et al., 1998; Zaccone et al., 2018). Under undisturbed conditions, the
89 organic matter content in peat is >65%, while organic carbon (C) ranges between 50–60% dry weight
90 (Loisel et al., 2014). Peatlands are thought to have a minor role in global carbon (C) cycling dynamics
91 since their atmospheric carbon sequestration capacity (a sink of $\sim 0.14 \text{ Gt yr}^{-1}$) (Gallego-Sala et al.,
92 2018) is equivalent to only $\sim 1\%$ of human fossil fuel emissions, and 3.1–5.4% of the current C sink
93 of all terrestrial ecosystems (Friedlingstein et al., 2022). However, despite their limited global extent,
94 peatlands have a major role in organic C storage, containing about 21–25% (610–644 PgC) of the
95 global soil C stock (Leifeld & Menichetti, 2018; Loisel et al., 2021), with $\sim 550 \text{ PgC}$ of this being in
96 boreal peatlands alone (Yu et al., 2010). This large and dense C store accumulated over millennia due
97 to the slow process of belowground peat accumulation under water saturation, particularly during the
98 Holocene following the Last Glacial Maximum (LGM)(Cobb & Cecil, 1993; Lyons & Alpern, 1989).
99 The capacity to sequester atmospheric C over extended periods, acting as a cooling mechanism for
100 Earth’s climate throughout most of the Holocene (Frolking et al., 2006; IPCC, 2013), combined with
101 the present large C reserve, make peatlands a crucial element of C balance in the global climate
102 change scenario.

103 A peat profile shows a fossilized record of vegetational changes, consisting of macrofossils (*e.g.*,
104 partially decomposed plants, charcoal particles, and animal remains) and microfossils (pollen grains,
105 spores, and other unicellular or very small multicellular organisms), which collectively provide a
106 wealth of information and evidence about the development of the peatland and environmental changes
107 through time (Figure 2a). In particular, ombrotrophic peatlands (*i.e.*, bogs) are only fed by dry and
108 wet atmospheric depositions and isolated from groundwater (Clymo, 1984; Damman, 1978).
109 Consequently, they are considered precious archives to study climate-environment relationships since
110 their genesis is directly linked to the atmospheric conditions during peat formation (Magnan et al.,
111 2018; Naafs et al., 2019; Zaccone et al., 2011).



112

113 **Figure 2** A. Scheme of a peatland profile and the main target organisms of molecular methods; B. Molecular techniques to analyse eDNA from peat samples, with a focus on their
 114 main characteristics; C. Complete workflow to analyse samples using the eDNA metabarcoding technique; D. Complete workflow to analyse samples using the shotgun
 115 metagenomics technique.

A common approach in palaeoecology and palaeoclimatology is to use different proxies and methods (*i.e.*, a multi-proxy approach: Davies et al., 2018; Lamentowicz et al., 2008; Poto et al., 2013), which allows cross-checking of results and understanding uncertainties of single proxies (Jansen et al., 2007; Jones et al., 2009). Several physical, chemical, and biological proxies can be used to infer the environmental conditions that occurred in the past (Chambers et al., 2012). However, morphological identification analyses of plant and animal residues are time-consuming and require taxonomic expertise. Moreover, peatlands are rich in prokaryotic and eukaryotic microorganisms (Figure 2a) that are rarely considered in palaeoecological reconstructions, such as archaea, bacteria, and fungi (including both yeast and filamentous life forms). As these microbial cells may move through the peat profile due to porewater fluctuation/percolation, the distinction between living vs. dead/fossil microorganisms using traditional approaches can be difficult. The analysis of environmental DNA (eDNA) through different molecular techniques is a tool that can overcome these limitations.

These techniques allow the simultaneous study of different communities without the need for extensive taxonomic expertise (Holdaway et al., 2017; Thomsen & Willerslev, 2015). In addition, molecular techniques such as eDNA metabarcoding and shotgun sequencing can be automated, leading to reduced time and costs (Holdaway et al., 2017). Furthermore, shotgun sequencing allows the inclusion of fungi and bacteria through the use of specific software that can predict the age of the DNA, thus establishing whether it is ancient or the result of contamination by modern organisms (Jónsson et al., 2013).

These approaches could foster access to palaeoecological studies and could take advantage of many more informative biological proxies such as arthropods, archaea, bacteria, and fungi.

Here, we review current methodologies used in palaeoecological studies of peatlands, proposing alternative approaches (Figure 2b) to the classical morphological identification of plant residues and molecular approaches that would allow the use of arthropod-, fungi-, bacteria-, and archaea-related proxies, which have rarely been used in paleoenvironmental reconstructions so far.

2. Proxies and main classical techniques

Peatlands are reservoirs of many inorganic elements and organic residues that can be used as proxies to study the evolution of a peatland and its surrounding environment. Peat accumulation is a function of the imbalance between net productivity and decay rate (Clymo, 1983), which both vary spatially and temporally because they are influenced by changing climate regimes, autogenic factors (*e.g.*, vertical growth and litter quality), and natural (*e.g.*, fires) and anthropogenic disturbance (*e.g.*, logging, harvesting, drainage practices, and deposition of dust and pollutants) (van Bellen et al., 2020).

The upper, predominantly aerobic, section of a peat column is often referred to as the acrotelm (Ingram, 1978) and is generally subjected to oxidation processes (Belyea & Clymo, 2001; Clymo, 1984) and shows a higher apparent accumulation rate of organic matter compared to the deeper, anoxic section (the catotelm) in which decomposition is incomplete. In the acrotelm, ~90% of net primary production may be decomposed before being incorporated into the catotelm (Laiho, 2006). Therefore, peat humification may indicate preponderant palaeohydrological conditions when the upper layer of peat was accumulated (Chambers et al., 2011). At the same time, the water table level is highly dynamic, and changes may cause a shift between acrotelm and catotelm, thus retroactively affecting peat decomposition (Frolking et al., 2014).

One of the main difficulties in the study of changes in peat decomposition and humification is its possible evolution towards different directions, mainly depending on differences in peat-forming vegetation, climatic conditions, peat depth, trophic status, pH, and age (Zaccone et al., 2018). The von Post scale (H1–H10), based on both the colour/turbidity of the porewaters and the structure of remaining peat material following squeezing, has been widely used for decades as one of the reference systems to describe peat humification in the field (von Post, 1922, 1924). According to Chambers et al. (2012), dark coloured and highly humified layers could reflect warm or dry climatic conditions in which the material persisted for longer in the acrotelm with rapid decomposition; light-coloured layers, instead, are generally formed under wet or cool conditions, with fast translocation down into the anaerobic catotelm, or a slow decay rate. More reliable and reproducible proxy-climate information either directly or indirectly related to the C cycle can be inferred from chemical, spectroscopic and thermal techniques. For example, the increase in peat decomposition and humification is reported to be associated with a decrease in some elemental ratios (*i.e.*, C/N, H/C and O/C) and a residual enrichment of more recalcitrant aromatic and aliphatic compounds (Stevenson, 1994). The signature of stable isotopes (mainly H, O and C) in bulk peat is descriptive of critical hydrological changes, C cycle perturbation and vegetation changes (Chambers & Charman, 2004; Dodson, 2010), although sometimes it may fail to provide unambiguous information in deeper or highly humified layers (Biester et al., 2014; Zaccone et al., 2011). More informative proxies of climatic changes are $\delta^{13}\text{C}$, $\delta^{18}\text{O}$ and δD recorded in specific compounds (*e.g.*, *n*-alkanes; Bingham et al., 2010; Moschen et al., 2009; Xie et al., 2004). Other approaches have been used to find potential descriptors of peat humification vs. climate change, including bulk density, diluted alkaline extraction followed by UV–Vis absorption and molecular fluorescence, Fourier Transform Infrared (FT-IR) and Nuclear Magnetic Resonance (NMR)

spectroscopy, Gas Chromatography (GC) and GC-Mass Spectrometry (GC-MS), and thermal analysis. More details about the application of these techniques can be found in specialized literature (Chambers et al., 2011; Zaccone et al., 2018).

Variations in dust fluxes and mineralogy over time are also used as proxies for palaeoclimate reconstructions (Björck & Clemmensen, 2004; Le Roux et al., 2012; Marx et al., 2009), although in some cases the extent of changes observed along a profile could also reflect differences in the rate of plant growth or peat accumulation, in the botanical composition of peat-forming plants, or in decomposition and humification degree (Zaccone et al., 2012, 2013). Mineralogy peculiarity of the source allows the use of titanium (Ti) and other conservative elements such as scandium (Sc), thorium (Th), and zirconium (Zr) as a proxy for dust influx, thus allowing the inference of atmospheric circulation patterns.

All proxies must be dated to relate a particular climate condition to a given point in the past. However, the stratification along the peat bog profile is not always reliable. Bio-disturbance and other physical mixing agents (*e.g.*, cryoturbation) often do not allow an accurate dating; thus, some age models must be deduced through interpolation, such as linear accumulation, convex models, concave models, and flexible Bayesian 'Poisson' models, each with their own advantages and limitations (Bennett & Fuller, 2002; Blockley et al., 2007; Davies et al., 2018; Telford et al., 2004; Yeloff et al., 2006).

Together with the above-mentioned proxies, peatlands are rich in biological proxies (Chambers & Charman, 2004; De Jong et al., 2010). The most used are plant macrofossils, pollen, testate amoebae, and diatoms, which are identified by comparing organic residues with reference materials (Katz et al., 1977; Mauquoy & van Geel, 2013; Smith, 2004).

Dominant taxa in ombrotrophic peatlands are represented by the moss species *Sphagnum*. These species represent the foundation of peatlands due to their ability to store a large amount of water. Beyond this key role, they are also fundamental for reconstructing the evolution of peatlands; for that reason, plant macrofossils of mosses, shrubs and graminoids are used as local vegetational indicators to determine bog successional dynamics (Hughes & Barber, 2004) as well as a proxy for water table level variations (Mauquoy et al., 2008; Swindles et al., 2007). In addition, the analysis of macrofossil residues can help to assess the role of human impact and climate change on C sequestration and environmental changes in peatlands (Chambers et al., 1999; Chambers et al., 2007a; Chambers et al., 2007b; Heijmans et al., 2008; Sannel & Kuhry, 2009; van Bellen et al., 2020).

Together with the analysis of plant macrofossils, pollen analyses are widely used to provide information about local vegetation history, past climate events, and human activities/impacts. Due to their high taxonomic identifiability and excellent preservability in sediments, pollen grains are particularly useful for describing not only the development of the peatland itself but also the development of the surrounding environment (Bradley, 2014).

Among other organisms, testate amoebae (and diatoms) are commonly used as indicators of past environmental changes in peatlands (Mitchell et al., 2008; van Bellen et al., 2018). An external shell, called the “test”, allows their preservation for thousands of years and these unicellular organisms are decay-resistant and respond rapidly to environmental changes associated with hydrological conditions. The community composition, usually based on the ratio between mixotrophic (related to high water table depth, open peatlands, presence of wet *Sphagnum* and high C sequestration) and heterotrophic (related to low water table depth, low C accumulation, and forested peatland) (Marcisz et al., 2020) taxa, is strongly related to the variation from dry to wet

peat bog conditions (Booth et al., 2010; Charman et al., 2000). This makes them particularly suitable for quantitative reconstruction of water table depth (Charman, 2001; Mitchell et al., 2008).

In addition, peatlands are also rich in arthropods, fungi, bacteria, and archaea (Figure 2a).

Arthropods have been rarely considered for paleoecological reconstructions, likely due to their numerous species and taxonomic groups and the challenges associated with the morphological identification of each organism. In fact, in addition to those species closely associated with peat bogs, more generalist species may exploit the habitat as a source of food and/or to deposit eggs, thus fully falling within the community and food web of the peat bog (Desrochers & van Duinen, 2006). This implies that some taxa may only be detected by the presence of slight traces or organic residues, making their identification by morphological recognition even more complex. However, to understand the role of such organisms in peatland systems and to obtain information on the ecological and climatic history of investigated sites, their inclusion in palaeoecological studies would be significant (Chambers & Charman, 2004; Desrochers & van Duinen, 2006).

Among the microorganisms, fungi, bacteria, and archaea represent the main “engine” of peatlands, because they contribute to their formation and growth (Rydin & Jeglum, 2006). Among fungi, the predominant phyla are Ascomycota and Basidiomycota, generalist and fast-growing organisms divided, from a functional point of view, into saprophytic and mycorrhizal (Thormann, 2006b, 2006a; Thormann & Rice, 2007). The former are responsible for the degradation of organic matter (Baldrian, 2009; Baldrian & Valášková, 2008; Thormann, 2006a; Thormann & Rice, 2007), while the latter are symbionts of vascular plants, which is advantageous for surviving in such an extreme environment (Martino et al., 2018; Read et al., 2004). Acidobacteria and proteobacteria represent the dominant bacterial phyla, while methanogens are the dominant archaeal group occurring in deeper profiles (Lin et al., 2012; Urbanová & Bárta, 2014). Proteobacteria are mainly involved in

the C and nitrogen (N) biogeochemical cycles (Too et al., 2021), while methanotrophic bacteria found in many natural peatland ecosystems contribute to global methane production (Song et al., 2021). Species adapted to thrive under extreme conditions and species with close similarity to xenobiotic-degrading strains were also reported (Puglisi et al., 2014).

The variety of organic residues extracted from peat makes them useful for an overall interpretation of past climatic conditions and vegetation development. However, the classic morphological identification of microorganisms and organic residues has several limitations: i) it is expensive and time-consuming, ii) it requires strong taxonomic expertise, iii) it does not always allow identification of organisms at the species level (particularly for arthropods), and iv) it does not allow to ascertain whether organisms are dead/ancient or alive, as they may have moved (actively or passively) through the profile. For those reasons, the use of arthropods, fungi, bacteria, and archaea can limit palaeoecological reconstruction. Therefore, new methods are necessary to speed up the identification process and allow the use of organisms that are currently excluded from this type of study.

3. Modern and ancient environmental and sedimentary ancient DNA

In recent years, the advent of High Throughput Sequencing (HTS) has fostered the development of eDNA metabarcoding (Figure 2c). This technique has been widely used to monitor modern plant and arthropod communities from water and soil samples (Coghlan et al., 2021; Kirse et al., 2021; Lacoursière-Roussel et al., 2018; Leontidou et al., 2021; Oliverio et al., 2018) and to characterize past plant and microbial communities from ice cores, permafrost, and lake sediments (Afouda et al., 2020; Ficetola et al., 2018; Parducci et al., 2017; Varotto et al., 2021; Willerslev et

al., 2003). Only a few NGS studies have been conducted on peatlands (Concheri et al., 2017; Garcés-Pastor et al., 2019; Parducci et al., 2015), leaving them largely unexplored.

Compared with morphological identification, the reliability of HTS-based techniques is strictly dependent on rigorous exogenous contamination control. It is, therefore, highly desirable to manipulate all eDNA samples as putative ancient DNA (aDNA) by working in ancient DNA dedicated laboratories and following strict procedures to limit contaminations. In particular: i) all laboratory analyses must be conducted in facilities in which the physical separation between sample preparation and DNA extraction, and DNA amplification rooms, is guaranteed; ii) all rooms must be sterilized with a UV lamp (where possible), and all surfaces and instruments must be sterilized using ethanol and bleach (and UV where possible) before and after each use; and iii) negative controls must be introduced during DNA extraction, amplification, and sequencing (Taberlet et al., 2018; Thomsen & Willerslev, 2015) to monitor reagent, cross-sample and environmental contaminations.

Primers are a second fundamental aspect to consider in order to obtain high quality data. Over the years, several primer pairs have been developed for both plants and arthropods (CBOL Plant Working Group, 2009; Elbrecht et al., 2019; Guardiola et al., 2015; Han et al., 2013; Taberlet et al., 2007; Timpano et al., 2020). Each barcode, however, has different taxonomic identification power depending on the target and fragment length. Among the most widely used markers in plant species detection are:

- 1) matK: best resolution for the detection and identification of angiosperms, but it is lacking in identification for gymnosperms and cryptogams (CBOL Plant Working Group, 2009).
- 2) rbcL: effective in the identification of terrestrial plants (CBOL Plant Working Group, 2009).

- 3) trnL: good resolution for terrestrial plants, and its short length (about 70 bp) makes it suitable for studies based on degraded DNA, such as peatland DNA (Taberlet et al., 2007).
- 4) ITS2: longer than trnL, it was found to excel in the amplification of degraded DNA with a higher resolution than matK and rbcL (Han et al., 2013; Timpano et al., 2020).

Arthropods are usually identified by the CO1 (Elbrecht et al., 2019) and/or 18s rRNA (Guardiola et al., 2015) mitochondrial DNA fragments. However, Garcés-Pastor et al. (2019) found CO1 to perform better than 18s rRNA; 18s rRNA proved too unspecific (amplifications of plants and organisms outside of arthropods were shown) and, therefore, have a lower taxonomic resolution. CO1 is also the most frequently used marker, with a wide range of possible primer pairs (for details, see Elbrecht et al., 2019).

Finally, to achieve genus- or species-level resolution in taxonomic identification, barcodes with complete and curated reference databases are required since they usually include high numbers of sequences corresponding to most of the flora and fauna in a specific habitat (Schenekar et al., 2020).

However, even this technique is not free of drawbacks. For example, preferential amplification of the most abundant taxa can occur, masking the presence of less represented (or under sampled) organisms (Fulton & Shapiro, 2019; Garcés-Pastor et al., 2019), while the absence of complete and curated public databases can lead to an incomplete (or even failed) identification (Schenekar et al., 2020). Despite these shortcomings, the technique is promising and in continuous development. To overcome the limitations, alternative strategies can be adopted; example, two barcodes can be combined to increase the identifiable targets and thus the resolution, while PCR-free techniques are being developed to overcome preferential amplification. One such technique could be shotgun sequencing; however, higher sequencing depth per sample is required to obtain

enough reads to identify groups of organisms with low abundance using this technique. Moreover, for most paleo-ecological studies, >90% of the reads remain unassigned due to incomplete genomic and plastid databases (Ahmed et al., 2018; Pedersen et al., 2016; Wang et al., 2021).

In recent years, multiple studies have combined barcoding principles with shotgun methods by targeting barcoding genes (*e.g.*, Armbrrecht et al., 2021). This offers the advantages of the shotgun approach, such as the retention of ancient DNA damage patterns for authentication, the reduction of false positives and negatives, and fragments are not limited by the availability of primer binding sites.

This approach is based on a probe capture strategy (Vernot et al., 2021) and requires prior knowledge of sequence diversity to design (RNA/DNA)-baits complementary to the target DNA sequence of interest. Synthesised probes are biotin-labelled and incubated with genomic eDNA libraries, where they hybridise into complementary sequences. The metallic beads are then immobilised by a magnet while non-targeted library molecules are washed away. The captured molecules are then subjected to HTS, resulting in a net increase (enrichment) in the number of DNA reads containing the target DNA regions. Though at earlier stages than PCR-based metabarcoding and shotgun sequencing, the sequence-capture barcode enrichment approach appears to be very promising, especially for organisms such as plants, requiring the use of multiple barcode markers for robust taxonomic identification.

Despite their great versatility, these two techniques utilize only a tiny fraction of all extracted DNA, which limits the analysis. In addition, eDNA metabarcoding and sequence capture are not suitable for the taxonomic identification of microorganisms (*i.e.*, fungi, bacteria, and archaea). Since these groups can move and survive along the peatland profile, using eDNA metabarcoding makes it difficult to determine their actual presence in the oldest and deepest samples (as the DNA

could derive from modern organisms), while a sequence capture approach is time- and cost-inefficient for their identification. In this respect, shotgun metagenomics is a technology that allows the detection of ancient environmental DNA from soils, lakes, and sediments (Figure 2d and Figure 3), providing a more accurate authentication via computing ancient DNA deamination patterns (Dabney et al., 2013) and *de-novo* assembly of genomes from ancient organisms (Seitz & Nieselt, 2017).

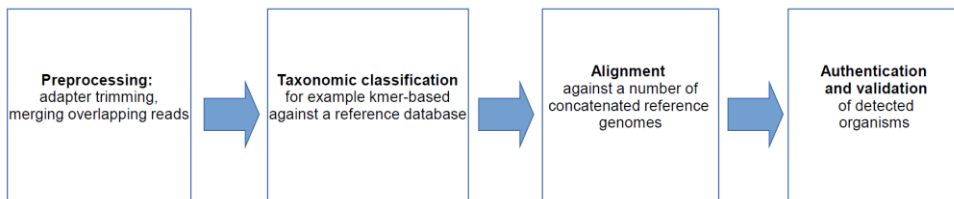


Figure 3 A typical ancient metagenomics workflow includes data pre-processing, taxonomic (kmer-based) classification, alignment against many concatenated and indexed reference genomes, and finally, authentication and validation analysis (deamination pattern, read length distribution, edit distance, evenness and breadth of coverage).

Nevertheless, accurate quantification and authentication analysis of microbial life forms remain challenging even in shotgun metagenomics studies. This is related to limited amounts of microbial aDNA and an unprecedented variety of endogenous and modern (entered *post-mortem*) microbial communities that have been populating ancient samples for centuries to millennia. Potential modern contamination can be detected via computing damage/deamination pattern and read length distribution using, for example, the mapDamage (Jónsson et al., 2013) tool. Furthermore, the misalignment edit distance statistic is often used to quantify similarity of query aDNA sequences for reference genomes of potential candidates as it is implemented in the HOPS ancient microbiome pipeline (Hübler et al., 2019). Finally, perhaps the most important authentication and

validation step is to compute the breadth/evenness of coverage of query aDNA sequences aligned to reference genomes of potential candidates.

Alternatively, without an explicit alignment, the breadth of kmer coverage using a classification approach via the KrakenUniq tool can be utilized (Breitwieser et al., 2018). Although this step is not specific to aDNA analysis, it ensures that the candidate (ancient or modern) organism is truly present in a sample.

A peculiarity of detecting ancient organisms using environmental and sedimentary DNA is the absence of a clear host, which differs from traditional bone artifact based aDNA studies in which most DNA typically comes from the host. Therefore, a large database with reference sequences equally representing all groups of organisms should be used for unbiased metagenomic profiling. If a group of organisms (*e.g.*, microbial pathogens) becomes dominant in a database, the presence of this group member in ancient samples can be erroneously reported because other organisms that might have been the true origin of aDNA were not included in the analysis. Since alignment against a large database is resource- and time-demanding, a classification approach against largest possible databases is often applied, such as NCBI NT with KrakenUniq (Breitwieser et al., 2018) or Kraken2 (Wood et al., 2019) tools that also allow fast filtering out of false positive hits via breadth and depth of coverage statistics computed by the tools.

In summary, the typical workflow for the analysis of ancient microbiota includes classification, alignment, and *de-novo* assembly. While the first two are already widely used, *de-novo* assembly is being rapidly developed (Seitz & Nieselt, 2017) and delivers interesting new methods for the authentication of assembled contigs such as pyDamage (Borry et al., 2021). One significant promise of this analysis is the reference-free reconstruction of genomes of extinct

(micro)organisms that might be genetically very different from modern homologs and hence would be difficult to analyse by classification and alignment reference-based approaches.

4. Conclusions

This review has highlighted how molecular techniques can support the classical techniques previously used to study the evolution and the biodiversity of peatlands. Moreover, classical techniques are difficult to apply to organisms with common morphologies, especially if identification is conducted from organic residues that have been archived in the peat environment for a long time. DNA, even if only present in trace amounts, can be detected, quantified, and classified with appropriate techniques to at least the level of genus or family. Nowadays, eDNA metabarcoding is, therefore, one of the best solutions to classify residues of plants and arthropods, as it offers a wide range of genetic markers and does not require a large investment of time and money. However, developing the sequence capture technique may overcome the limitations of eDNA metabarcoding by including PCR-free steps and allow the use of probes capable of targeting various fragments in a single experiment. Finally, shotgun sequencing is a better identification tool for fungi (including yeast and filamentous life forms), bacteria, and archaea. Since these organisms are alive and able to move along a peat profile, an extra control step is required to determine whether the DNA is ancient or derived from modern organisms. Although still under development, molecular techniques would make these studies accessible to more research groups and would favour the inclusion of organisms that have rarely been used for dating and that can provide important information about the development of a peat bog and its communities. Initially, it will be necessary to use molecular techniques alongside the classical techniques to evaluate their outcomes and improve the methodologies. However, due to the continuous development of

pipelines, new genetic markers, and improvements in techniques, eDNA metabarcoding, sequence capture, and shotgun sequencing could make paleoecological reconstructions much more rapid, informative, and reliable.

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