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Invited review

Subfossil peatland trees as proxies for Holocene palaeohydrology and palaeoclimate



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ABSTRACT

Due to the scarcity of reliable and highly resolved moisture proxies covering much of the Holocene, there has been increased interest in the study of living and subfossil peatland trees sensitive to gradual and extreme changes in hydrology, precipitation, and related environmental processes. Peatland development and the associated carbon accumulation, which are strongly influenced by hydrological fluctuations, are also of prime importance as peatlands represent long-term sinks of atmospheric carbon. Improved knowledge of peatland development and soil moisture variability during the Holocene is therefore essential to our understanding of long-term hydroclimate changes, the terrestrial carbon cycle, and to enable more robust predictions of peatland response to future climate changes.

Here, we review the existing mid- to late Holocene peatland tree-ring chronologies that have been used to study climate variability on (sub-)annual to centennial scales with a primary focus on northern Europe. Since the 1970s, absolutely dated tree-ring chronologies covering substantial parts of the Holocene have been developed from excavated remains of oak (*Quercus* spp.) and pine (*Pinus sylvestris* L.). The annual tree-ring patterns of these trees are often characterized by periods of depressed growth reflecting annual to decadal hydroclimatic changes. In addition, changes in the spatio-temporal distribution of trees throughout the Holocene are often found to reflect decadal to centennial climate and hydrological changes. Moreover, synchronicity between tree-ring chronologies and tree-population dynamics over larger geographical areas show periods of coherent regional climate forcing, especially during the mid-Holocene.

This review (i) provides an overview of pioneering and recent studies presenting tree-ring chronologies developed from subfossil peatland trees, and (ii) presents recent developments in the fields of dendroecology (i.e. the response of tree growth and changes in vitality as a result of changes in climatic variables) and dendroclimatology (i.e. the reconstruction of climate fluctuations based on tree-ring analyses) in peatland regions. Moreover, we (iii) use long-term climate reconstructions based on alternative proxies for comparison, and (iv) present different ways to analyse tree-ring records to generate novel information on annual to centennial timescales. This analysis is based on an unprecedented network of tree-ring chronologies from Denmark, Finland, Germany, Great Britain, Ireland, Lithuania, the Netherlands, Poland, Sweden, and Canada, as well as a wealth of old and previously (un) published literature from Scandinavia and Germany, which has not been accessible to a wider audience in the past due to inaccessibility or linguistic barriers. Finally, a map of possible hotspots for the assessment of continuous peatland-tree studies is presented, along with suggestions for new research directions in the field.

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1. Introduction

A prerequisite for any effort to distinguish natural climate variability from anthropogenic effects is to reconstruct past climatic variations prior to industrialization (Jansen et al., 2007; Marcott et al., 2013). In recent decades, improved palaeoclimatic methodologies and chronological techniques have enabled the development of robust, accurate and detailed climate and ecosystem reconstructions, and thereby increased our knowledge of climate dynamics over the course of the Holocene (Wanner et al., 2008; Marcott et al., 2013). Several multi-proxy temperature reconstructions have been created both in the northern and southern hemispheres for the last two millennia (Moberg et al., 2005; D'Arrigo et al., 2006; Mann et al., 2008; Birks et al., 2014; Stoffel et al., 2015), many of them being derived from tree rings and with annual resolution. The vast majority of dendroclimatic studies have been used to infer past temperatures at high latitudes (Briffa et al., 1990; D'Arrigo et al., 2006; McCarroll et al., 2013; Linderholm et al., 2014). A much smaller proportion of time series can be used for the reconstruction of long-term, highly resolved precipitation series (Büntgen et al., 2014; Cook et al., 2015), thereby hampering our understanding of past moisture or hydrological variations.

Tree growth in natural peatlands strongly depends on water-table depth (Boggie, 1972; Linderholm et al., 2002), such that rising water tables cause reduced growth due to hypoxia or anoxia, whereas lowered water tables create relatively well-oxygenated peat-surface layers promoting tree growth (Boggie, 1972; Leuschner et al., 2002). As a consequence, trees growing on peatlands have been shown to respond to hydrological changes (Leuschner et al., 2002; Eckstein et al., 2009; Edvardsson et al., 2015a) and can therefore be used for the construction of time series of past moisture fluctuations.

Peatlands are not only valuable long-term climate archives (Aaby, 1976; Barber, 1981; Charman et al., 2009). With an approximate coverage of 4 million km² across Eurasia and North America (Lappalainen, 1996; MacDonald et al., 2006), they also constitute an important sink for atmospheric carbon dioxide (CO₂) and a considerable source of methane (CH₄) (MacDonald et al., 2006; Yu et al., 2010; Limpens

et al., 2011). In fact, peatlands store twice as much carbon (C) as forests (Joosten and Couwenberg, 2008). Spatio-temporal dynamics of CO₂ and CH₄ fluxes in peatlands are mainly driven by hydrological conditions, which can be expressed by water-table levels (Mitsch et al., 2013). In addition to driving the carbon flux, water-table fluctuations in peatland ecosystems also influence a wide range of environmental processes such as vegetation patterns, the fixation of nitrogen, and the chemical composition of water passing through peatlands (Limpens et al., 2011; Waddington et al., 2014). Consequently, reconstructions of past water-table variations based on tree-ring records are of prime importance not only to improve our understanding of climate variability, but also to the assessment of the functioning of peatlands in a context of changing climatic conditions and under increasing levels of greenhouse gases.

In this context, the specific aims of this paper are to:

- (1) Synthesize current knowledge on relationships between tree growth, hydrology, and climate changes in peatlands from both an ecophysiological and dendroecological perspective, to evaluate and document the potential of peatland trees as a proxy for water table and/or regional hydroclimatic reconstructions;
- (2) Review and map past work on peatland tree-ring chronologies across the Northern Hemisphere. We include studies from e.g. Germany and Scandinavia, written in languages other than English, to make them accessible to a wider audience;
- (3) Compare the spatial and temporal distribution of peatland forests at regional to hemispheric scales, to remove site effects and to interpret results in a longer-term climatic context;
- (4) Compare regional patterns of change with hydrological proxies covering the same period to test how the tree-ring records capture changes in (hydro)climatic variables;
- (5) Discuss the potential of tree-ring records derived from peatland trees for palaeoclimatic and palaeohydrological reconstructions over the course of the Holocene, and to illustrate related possibilities, benefits, and limitations of subfossil peatland trees in achieving these goals;

- (6) Conclude with a call for further research directions and for work in new geographic regions.

2. Peatlands, peat, structure and development

Peat can be defined as a natural substance that is formed by partially decomposed remains of plants and contains <20–30% of minerals (=ash content) (Warner, 2003). The chemical and physical properties of peat are highly variable in space and time, depending on the type of plant species contributing to its formation, the degree of decomposition, and the geochemistry of water supply. In an undisturbed peatland, peat is primarily composed of water (88–97%), dry matter (2–10%), and gas (1–7%). Peat changes in composition over time with very slow decomposition, compaction, and geochemical alteration, such that it eventually forms coal after several million years. Based on the dominant botanical composition and degree of decomposition, four main categories of peat can be described: moss, herbaceous, wood, and humified peat (Charman, 2002; Loisel et al., 2014). In humified peat, the plant remains are so decomposed that the bulk of plants are no longer identifiable.

A peatland can be defined as an area covered by at least 30 cm of peat (Joosten and Clarke, 2002; Charman, 2002). Peatlands, in a broader context, are a type of wetland characterized by organic soil. The term “mire” is sometimes used to indicate a peatland with active accumulation of peat, but for our purposes the two terms are equivalent. On a global scale, three main regions of peatland development can be distinguished; northern peatlands, primarily distributed in boreal and subarctic climate in the Northern Hemisphere (Fig. 1), tropical peatlands (primarily distributed in Southeast Asia, but also in South America and Africa), and Southern peatlands (primarily distributed in Patagonia, but also in temperate Australasia) (Yu, 2011). Estimates of the global peatland area are highly variable due to the different wetland classification systems and insufficient survey data (Lappalainen, 1996; Rydin and Jeglum, 2006), but it is generally agreed that total peatland area is approximately 4 million km², corresponding to c. 2.7% of the Earth's land surface (Lappalainen, 1996; MacDonald et al., 2006). Estimates for tropical regions are subject to much greater error than those for northern peatlands. Of the total peatland area, 1.5% is found in Africa, 28% in Asia, 0.4% in Australia and Oceania, 2.6% in Central and South America, 24% in Europe, and 44% in North America (Lappalainen, 1996).

Peatland initiation patterns differ for the three main regions because of different histories of ice cover recession and climate change over the

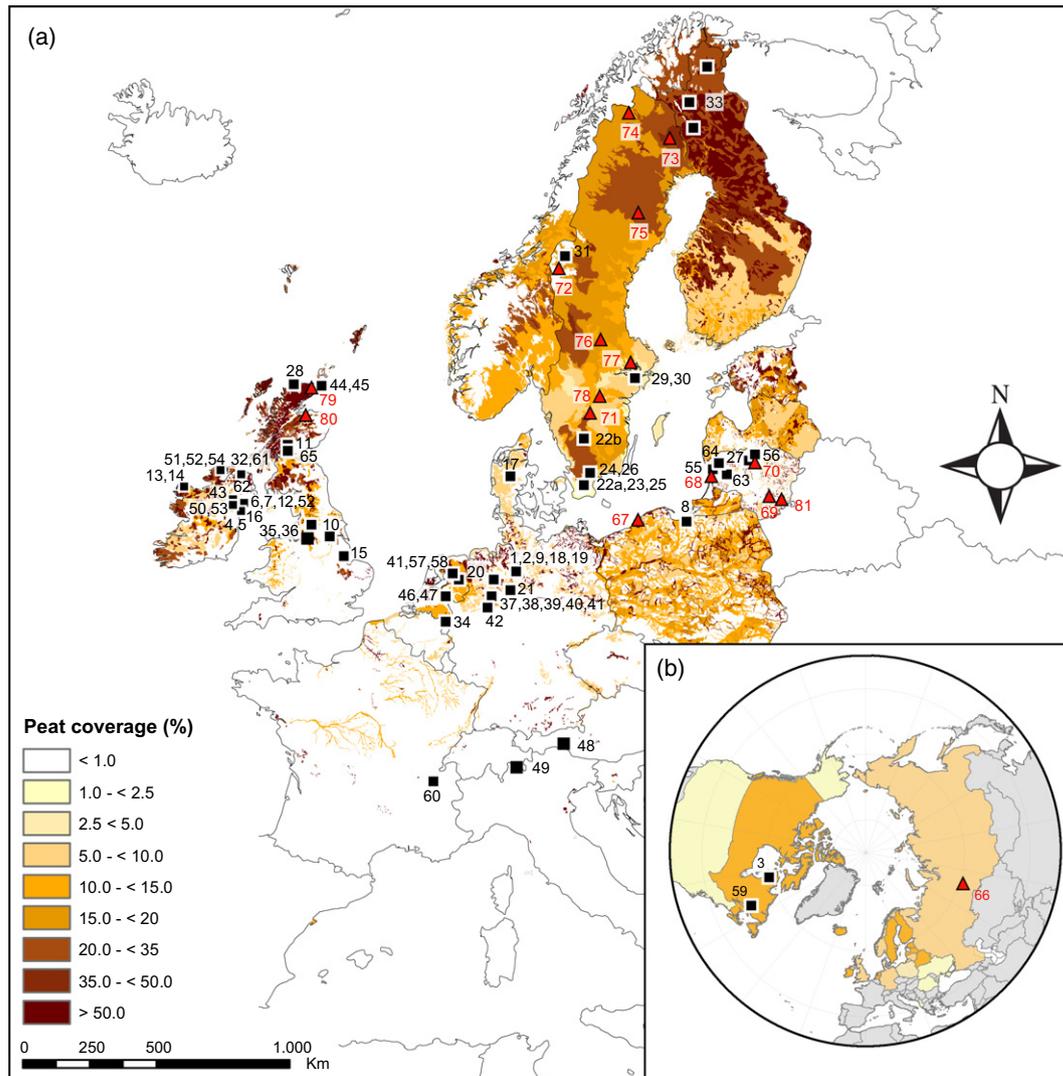


Fig. 1. (a) Location of the main peatlands referred to in Tables 1 and 2 (Id. No. 1–81). Sites from which subfossil trees have been sampled are shown by black squares whilst sites from which living trees have been sampled are shown by red triangles. (b) Map over peatlands outside northwest Europe. Peat coverage is based on Montanarella et al. (2006).

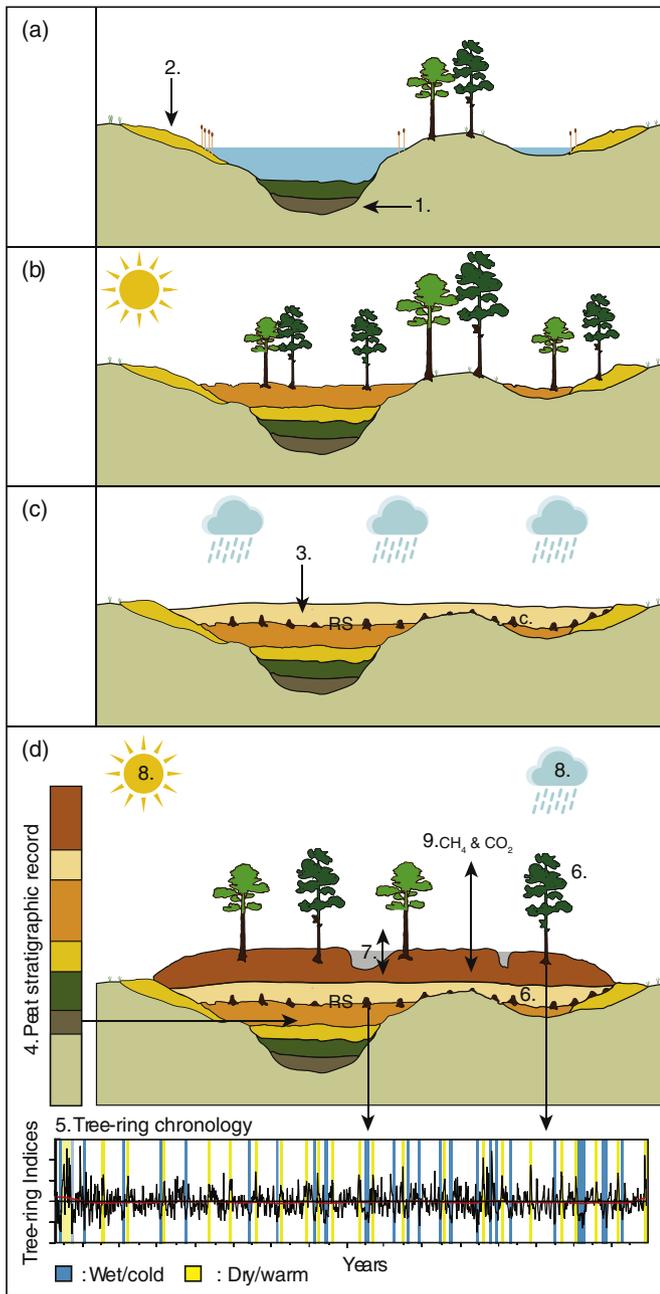


Fig. 2. (a) During the early Holocene, many topographic depressions were occupied by lakes in which organic layers consisting of e.g. gyttja (1) was deposited. In the shallow areas along the shores, reed or fen peat was developed (2). (b) During the mid-Holocene, relatively warm and dry conditions allowed trees to colonize many peatlands. (c) Accelerating peat growth following wet-shifts can often be observed as recurrence surfaces (RS) in stratigraphic records. Such hydrological changes may cause tree dying-off phases. Stumps and trunks from these trees can be preserved by the growing peat (3). (d) At present peatlands are valuable climate archives. Peat stratigraphic records (4) generate long-term information showing environmental changes, whereas tree-ring chronologies (5) can generate annually resolved information. The tree-ring chronologies (example from Edvardsson, 2016) can be developed from both living and subfossil trees (6). Tree growth is usually influenced by hydrological variations (7) related to climate (8). Moreover, climate, hydrology, and tree growth ultimately influence the carbon budget (9) of the peatlands.

glacial-interglacial transition (Fig. 2). Northern peatlands show an initiation peak around 9050–7050 BCE (11,000–9000 years before present, BP), South American peatlands around 15,050–12,550 BCE (17,000–14,500 years BP), and many tropical peatlands started to form > 18,050 BCE (20,000 years BP; Yu et al., 2010). The average peat accumulation rate is c. $13 \text{ g C m}^{-2} \text{ yr}^{-1}$ in tropical peatlands and c.

$19\text{--}22 \text{ g C m}^{-2} \text{ yr}^{-1}$ in northern and southern peatlands (Yu et al., 2010; Loisel et al., 2014). A conservative estimate of overall peat C pool indicates that world peatlands store c. 610 GtC, primarily in northern peatlands (c. 89%) with a small amount in tropical (c. 8%) and southern (c. 3%) peatlands (Yu et al., 2010). Overall, although covering only c. 2.7% of the Earth's land surface, peatlands store at least 25% of global soil organic C (Hiederer and Köchy, 2012).

On the basis of vegetation composition, hydrology, peat, and water chemistry, northern peatlands (which are the focus of this review) can be distinguished into two major types: minerotrophic peatlands (= fens) and ombrotrophic peatlands (= bogs). Minerotrophic peatlands receive their water and nutrient input from both atmospheric deposition and surrounding groundwater, whereas ombrotrophic peatlands are fed entirely from atmospheric deposition (Rydin and Jeglum, 2006). The main consequence of such different hydrological pathways is that fens are richer in dissolved minerals and have a higher water pH than bogs. These geochemical differences are reflected in the floristic composition; fens are typically dominated by vascular plants (particularly sedges) and brown mosses (Amblystegiaceae family), whereas bogs are usually dominated by peat mosses (Sphagnaceae family) and a smaller vascular plant component. The role of vascular plants, such as dwarf shrubs, has however gained increased interest recently because they seem to have competitive advantages in response to climate warming (Breeuwer et al., 2010; Buttler et al., 2015). In both fens and bogs, tree cover is often limited, but there are densely tree-covered peatlands in the boreal region (Fig. 3). Under natural conditions, the most common tree species colonizing peatlands in Eurasia are Scots pine (*Pinus sylvestris* L.), Mountain pine (*Pinus uncinata* Ramond ex DC.), Dwarf mountain pine (*Pinus mugo* Turra), and Siberian pine (*Pinus sibirica* Du Tour), whereas Mountain birch (*Betula pubescens* Ehrh.), willow (*Salix* spp.), and black alder (*Alnus glutinosa* L.) often colonize fens. Other tree species on northern peatlands include black spruce (*Picea mariana* (Mill.) Britton, Sterns and Poggenb.), whereas Tamarack (*Larix laricina* (Du Roi) K. Koch) sometimes colonizes fens. In this review, Scots pine and oak (*Quercus robur* L. and *Q. petraea* L.) will be in primary focus, as these species are commonly excavated in northern peatlands and are suitable for dendrochronological studies (Table 1). Excavated trunks and plant macrofossils show that oak trees once colonized significant peatland areas in northwest Europe (Pilcher et al., 1984; Leuschner et al., 2002). However, analogous peatland ecosystems do not appear to exist any longer (Sass-Klaassen and Hanraets, 2006).

The presence of *Sphagnum* is particularly important for peat accumulation in ombrotrophic peatlands. *Sphagnum* plants have the capacity to acidify the surrounding water as a result of an extremely efficient cation exchange capacity (van Breemen, 1995; Rydin and Jeglum, 2006). This enables *Sphagnum* to absorb nutrients from very low concentrations in the water source, and produces a litter that is resistant to decay. *Sphagnum* also increases soil anoxia by storing water in empty cells (hyalocysts). Because *Sphagnum*, like all bryophytes, cannot regulate their water balance, their development is possible whenever there is a surplus of water. In addition, because they are competitive under acidic conditions (pH < 4–5), most *Sphagnum* species benefit from the presence of low mineral content. This combination of hydrological and geochemical conditions is prevalent on ombrotrophic peatlands (van Breemen, 1995). The physiological requirements of *Sphagnum* are one of the key determinant of the global distribution of northern ombrotrophic peatlands, which are typically located north of 45° N, in particular at 50°–70° N (Yu et al., 2011), under climatic conditions and landscape morphology that promote a surplus of water and low mineral availability. However, whilst *Sphagnum* is a key taxon for northern peatland formation, the presence of *Sphagnum* is not a prerequisite for peat accumulation and some extraordinary examples exist where peat forms from plants such as e.g., Poaceae (Smith and Clymo, 1984). Peat can be formed by a range of other vascular plants as well, particularly sedges in fens and wood in peatlands with shrub

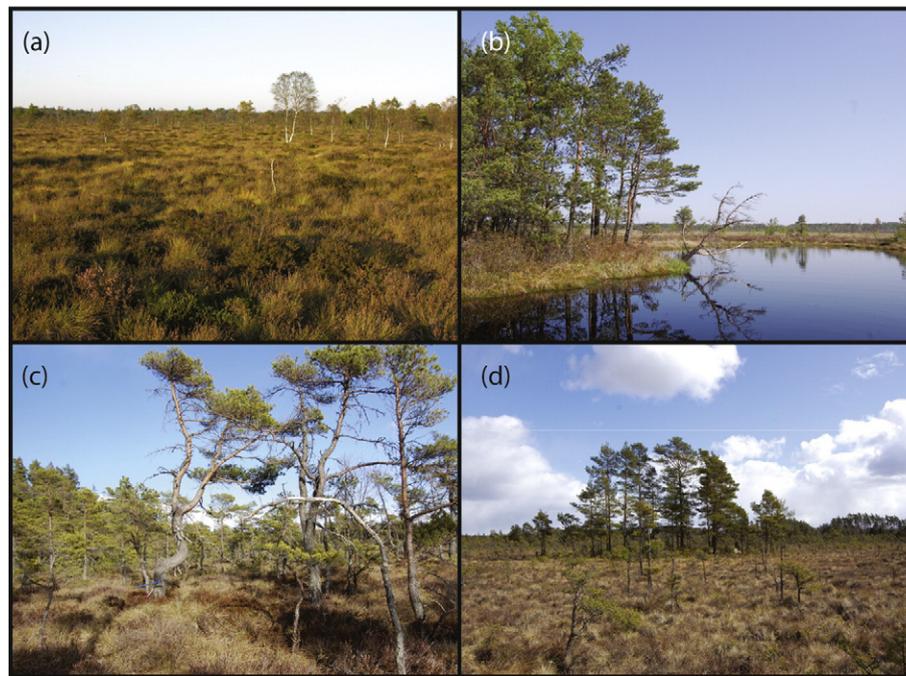


Fig. 3. (a) The natural raised bog Fjällmossen (S. Sweden) is characterized by scattered populations of birch and pine trees. (b) Open water ponds at the raised bog Aukštumala (Lithuania) show how close the water table is to bog surface and the root systems of the pine trees. (c) Peatland pines growing at Saxnäs Mosse, Sweden. (d) A till hummock in Hästhultsmossen (S. Sweden) generates stable and dry conditions favoring colonization of trees. The area surrounding the mineral soil hummock, however, is relatively wet, unstable and supports significantly smaller pine trees even though the trees are of same age.

and tree cover. Peat derived from woody plants is especially important in the tropics. Specific taxa, such as the restiad rushes in Australasia, are also important peat formers in some regions (Clarkson et al., 2004). Peat accumulation can be equally fast in these peat types (Loisel et al., 2014) and prevailing climate appears to be a more important driver of peat accumulation rates over millennial timescales than botanical composition (Charman et al., 2013, 2015). The presence of waterlogged conditions (persistent soil anoxia), low chemical quality of peat moss litter, and low pH, all hamper the microbial decomposition of plant remains, thereby favoring the long-term accumulation of peat (a sink of atmospheric C) and the preservation of plant macro- and micro-fossils creating an archive of past environmental conditions, especially in ombrotrophic northern peatlands (Chambers and Charman, 2004; Chambers et al., 2012).

A complex microtopography often develops on the surface of ombrotrophic peatlands, created by a process of differential growth and decay, sometimes enhanced by physical processes such as freezing. Microhabitats of pools, hollows, lawns, and hummocks are formed in relation to a water table gradient, which in turn drives vegetation composition and the spatial distribution of plants (Bragazza and Gerdol, 1999). Pools form in the wettest areas of peatlands (Fig. 3), characterized by standing water with only free-floating peat mosses and vascular plants. Hollows, lawns, and hummocks occur along a gradient of decreasing wetness and are often characterized by a continuous and dense layer of *Sphagnum* plants, and a sparse cover of vascular plants. Along the gradient from hollows to hummocks, *Sphagnum* species become more drought-adapted and vascular plants become more shrubby and abundant. In the driest locations, *Sphagnum* is absent and may be replaced by more drought tolerant mosses. In such a typical sequence of microhabitats on ombrotrophic peatlands, the presence of trees is determined by the moisture content of the peat due to the sensitivity of tree roots to anoxic conditions (Boggie, 1972; Vitas and Erlickytė, 2007).

Where hydrological conditions are stable, tree distribution is limited to the hummocks and individual trees tend to be small and slow growing. Where changes in hydrological conditions occur, the expansion of trees is favoured by any reduction in soil water content, such as

decreased precipitation or increased evapotranspiration (Boggie, 1972; Edvardsson et al., 2015a). Peatlands with consistently dry surface conditions can be heavily forested with relatively large trees, especially in boreal environments. The dominant hydrological control on tree growth means that the direct effect of temperature is less important, whereas lowering of the water table will promote expansion of tree cover and increased tree growth rates (Smiljanić et al., 2014; Edvardsson et al., 2015a, 2015b). This theoretical concept has been confirmed by observations of tree growth following peatland drainage (Dang and Lieffers, 1989; MacDonald and Yin, 1999; Freléchoux et al., 2000). Lowering of the water table increases soil temperature, improves soil aeration, and increases nutrient availability through organic matter mineralization (Grootjans et al., 1985; Choi et al., 2007; Weedon et al., 2012), with positive effects on tree growth.

Although success of tree seed germination does not differ between lawns (wet microhabitats) and hummocks (drier microhabitats), the performance of tree seedlings and the probability of maturation is greater on hummocks (Holmgren et al., 2015). Positive feedbacks have also been shown between tree recruitment and dwarf shrubs on hummocks (Holmgren et al., 2015). Once they are established, trees can cause a further drying of the peat due to enhanced transpiration (Moir et al., 2010; Limpens et al., 2014a), promoting even greater tree encroachment.

Peatland development over time is driven primarily by successional processes and climate dynamics (Fig. 2; Hughes, 2003). Historically, the conventional successional sequence is via terrestrialisation of aquatic systems and fen peat formation to bog peat (Walker, 1970), but it is now commonly accepted that a wide variety of successional sequences can occur in different peatlands. Paludification (i.e. the gradual spread of peatland through waterlogging of previously dry ground) is the other main process leading to peat formation particularly in many boreal peatlands and blanket bogs. The occurrence and preservation of trees is influenced by successional stages, with tree growth occurring most likely in the later stages of succession, when drier surfaces are more prevalent. In paludified peatlands, tree remains typically occur at the base of the sequence, as they were growing on the drier surfaces prior to peat formation. Moreover, trees can be preserved in peatlands even

Table 1

Representation of the main studies used in this review for comparison. Study areas include Austria (AU), Canada (CA), Denmark (DK), Finland (FI), France (FR), Germany (DE), Great Britain (GB), Ireland (IE), Italy (IT), Lithuania (LT), the Netherlands (NL), Poland (PL), Sweden (SE), and Switzerland (CH). Tree species presented are Alder (A), Ash (F), Larch (La), Oak (Q), Pine (P), and Spruce (Pi), and what context the material originates from, bogs/peatlands (b), mainly bogs/peatlands (m) and partly bogs/peatlands (p).

Id. no. and references	Country/latitude, longitude	Species/(b, m, p)	Main time span
1. Achterberg et al. (2015)	DE/52°50' N, 9°50' E ^a	P (b)	4629 BCE–502 CE
2. Achterberg et al. (2016)	DE/52°50' N, 9°50' E ^a	P, Q (b)	6703 BCE–931 CE
3. Arseneault and Payette (1997)	CA/57°44' N, 76°10' W	Pi (b)	500 BCE–present
4. Baillie (1973)	IE/54°50' N, 6°50' W ^a	Q (b)	5000–1380 CE
5. Baillie (1977)	IE/54°50' N, 6°50' W ^a	Q (b)	5000–1001 CE
6. Baillie et al. (1983)	IE/54°50' N, 6°50' W ^a	Q (b)	5000–1000 BCE
7. Baillie and Brown (1988)	IE/54°50' N, 6°50' W ^a	Q (b)	5300–200 BCE
8. Barniak et al. (2014)	PL/54°15' N, 19°44' E	P (b)	940–460 BCE ^b
9. Bauerochse et al. (2015)	DE/52°50' N, 9°50' E ^a	P, Q (b)	2600–1500 BCE
10. Boswijk and Whitehouse (2002)	GB/53°32' N, 0°57' W	P (b)	2921–2445 BCE
11. Bridge et al. (1990)	GB/56°52' N, 4°32' W ^a	P (b)	5900–1200 BCE ^c
12. Brown et al. (1986)	IE/54°50' N, 6°50' W ^a	Q (b)	5300–200 BCE
13. Brown and Baillie (1992)	IE/54°50' N, 6°50' W ^a	P, Q (b)	3600–2600 BCE
14. Brown and Baillie (2012)	IE/54°50' N, 6°50' W ^a	Q (m)	5200 BCE–present
15. Chambers et al. (1997)	GB/53°40' N, 0°53' W	P (b)	2900–2400 BCE
16. Charman (2010)	IE/54°60' N, 6°40' W ^a	Q (b)	5000 BCE–present
17. Christensen (2007)	DK/56°30' N, 9°50' E ^a	Q (m)	6000–200 BCE
18. Delorme et al. (1981)	DE/52°50' N, 9°50' E ^a	Q (b)	350–150 BCE ^b
19. Eckstein et al. (2009)	DE/52°50' N, 9°50' E ^a	P (b)	5600–2200 BCE
20. Eckstein et al. (2010)	DE/52°44' N, 8°17' E	P, Q (b)	2450–2050 BCE
21. Eckstein et al. (2011)	DE/52°70' N, 9°00' E ^a	P (b)	6500–1200 BCE
22. Edvardsson et al. (2012a)	SE/55°51' N, 13°49' E	P (b)	5219–4574 BCE
	SE/57°20' N, 14°35' E	P (b)	4839–3728 BCE
23. Edvardsson et al. (2012b)	SE/55°51' N, 13°49' E	P (b)	6100–4600 BCE
24. Edvardsson et al. (2014a)	SE/56°00' N, 14°00' E ^a	P (b)	4540–4460, 1320–1240 BCE
25. Edvardsson et al. (2014b)	SE/55°51' N, 13°49' E	P, Q, A, F (b)	4500–1000 BCE ^b
26. Edvardsson (2016)	SE/56°19' N, 13°55' E	P (b)	2667–1108 BCE
27. Edvardsson et al. (2016a)	LT/55°30' N, 23°50' E ^a	P (b)	4000 BCE–900 CE ^a
28. Gear and Huntley (1991)	GB/58°24' N, 4°3' W	P (b)	2450–1900 BCE ^b
29. Grudd et al. (2000)	SE/59°08' N, 17°55' E	P (b)	1700–1500 BCE ^b
30. Gunnarson (1999)	SE/59°08' N, 17°55' E	P (b)	1686–1483 ± 23 BCE ^b
31. Gunnarson (2008)	SE/63°16' N, 12°31' E	P (p)	5000–2000 BCE ^b
32. Hall et al. (1994)	IE/55°05' N, 6°34' W	P, Q (b)	6000–0 BCE ^b
33. Helama et al. (2004)	FI/67°50' N, 26°25' E ^a	P (p)	5600 BCE–present
34. Jansma (1996)	NL/50°83' N, 5°57' E	Q (p)	2258–1141 BCE
35. Lageard et al. (1999)	GB/53°40' N, 2°20' W ^a	P, Q (b)	3520–2462 BCE ^b , 3228–1891 BCE
36. Lageard et al. (2000)	GB/53°40' N, 2°20' W ^a	P (b)	2881–2639 BCE
37. Leuschner et al. (1987)	DE/52°40' N, 8°20' E ^a	Q (b)	6000 BCE–500 CE
38. Leuschner and Delorme (1988)	DE/52°40' N, 8°20' E ^a	Q (m)	6225 BCE–present
39. Leuschner (1992)	DE/52°40' N, 8°20' E ^a	Q (b)	6000 BCE–500 CE
40. Leuschner et al. (2000)	DE, NL ^a	Q (b)	6000 BCE–500 CE (GE), 6000–4500 BCE, 3000 BCE–500 CE
41. Leuschner et al. (2002)	DE, IE, NL ^a	Q (b)	6069 BCE–1596 CE
42. Leuschner et al. (2007)	DE/52°27' N, 8°10' E	P (b)	3050–2700 BCE
43. McGeever and Mitchell (2015)	IE/53°00' N, 7°00' W ^a	P (b)	6000 BCE–1000 CE ^c
44. Moir et al. (2010)	GB/58°90' N, 4°30' W ^a	P (b)	3200–3000 BCE
45. Moir (2005, 2012)	GB/58°90' N, 4°30' W ^a	P (b)	3200–2800 BCE
46. Munaut (1967)	NL/52°60' N, 6°30' E	P (b)	5000, 4000, 3000 BCE ^b
47. Munaut and Casparie (1971)	NL/52°60' N, 6°30' E	P (b)	5000, 4000, 3000 BCE ^b
48. Nicolussi et al. (2005)	AU/46°90' N, 10°70' E ^a	P (p)	7100–2100 BCE
49. Nicolussi et al. (2009)	AU, IT, CH ^a	P, Pi, La (p)	7100 BCE–present
50. Pilcher (1973)	IE/54°50' N, 6°50' W ^a	Q, P (b)	6000 BCE–present
51. Pilcher et al. (1977)	IE/54°50' N, 6°50' W ^a	Q (b)	4000–1000 BCE
52. Pilcher et al. (1984)	IE, GB, DE ^a	Q (m)	5218–158 BCE (present)
53. Pilcher et al. (1995)	IE/54°60' N, 5°90' W ^a	P (b)	3451–2569 BCE
54. Pilcher et al. (1996)	IE/54°60' N, 6°50' W ^a	Q (m)	5218–158 BCE
55. Pukienė (1997, 2001)	LT/56°05' N, 21°50' E	P (b)	200 BCE–present ^b
56. Pukienė (2003)	LT/56°12' N, 24°44' E	Q (b)	4600–4400 BCE ^b
57. Sass-Klaassen et al. (2005)	NL/52°31' N, 6°02' E	Q (b)	200 BCE–150 CE
58. Sass-Klaassen and Hanraets (2006)	NL/52°31' N, 6°02' E	Q, F (b)	600 BCE–200 CE
59. Simard et al. (2011)	CA/48° N, 71° W ^a	Pi (b)	3200 BCE ^b
60. Tessier et al. (1993)	FR/45°05' N, 5°92' E	P (p)	6000 BCE–present ^b
61. Torbenson et al. (2015)	IR/54°49' N, 6°30' W ^a	P (b)	6300–5600 BCE
62. Turney et al. (2005)	IE/54°60' N, 6°40' W ^a	Q, P (m)	5000 BCE–present
63. Vitas (2009)	LT/55°50' N, 22°17' E	Q, F (b)	4700–1500 BCE ^b
64. Vitas (2010)	LT/55°48' N, 21°53' E	F, A, Q, B (b)	3800–1290 BCE ^b
65. Ward et al. (1987)	GB/56°40' N, 4°18' W	P (b)	4500–1000 BCE ^b

^a Approximate coordinates as the chronology/chronologies are based on material from several study sites.

^b Approximate ages as the chronology/chronologies are dated by radiocarbon.

^c Approximate ages as of individual subfossil trees (no tree-ring chronologies) dated by radiocarbon.

Table 2
Papers in which comparative studies based on peat soil and mineral soil trees have been performed. For further information, see Figs. 1 and 8. Study areas include Great Britain (GB), Lithuania (LT), Poland (PL), Russia (RU), and Sweden (SE). Tree species included are *Pinus sylvestris* (PiSy) and *Pinus sibirica* (PiSi).

Id. no. and references	Country/site name	Latitude, longitude	Species
66. Blanchet et al. (2016)	RU/Mukhrino	60°54'N, 68°42'E	PiSy, PiSi
67. Cedro and Lamentowicz (2011)	PO/Słowińskie Błoto	54°21'N, 16°29'E	PiSy
68. Edvardsson et al. (2015a, 2015b)	LT/Aukštumala	55°23'N, 21°22'E	PiSy
69. Edvardsson et al. (2015a, 2015b)	LT/Kerėplis	54°27'N, 24°32'E	PiSy
70. Edvardsson et al. (2015a, 2015b)	LT/Rėkyva	55°51'N, 23°15'E	PiSy
71. Edvardsson and Hansson (2015)	SE/Store Mosse	57°14'N, 13°55'E	PiSy
72. Linderholm (2001)	SE/Lake Ånn	63°15'N, 12°30'E	PiSy
73. Linderholm et al. (2002)	SE/Augerusjärvi	67°38'N, 21°46'E	PiSy
74. Linderholm et al. (2002)	SE/Stortjäderberget	54°32'N, 19°00'E	PiSy
75. Linderholm et al. (2002)	SE/Årsön	63°15'N, 12°30'E	PiSy
76. Linderholm et al. (2002)	SE/Bredmossen	60°08'N, 16°05'E	PiSy
77. Linderholm et al. (2002)	SE/Hanvedsmossen	59°09'N, 17°55'E	PiSy
78. Linderholm et al. (2002)	SE/Anebymossen	57°51'N, 14°38'E	PiSy
79. Moir et al. (2011)	GB/Eilean Subhainn	58°41'N, 5°29'W	PiSy
80. Moir et al. (2011)	GB/Abernethy	57°14'N, 3°40'E	PiSy
81. Edvardsson (unpublished)	LT/Čepkeliai	54°07'N, 24°30'E	PiSy

if they were not growing on the surface. For example, trees can fall into the margins of ponds or fens and may therefore be preserved in peat and sediment formed during the early aquatic stages of peatland growth.

3. Historical background: pioneering to recent studies

Since the late nineteenth century, palaeobotanic and climatic research has been performed in peatlands, initially with a focus on Nordic countries (Dau, 1829; Vaupell, 1851; Blytt, 1876; Sernander, 1890, 1893; von Post, 1924, 1930), and later in other regions of the northern hemisphere (Lewis, 1906, van Geel, 1978; Barber et al., 1994; Yu et al., 2014; Loisel et al., 2014). Most often, such studies have been based on plant macrofossils, pollen grains or peat decomposition, but the attention of many pioneer researchers was attracted by the presence of subfossil trees (Figs. 2 and 4) in peat stratigraphy (Dau, 1829; Vaupell, 1851; Blytt, 1876; see also Birks and Seppä, 2010; Nielsen and Helama, 2012).

For example, Dau (1829) presented pioneering studies where he described the stratigraphic distribution of tree trunks in Danish peat bogs,

and Vaupell (1851) studied buried trees and their relationship with soil nutrients, sunlight, and moisture conditions (Nielsen and Helama, 2012). Steenstrup (1842) classified tree horizons on the basis of species composition and interpreted tree population shifts as environmental changes associated with temperature and hydrological shifts during the postglacial period (Birks and Seppä, 2010; Nielsen and Helama, 2012). For these observations, Steenstrup can be considered as one of the founders of Holocene palaeoecology and climate research (Birks and Seppä, 2010). In Norway, Blytt (1876) investigated tree horizons in relation to variations in peat decomposition, and interpreted synchronous changes as shifts controlled by climate. The Swedish researcher Sernander thereafter improved the methods introduced by Blytt (1876) and associated dark peat layers containing wood material with periods of relatively dry continental climate, whereas less humified peat layers without fossil trees were interpreted as humid climatic periods (Sernander, 1890, 1893). Sernander also developed a schematic model of postglacial climate change, known as the Blytt-Sernander scheme, which has been used by many generations of Quaternary geologists and palaeobotanists (e.g., Smith and Pilcher, 1973; Blackford and Chambers, 1991; Birks and Seppä, 2010). Outside Scandinavia, pine

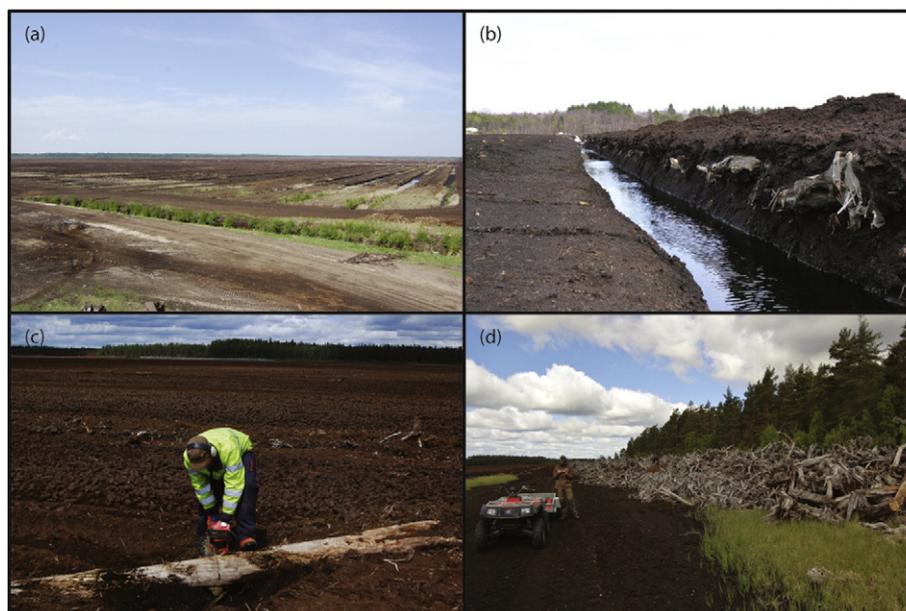


Fig. 4. (a) Several meters of peat have been harvested at the Rėkyva peat mining area (Lithuania) with the result that subfossil trees preserved in peat have been exposed. (b) Tree horizon at the Viss Mosse peatland (Sweden; Fig. 1, site 23) containing in situ pine stumps. These trees were growing at the bog surface between 7200 and 6500 years BP. (c) Field sampling of a c. 6000-years old pine tree at Hällaryds mossen (Sweden; Fig. 1, site 22b). (d) To enable continued peat mining, tree trunks and stumps are often stored in piles surrounding the peat mining area (Hällaryds mossen).

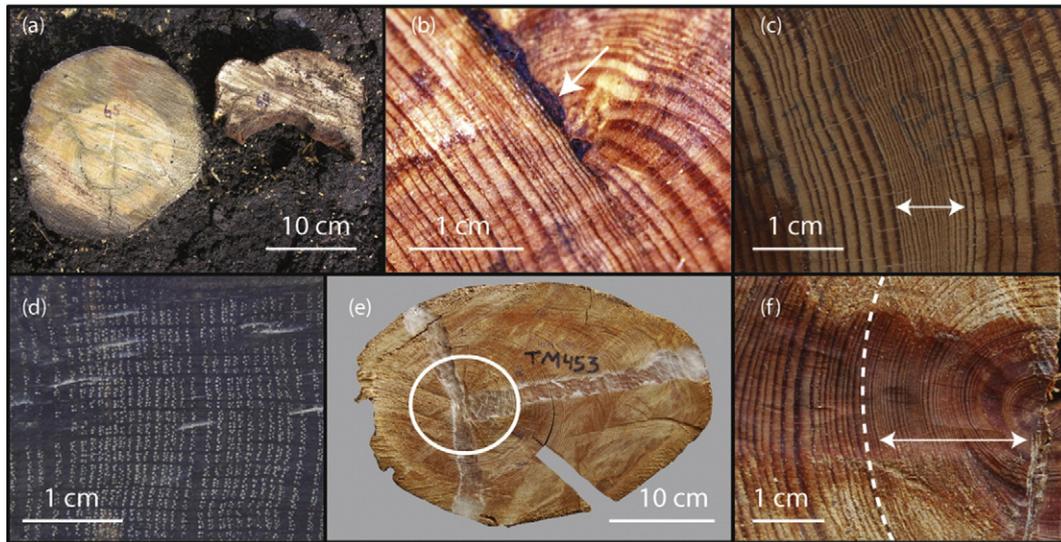


Fig. 5. Cross-sections and annual growth rings from subfossil trees exhibit different growth patterns and characteristics. (a) Two cross-sections from Scots pine (*Pinus sylvestris* L.) excavated at Viss Mosse (Fig. 1, site 23). The left hand sample contains a complete ring sequence from pith to bark corresponding to 5078–4970 BCE (7027–6919 BP). The right hand sample has degraded after death. The growth rings correspond to the period 4872–4716 BCE (6821–6665 BP), but approximately 50–70 rings towards the center and another 10–20 of the outermost rings are expected but have eroded away. (b) Fire scar dated to 4420 BCE (6369 BP). (c) Abrupt growth depression visible in a pine tree from the peatland Ábuamossen (Fig. 1, site 24). The growth depression most likely resulted from a period of extremely wet conditions between 1288 and 1270 BCE (3237–3219 BP) and is visible in all dated trees growing at the peatland. (d) Tree-ring sequence from a subfossil oak (*Quercus robur* L.). (e) Eccentric pine-stem cross-section characteristic for trees growing on unstable soils. The innermost 70 annual rings are circular, whereas about 4070 BCE (6020 BP) unstable conditions are evident having forced the tree to form reaction wood. (f) About 70 narrow annual rings (inside the circle) around the pith, indicating unfavourable conditions during establishment.

trees exposed in erosion scars in blanket peats across the Scottish Highlands (Lewis, 1906, 1908) were interpreted as evidence of constant changes in the character of the vegetation covering the Scottish peatlands.

During the early twentieth century, palaeoclimatological research was improved significantly by pollen analysis, introduced by von Post (1924, 1930). Moreover, stratigraphic studies by Granlund (1932) showed that abrupt peat humification shifts, referred to as “recurrence surfaces” (Fig. 2), were associated with rapid climatic shifts towards colder and wetter conditions. Following the introduction of radiocarbon dating, the studies by e.g., Aaby (1976) and Barber (1981) were able to link peat humification shifts to actual climate changes. Currently, climate reconstructions based on peatlands are common in the palaeoclimatic literature (e.g., Langdon and Barber, 2005; Mauquoy et al., 2008) and generally based upon several parameters such as peat humification, pollen data, plant macrofossils, and testate amoebae (e.g., Hughes et al., 2006; Swindles et al., 2013).

Even though tree horizons in peat deposits were discovered over a century ago and their potential role as indicators of environmental changes was rapidly realized, subfossil trees in peatlands remained an underutilized source of palaeoclimatic information for a long time. Then, in the late 1960s, a number of projects were initiated with the aim of developing tree-ring chronologies using subfossil trees excavated from peatlands in northwest Europe (Pilcher, 1973; Pilcher et al., 1977). This approach was made possible by the large number of well-preserved tree remains that have been exposed by peat extraction for fuel and horticulture (Figs. 4–5; Joosten and Clarke, 2002). During the 1970s and 1980s, oak samples from such peatlands in Ireland and Germany were used for the establishment of the first multi-millennial peatland tree-ring chronologies (Pilcher, 1973; Pilcher et al., 1977, 1984; Leuschner and Delorme, 1984). At a very early stage, dendrochronological studies proved that subfossil wood material originating from different Irish peatlands could be cross-dated (Pilcher, 1973; Pilcher et al., 1977), which encouraged further work. Cross-dating is a standard procedure in dendrochronology in which individual tree-ring width (TRW) series are statistically and visually compared (Douglass, 1941; Fritts, 1976; Wigley et al., 1987). Several statistical parameters are normally tested, of which the *t*-test (Baillie and Pilcher, 1973) is the most

commonly used (Table 1) and referred to when cross-dating statistics are presented (Figs. 6–7).

During the 1970s, floating tree-ring chronologies were developed from oaks found in multiple peatlands across Ireland (Pilcher, 1973; Pilcher et al., 1977). In parallel, an Irish oak chronology from living and archaeologically excavated trees was developed by Baillie (1973, 1995), which would later enable absolute dating of some of the floating chronologies to obtain a continuous tree-ring chronology spanning 7272 years (Pilcher et al., 1984). The chronology proved to be a valuable calendric climate record and provided a standard for the radiocarbon calibration curve (Pilcher et al., 1984; Pearson et al., 1986; Reimer et al., 2013). As the Holocene record of subfossil peatland trees is of significance to both palaeoclimatologists and archeologists, the literature contains a mixture of chronologies that quote ages as both BP and AD/BC. Although, for the purpose of a review it may seem appropriate to adopt one scheme or the other, however, this has inherent problems for both of the relevant communities. Consequently, in this study where we refer to an absolute age we quote the age in AD/BC with the BP alternative in brackets, but where an event is known by a BP age, we quote the cal. BP age (calibrated years before 1950 CE) and refer to an approximate BC age in brackets.

Meanwhile, tree-ring chronologies for environment and climatic reconstructions were also constructed in Germany (Bauerhchse et al., 2015). In this case, thousands of trees preserved in central and north German riverine sediments (Becker and Schirmer, 1977; Becker, 1983; Friedrich et al., 2004) and in north German peatlands (Leuschner and Delorme, 1984) were used. Due to stepwise and long-distance cross-dating it was possible to age determine previously undated material and to correct problematic and falsely dated sections (Figs. 6–7; Pilcher et al., 1984; Brown and Baillie, 2012). Ever since then, the use of stepwise cross-dating has given an absolute age to tree-ring chronologies from England (Chambers et al., 1997; Lageard et al., 1999; Boswijk and Whitehouse, 2002), Scotland (Moir et al., 2010; Moir, 2012) the Netherlands (Jansma, 1996; Sass-Klaassen and Hanraets, 2006), Denmark (Christensen, 2007) and Sweden (Edvardsson et al., 2012a, 2014b).

In the late 1960s, Munaut (1967) and Smith et al. (1972) successfully developed the first tree-ring chronologies from subfossil peatland

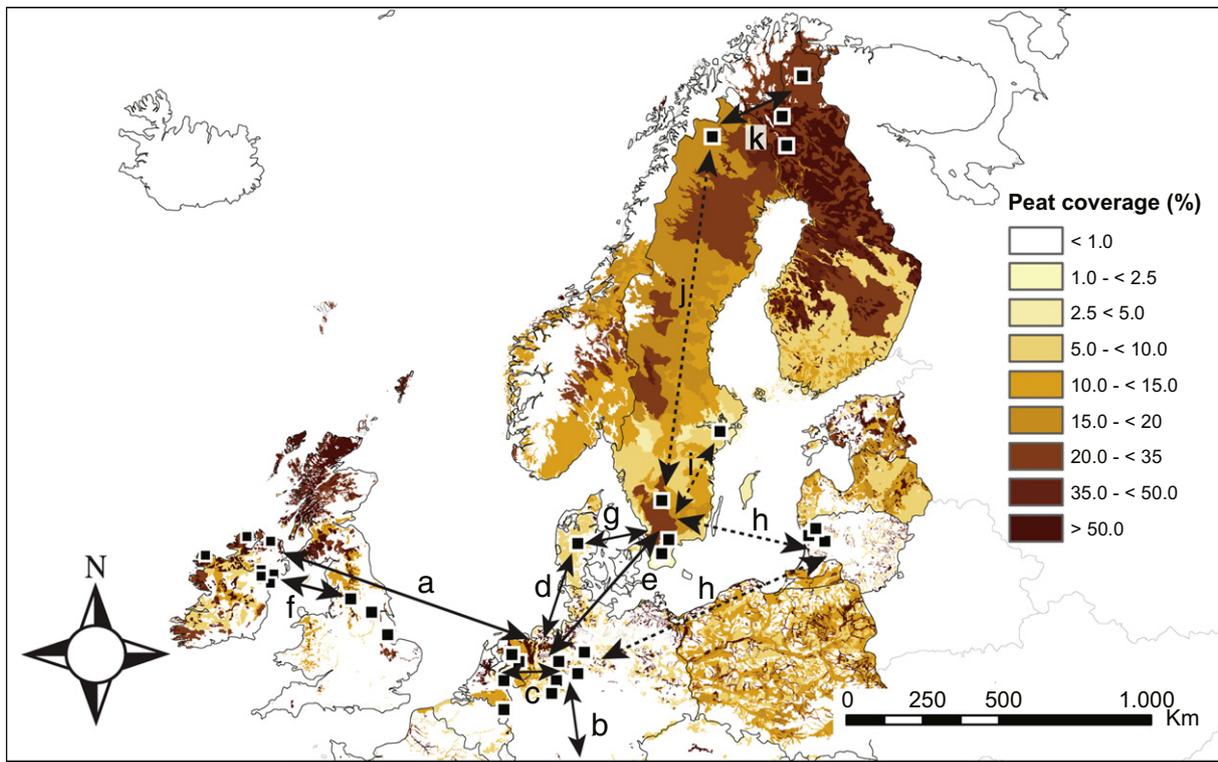


Fig. 6. Significant cross-dating statistics between continental and Irish peatland and oak chronologies have been described by Pilcher et al. (1984) and Leuschner et al. (2002; arrow a). German peatland-oaks also cross-date oaks from River Main (Friedrich et al., 2004, arrow b), the Netherlands (Sass-Klaassen and Hanraets, 2006; arrow c), Denmark (unpublished, see Fig. 7; arrow d), and Swedish pine (Edvardsson, 2016; arrow e), whereas the Irish chronologies (oak and pine) cross-date with the material from Great Britain and Scotland (e.g. Boswijk and Whitehouse, 2002; arrow f). Some of the Danish and Swedish oak chronologies also cross-date (Edvardsson et al., 2014b; arrow g). Furthermore, the Swedish and German pine chronologies generated strong cross-dating statistics (Edvardsson et al., 2012a; arrow e). Attempts to cross-date Baltic pine chronologies using material from Germany and Sweden have, however, failed (Edvardsson et al., 2016a; dashed arrows h). Tests to cross-date south Swedish pine chronologies with peatland pines described by Gunnarson (1999; dashed arrow i) and subfossil mineral soil pines from Torneträsk (Grudd et al., 2002; dashed arrow j) failed as well. By contrast, the north Swedish and Finnish chronologies (Helama et al., 2005; arrow k) indeed cross-date well. Peat coverage is based on Montanarella et al. (2006).

pinus. However, pine trees were often considered as unreliable for chronology construction due to problems such as missing and wedging rings (Fig. 5). Attempts in Scotland during the 1980s, for example, failed

to cross-date approximately 200 samples (Bridge et al., 1990). Radiocarbon dates later showed that the samples had a large temporal range, which explained parts of the problems with cross-dating. By contrast,

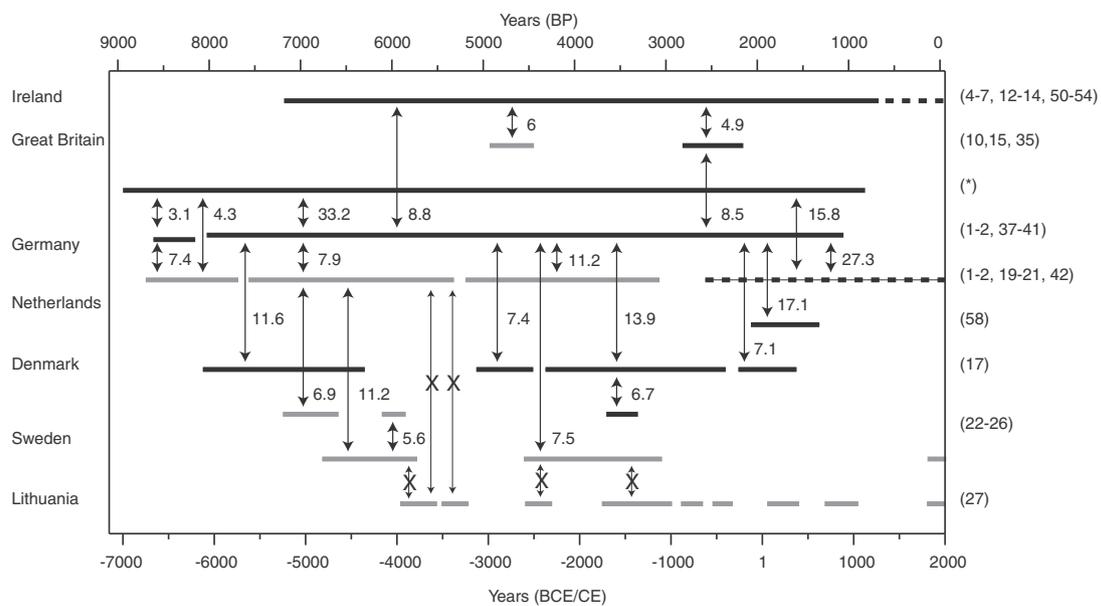


Fig. 7. Stepwise cross-dating of tree-ring chronologies from northwest Europe. The t-values between different chronologies are presented next to the arrows. Oak chronologies are shown in black, pine in grey, and dashed lines represent historical material anchored in present. The figures to the right correspond to the site IDs in Fig. 1 and Table 1. The River Main oak chronology (*, Friedrich et al., 2004) is also included in the figure.

more recent studies focusing on Irish, Scottish, and British peatland pine chronologies have been successful in cross-dating tree-ring records (Pilcher et al., 1995; Lageard et al., 2000; Moir et al., 2010).

The interest in peatland pines increased, especially as they were found to have the potential to extend further back in time than the Irish oak chronology (then at 5452 BCE or 7401 BP; Pilcher et al., 1995). In the Lower Saxony area, northwest Germany, extensive work was initiated on peatland pines (Leuschner et al., 2007; Eckstein et al., 2009, 2011; Achterberg et al., 2015, 2016). The German pine chronologies have been constructed from some 4000 peatland trees (Bauerchse et al., 2015) and show a temporal spread over the period 6703–1165 BCE (8652–3114 BP; Achterberg et al., 2016). Scots pine has been shown to represent by far the most common tree species in Scandinavian (Gunnarson, 1999; Edvardsson et al., 2012a) and Baltic (Pukienė, 1997; Edvardsson et al., 2016a) peatlands and in northern Sweden, pine remains in peaty environments have been used for treeline reconstructions during the Holocene (Kullman, 1987). However, these treeline trees have proved to be unsuitable for chronology development due to the smaller sample number and wide temporal range. In central and southern Sweden, by contrast, peatland pines have been used successfully for the development of multi-millennial tree-ring chronologies (Gunnarson, 1999, 2008; Edvardsson et al., 2012a, 2012b). In northern Finland, subfossil pine remains have been recovered from peatlands and lacustrine sediments of lakes with thick layers of organogenic riparian substrate (Eronen et al., 1999). Dendrochronological analyses of this material yielded a continuous tree-ring chronology over the mid- and late-Holocene (from 5634 BCE, Eronen et al., 2002; Helama et al., 2008), with indications that pine population density and hydrologic conditions varied over time (Helama et al., 2005). The suitability of subfossil peatland pines for long-term climate and palaeohydrology reconstructions has now been shown in a range of studies (Pilcher et al., 1995; Lageard et al., 2000; Boswijk and Whitehouse, 2002; Leuschner et al., 2007; Eckstein et al., 2009; Moir et al., 2010; Edvardsson et al., 2012a; Achterberg et al., 2016).

4. General interpretations of peatland tree-growth dynamics

4.1. Tree growth, climate and hydrology

High water levels in peatlands have profound effects on seed germination and seedling development (Kozłowski, 1997; Holmgren et al., 2015). Indeed, the activation of the physiological processes required for seed germination depends on oxygen (O₂) supply. A water table located close to the peat surface will restrict O₂ availability to the embryo and thereby prevent or postpone seed germination (Dang et al., 1991; Kozłowski and Pallardy, 1997; Fragnière et al., 2015; Kozłowski et al., 2015). Only once the seeds germinate will fluctuations in water level determine seedling survival and modify the capacity of seedlings to elongate rapidly and protrude above the water level (Sacchi and Price, 1992). As a consequence, lowered water tables are typically associated with the colonization of trees due to improved growth conditions (Freléchoux et al., 2000; Eckstein et al., 2009; Edvardsson et al., 2015b).

Most often, the annual growth of peatland trees is highly dependent on the depth and variability of the water table beneath the tree root system (Boggie, 1972; Eckstein et al., 2009). Wetter conditions are usually characterized by growth patterns showing recurrent, narrow annual growth rings, multi-annual growth depressions, and sometimes missing rings (Leuschner et al., 2002; Fig. 5). Such moist and unfavourable growth conditions are associated with physical, chemical, and biological restrictions on tree growth, of which reduced availability of nutrients in the water unsaturated zone probably represents the most important limiting factor (Boggie, 1972; Mannerkoski, 1991; Linderholm, 2001). Moreover, nitrate is rapidly depleted by denitrification under conditions of soil hypoxia (Kozłowski and Pallardy, 1984). By contrast, the uptake of iron (Fe) and manganese (Mn) is increased because of an increase in soluble ferric and manganic forms. Yet, abundant ferrous and

manganous ions in wet soils may be toxic to some tree species (Crawford, 1989). Moist conditions reduce root growth of most woody plants by inhibiting root formation and branching, repressing growth of existing roots and mycorrhizae, and by promoting root decay (DeBell et al., 1984; Kozłowski, 1984; Kozłowski and Pallardy, 1997; Eckstein et al., 2011). Tree growth is inhibited by the lack of O₂ (Dang et al., 1991; Kozłowski and Pallardy, 1997) and in particular, reduced macronutrients uptake (especially nitrogen, phosphorus, and potassium) driven by a reduction in O₂ supply to the roots (e.g., Osundina and Osonubi, 1989). Finally, a variety of toxic compounds such as aldehydes, organic acids, and ethanol accumulated in wet soils have been demonstrated to variously contribute to injury, growth reduction, and mortality of woody plants (Kozłowski, 1997; Vitas and Erlickytė, 2007).

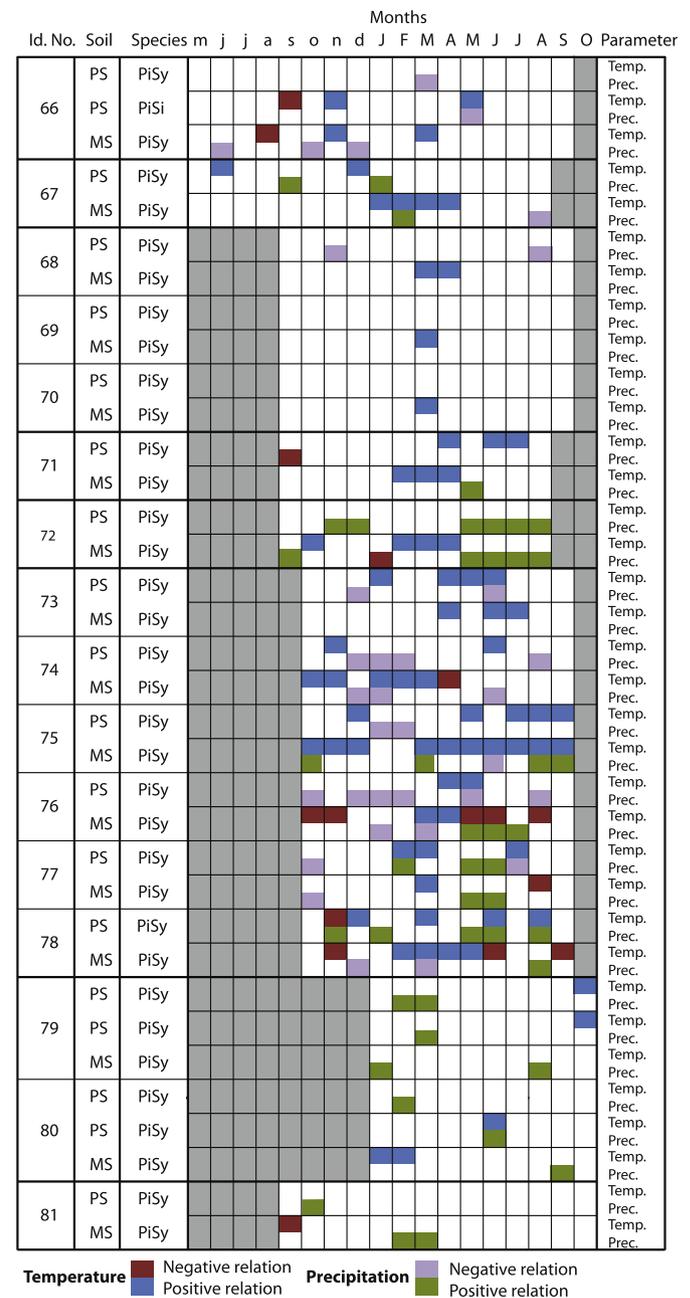


Fig. 8. Comparisons between tree-ring width (TRW) and meteorological records (monthly temperature and precipitation data). Sites from which both tree growth at mineral soils (MS) and peat soils (PS) could be compared are presented. The identification numbers (Id. no.) corresponds to those presented in Fig. 1 and Table 2.

Consequently, a change towards wetter climatic conditions would lead to rising water tables, causing shallower unsaturated zones (Schouwenars, 1988; Hunt et al., 1999), and thereby reduce recruitment of new trees and growth reductions in trees already growing at the peat surface (Boggie, 1972; Linderholm et al., 2002; Edvardsson et al., 2015a). Soil moisture is therefore a key driver of both radial tree growth and tree population dynamics in peatlands. Growth depressions and dying-off phases in subfossil chronologies are therefore an expression of unfavourable growth conditions, linked to changes in site hydrology towards moister conditions (Leuschner et al., 2002; Edvardsson et al., 2012b; Scharnweber et al., 2015). Lowered water tables, on the other hand, are typically associated with enhanced radial growth or the colonization of peatland trees (Freléchoux et al., 2000; Eckstein et al., 2009; Edvardsson et al., 2015b). This hypothesis is supported by a comparison of climate-growth relationships obtained for pine trees growing on peat and adjacent mineral soils (Fig. 8). This comparison also clearly demonstrates that tree growth on mineral soils is significantly correlated with winter and early summer temperatures, whereas a more complex, weaker and clearly site-dependent response to monthly temperature and precipitation is detected in peatland trees. The latter presumably reflects the multiannual synthesis of moisture variability and changing hydrology (Fig. 9), which could be further complicated by a hydrological lag and/or feedback response in peatlands (Linderholm et al., 2002; Edvardsson et al., 2015a; Edvardsson and Hansson, 2015).

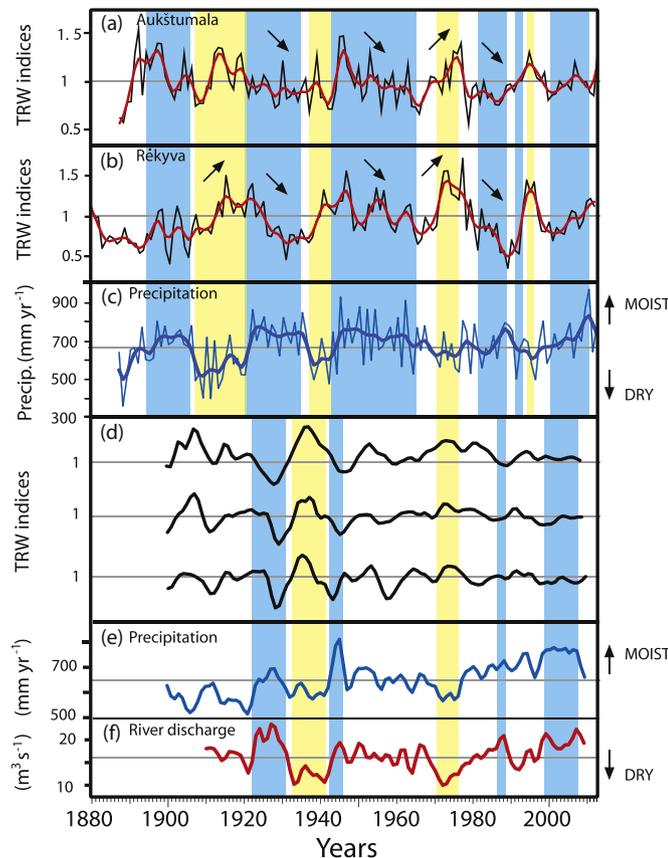


Fig. 9. (a–b) Examples of TRW chronologies from living trees growing at Aukštumala and Rékyva (Edvardsson et al., 2015a). (c) Precipitation data from the meteorological station in Vilnius. (d) TRW chronologies from Buxabygd's Mosse, Saxnäs Mosse and Store Mosse, Sweden (Edvardsson and Hansson, 2015). (e) Local precipitation data and (f) river discharge data. The blue bars emphasize moist periods associated with positive precipitation anomalies, grey lines represent average values. Growth depressions or trends towards narrower growth rings can often be observed during phases associated with positive precipitation/wet anomalies.

Studies exploring climate-growth relationships have not been realized for subfossil peatland oaks so far. Indeed, during extended periods of the Holocene, deciduous oaks have established in peatlands across northwestern Europe (Pilcher et al., 1984; Leuschner et al., 2002), but any detailed interpretation of the subfossil oak data has long been problematic due to the absence of modern peatlands with oak tree cover (Sass-Klaassen, 2004). In a study by Scharnweber et al. (2015), however, a catastrophic rewetting of a drained, oak covered peatland in north-east Germany has provided the opportunity to study growth responses in oaks following well-documented hydrological changes. Similar to the work on pine, moisture is also shown to be the main growth-limiting factor in peatland oak trees.

4.2. Hydrological lag effects

Several studies show that a hydrological lag response to changing precipitation in peatlands exists, meaning that some delay can be observed between actual climate changes and related hydrological shifts in the peatlands (Kilian et al., 1995; Waddington et al., 2014). Such delayed responses have in the past been attributed to (i) water transport in soils towards the peatlands (e.g., Cowan, 1965; Hillel, 1971), (ii) water interception or accumulation in plants (Shukla and Mintz, 1982; Seneviratne et al., 2010), (iii) delays between snowfall and associated snowmelt (Price and Schlotzhauer, 1999), and (iv) the process by which water is replacing air in the relatively large pore spaces of the unsaturated zone of peat (Ingram, 1983; Almendinger et al., 1986). In addition, it is known that (v) peat soils are compressible such that changes in water content may result in volumetric fluctuations and thereby variations in surface elevation, which in turn can vary depending on the amount of water stored in the peat (Almendinger et al., 1986; Price and Schlotzhauer, 1999). These slow hydrological changes may therefore result in monthly to multiannual lags between climate and tree growth responses, as observed and discussed in studies by Linderholm et al. (2002), Edvardsson et al. (2014a, 2015a), or Edvardsson and Hansson (2015). Knowledge about such delays is important for our understanding of relations between hydrological variability and tree growth, and for all studies aiming at: (i) reconstructing past and future hydroclimate changes, (ii) long-term carbon storage capacity of northern peatlands, (iii) the prediction of future peatland vegetation dynamics, and (iv) an improved understanding of peatland vulnerability to changing climate (Waddington et al., 2014).

4.3. The influence of trees on peatland hydrology

As discussed, surface moisture in peatlands is the most important factor governing tree growth and colonization (Boggie, 1972; Edvardsson et al., 2015b). Tree density may in turn influence surface moisture and ultimately carbon sequestration in the peatlands, as a result of feedback effects (Limpens et al., 2014a; Holmgren et al., 2015). Trees can affect the moisture status of peatland environments through transpiration and interception (Limpens et al., 2014b). Colonization by trees therefore has the potential to cause a positive drying feedback, whereby increased root uptake for transpiration demand causes a lowering of the water table, in turn promoting improved tree growth and seedling recruitment and/or shrubification as root oxygenation and root zone thickness increase (Limpens et al., 2014b). This positive feedback is amplified further by: (i) increased soil nutrient availability by litter fall, (ii) increased levels of interception with increased canopy (Dubé et al., 1995), and (iii) reduced aerodynamic resistance (by e.g., wind) favoured by higher stand density which increases evaporation (Kellner, 2001). The change in hydrology may also lead to increased decay rates in the upper peat profile due to a deepening of the aerobic zone. Changes in tree cover can therefore be a fundamental shift in the peatland carbon cycle and it is possible that tree-covered peatlands could become net sources of carbon if increased net photosynthetic rates and carbon fixation are lower than increased peat decomposition

rates (Juutinen et al., 2010). The effects that tree density has on water loss have important implications for the structure and functioning of peatlands but the relation between evapotranspiration and tree density is non-linear (Limpens et al., 2014b). This is because increasing density of tree stands can result in shading of the peat surface, thereby reducing the energy available for evaporation (Ohlson et al., 2001; Strakova et al., 2012).

5. Climate – peatland relations: drawing a continental-scale picture

The present interglacial, the Holocene, started about 11,700 cal. BP (calibrated years before 1950 CE) with a rapid transition from the cold Younger Dryas to subsequent conditions characterized by significantly warmer and more stable conditions (Bond et al., 2001; Wanner et al., 2008; Marcott et al., 2013). At the millennial timescale, the climate of the Holocene has been influenced strongly by hemispheric trends in solar insolation, but was also interrupted by shorter centennial events related to other drivers such as solar and volcanic forcing (Dansgaard et al., 1989; Bond et al., 2001; Wanner et al., 2011). High spatial and temporal variability in temperature and moisture records covering the Holocene have been reconstructed from archives such as ice cores, ocean, lake, and peat sediment cores, speleothems and glacier fluctuations (Wanner et al., 2011). Climatic and environmental mismatches or delays between different geographical regions, however, underline the importance of multiple site studies and call for high-resolution reconstructions using proxies such as tree rings, which remain the most widespread source of annual resolution, precisely dated palaeoclimatic data. In the following discussion, the Holocene is subdivided into the early (c. 9750–6250 BCE or 11,700–8200 cal. BP), mid (c. 6250–2250 BCE or 8200–4200 cal. BP), and late (c. 2250 BCE or 4200 cal. BP to present) Holocene as suggested by Walker et al. (2012).

5.1. The early Holocene

Subfossil peatland trees from the early Holocene are scarce for obvious reasons, primarily due to the fact that most northern peatlands were not ombrotrophic until later periods of the Holocene due to slow peat formation and accumulation (Barber et al., 2003; Yu et al., 2010). Despite this limitation, radiocarbon dated pine trees as old as c. 9050 BCE (11,000 cal. BP) have been discovered in northwestern German peatlands (Achterberg et al., 2016). The formation of raised bogs in this region, however, only began about 2000 years later (Petzelberger et al., 1999; Eckstein et al., 2011), which suggests that the material consists of mineral soil pines overgrown by and preserved in expanding peatlands. Tree colonization directly on peat soils of northwestern Germany has, however, been recorded about c. 6750 BCE (8700 cal. BP), evident from peatland pines dated to 6703 BCE (8652 BP; Achterberg et al., 2015) and oaks dated to 6627 BCE (8576 BP; Leuschner et al., 2002; Achterberg et al., 2015). Oak trunks from this period, but dated by radiocarbon, have also been discovered in Denmark (Christensen, 2007). Some centuries later, about 6350 BCE (8300 cal. BP), minor periods of pine establishment have been noted in the Irish and Scottish pine material (Bridge et al., 1990; Torbenson et al., 2015). Otherwise, few establishment phases have been recorded prior to the 8200 cal. BP cold event (referred to as the 8.2 ka event, c. 6250 BCE; Alley et al., 1997), which may have generated moist and unfavourable conditions for tree colonization at the peatlands. The 8.2 ka event is recorded on a hemispheric scale in a broad range of proxy records (Alley et al., 1997; Veski et al., 2004; Nicolussi and Schlüchter, 2012). The number of German pines recorded (replication in Fig. 10) drops during (or slightly after) the 8.2 ka event and a 108-year gap has been documented in the German bog oak record (Achterberg et al., 2016), indicating a shift towards unfavourable conditions for peatland tree growth (Fig. 10). Although from a different context, the lowest tree replication in the Alpine tree-ring chronology by Nicolussi et al. (2009) is observed around 6100 BCE, very close to the

8.2 ka event. In a similar way, Helama et al. (2008) also suspect that the lack of subfossil trees in Finnish Lapland was caused by the same climatic effect and that it would likely have decelerated pine colonization in the region.

5.2. The mid-Holocene

About 8100 years ago, following the cold 8.2 ka event (Alley et al., 1997), tree establishment has been recorded in various peatlands in northwestern Europe, namely in Ireland (Pilcher et al., 1995; Torbenson et al., 2015), Germany (Leuschner et al., 2002; Eckstein et al., 2009; Achterberg et al., 2015), Denmark (Christensen, 2007), and Sweden (Edvardsson et al., 2012b). These initial pulses of tree establishment were followed by continuous and fluctuating mid-Holocene tree colonization across northwest European peatlands (Fig. 8).

During the mid-Holocene, cross-dating between series from different regions yields statistically significant results and points to striking similarities in annual growth and tree population dynamics over substantial parts of northwestern Europe, especially for the period 5300 to 2500 BCE (7250–4550 BP; Figs. 6–7). The successful cross-dating between various sites, sometimes separated by hundreds of kilometres, also indicates that similar year-by-year climate variability has influenced environmental conditions at these peatlands, and thereby radial growth of trees (Pilcher et al., 1977, 1984; Leuschner et al., 2002; Eckstein et al., 2009; Edvardsson et al., 2012a). Similarities in tree replication records on the other hand, show coinciding regeneration and later life stages, whereas mean-age records indicate changes in the age structure of tree populations. The German pines, for instance, were not randomly distributed over time. Instead, woodland establishment and dying-off phases were periodic, as detected in pine populations from 36 different German peatlands (Eckstein et al., 2009). Together, the significant cross-dating statistics and similarities in tree population dynamics imply similar high- (i.e. annual to decadal scale) and low-frequency variability (i.e. decadal to centennial scale) governed hydroclimatic forcing mechanisms influencing peatland hydrology and associated tree growth over a large geographic region (Figs. 6 and 10). Moreover, widespread colonization also points to relatively dry and therefore favourable growth conditions for peatland trees, which is underlined by the main woodland phases at German and Swedish peatlands between 5300 and 3700 BCE (7250–5650 BP; Eckstein et al., 2009, 2011; Edvardsson et al., 2012a, 2012b).

Pine records from the Alps show colonization at unusually high elevations (Tessier et al., 1993) and strong replication (Nicolussi et al., 2009) during the same period. A combination of high-altitude occurrence and an increased replication of subfossil pines is also evident in northern Finland from 4200 to 2200 BCE (6150–4150 BP; Helama et al., 2004, 2010). The pine colonization of peatlands in northern Scotland occurred around 5000 years ago, and has been interpreted as a regional phenomenon (Gear and Huntley, 1991; Charman, 1994; Daniell, 1997; Huntley et al., 1997). By contrast, both oak and pine trees colonized Baltic peatlands during the mid-Holocene (Pukienė, 2003; Vitas, 2010; Edvardsson et al., 2016a), and therefore add further evidence of widespread impacts of favourable climatic conditions.

These favourable growth conditions for peatland trees during the mid-Holocene were probably closely linked to a relatively warm and dry climate regime, which commonly is referred to as the Holocene Thermal Maximum (HTM; Seppä et al., 2005; Renssen et al., 2009). The onset and termination of the HTM varies clearly between different geographical regions and studies, but is generally dated to the period c. 6850–2450 BCE (8000–4400 cal. BP) across northern Europe (Jessen et al., 2005; Seppä et al., 2005; Renssen et al., 2009; De Jong et al., 2009). The comparably high air temperatures and dry conditions in northwestern Europe were probably caused by (i) an orbitally-forced increase in summer insolation, and (ii) a stronger meridional overturning circulation and intensified northward ocean heat transport

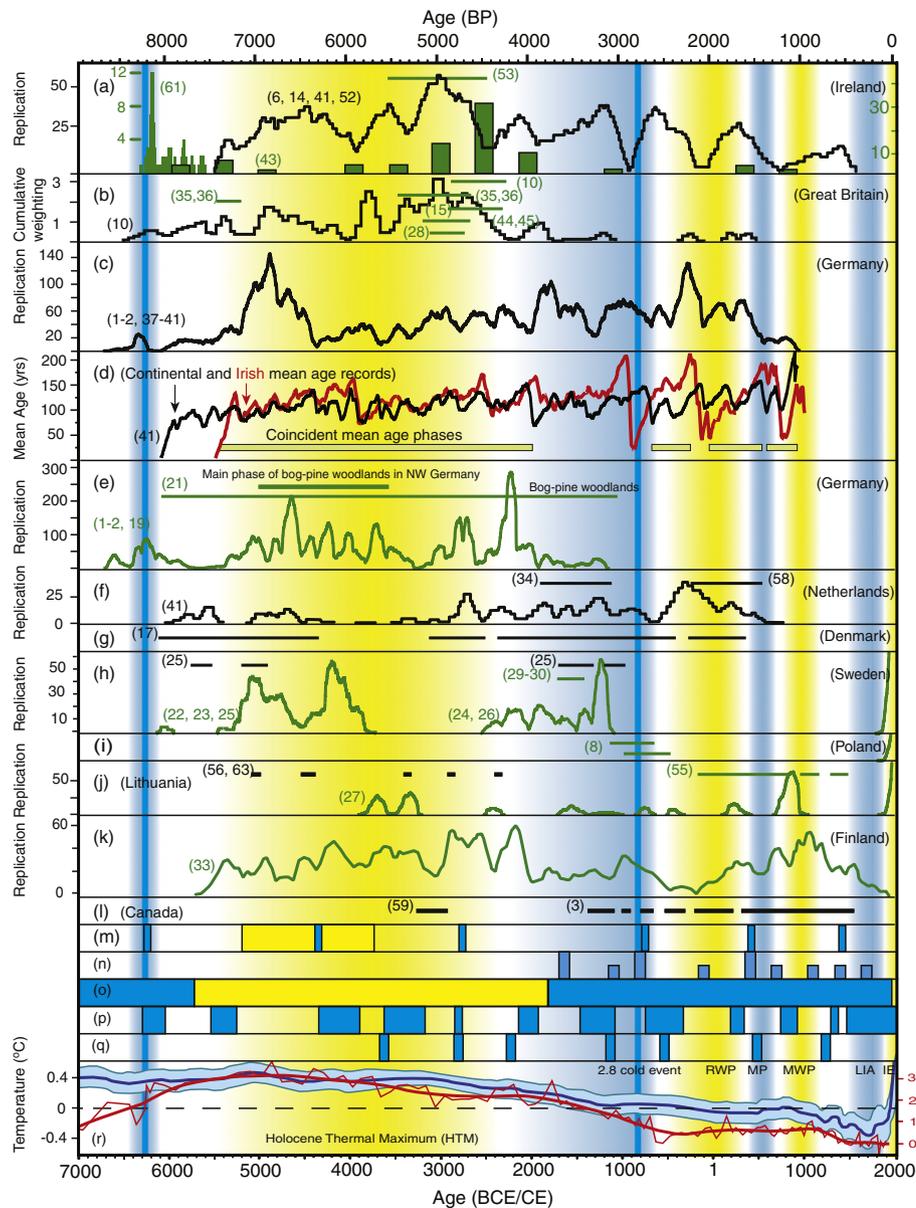


Fig. 10. Main data series compared in the discussion, oak in black, pine in green, and numbers in brackets correspond to those in Table 1. (a) Irish data series, in black Irish oak replication, in green pine establishments, and cumulative radiocarbon dated pine samples (green/black squares). (b) Cumulative weighted Scottish peatland trees dated by radiocarbon and coverage of peatland pines chronologies. (c) German peatland oaks. (d) Continental and Irish oak mean-age records. (e) German pine replication and woodland phases. (f) Replication and temporal spread of oak from the Netherlands. (g) Periods covered by Danish peatland oaks. (h) Swedish pine replication and periods covered by oak chronologies. (i) Polish pine chronologies. (j) Lithuanian pine replication as well as pine and oak coverage. (k) Pine replication from Finland. (l) Spruce coverage from Canada. (m) Dry and wet shifts highlighted in yellow and blue respectively (Wanner et al., 2011). (n) Wet shifts detected in peat bogs from northern Britain (Charman, 2010). (o) Lake levels in the Baltic region (Sohar and Kalm, 2008). (p) High lake-level phases in mid-European lakes (Magny, 2004, 2013). (q) Wet shifts detected as recurrence surfaces in Swedish peat bogs (Borgmark and Wastegård, 2008). (r) In blue, temperature anomalies in relation to the average (Marcott et al., 2013) and in red, a pollen based temperature reconstruction by Heikkilä and Seppä (2010).

after the Laurentide Ice Sheet had vanished (Snowball et al., 2004; Renssen et al., 2009; Wanner et al., 2011). Temperature reconstructions based on stable isotopes from ice-cores as well as pollen data from lake sediments and peat cores all point to summer temperatures which would have been approximately 2–3 °C above present value/The comparably high air temperatures and dry conditions is across most parts of northwestern Europe and Scandinavia (Huntley and Prentice, 1988; Seppä et al., 2005; Brown et al., 2011; Helama et al., 2012). At the same time, moisture records indicate a dry phase at about 5250 to 3750 BCE (7200–5700 BP; Wanner et al., 2011), which is confirmed indirectly by lake level proxies pointing to generally low water levels

(Digerfeldt, 1988; Hammarlund et al., 2003; Magny, 2004, 2013; Sohar and Kalm, 2008).

The annual resolution and accurate dating of the tree-ring chronologies allow detailed studies of rapid climatic events during the HTM, which may be missed in lower resolution proxies. Several peaks in the Irish replication records have, for instance, been recorded about 6050, 5350, 4250, and 1250 BCE (8000, 7300, 6200 and 3200 BP; Turney et al., 2006), and are consistent with peaks and establishment phases detected in replication records from Germany, the Netherlands, and Sweden (Fig. 10). Moreover, many dying-off phases described in the German records (Leuschner et al., 2002; Eckstein et al., 2009;

Bauerochse et al., 2015; Achterberg et al., 2015) can be found in other records from northwestern Europe. For instance, the dying-off phase between 4600–4550 BCE (6550–6500 BP) described by Achterberg et al. (2015) is also visible in the oak records from Germany and the Netherlands (Leuschner et al., 2002), as well as in the Scottish (Bridge et al., 1990) and Swedish (Edvardsson et al., 2012a) pine records.

Towards the end of the HTM, shifts towards wetter conditions about 3250 BCE and 2250 BCE (5200 and 4200 cal. BP) have been described in the literature (referred to as the 5.2 and 4.2 ka events; Roland et al., 2014, 2015). The 5.2 ka event (c. 3250 BCE) has been identified as a coherent shift towards wetter conditions caused by prolonged positive North Atlantic Oscillation conditions, and was found in stable isotope, testate amoebae, plant macrofossil, and humification records from peatlands in Northern Ireland (Roland et al., 2015). Evidence for such a wet shift is lacking in the Irish oak replication records, whereas a decrease in German peatland pines and a dying-off phase in Lithuanian pines can be observed (Fig. 10). Moreover, a coincident phase of lowered replication of subfossil pines is evident in northern Finland (Helama et al., 2004, 2010). Several synchronous and massive dying-off phases can also be detected about 2500 BCE (4450 BP) in Scotland (Gear and Huntley, 1991; Charman, 1994; Daniell, 1997), Ireland (Pilcher et al., 1995), Great Britain (Lageard et al., 1999; Boswijk and Whitehouse, 2002), Germany (Eckstein et al., 2011; Bauerochse et al., 2015), and Sweden (Edvardsson et al., 2014b), and thus point to a spatially structured, regional environmental change. By way of example, the British peatland pine chronologies from Garry Bog (2569 BCE; Pilcher et al., 1995), White Moss (2559 BCE; Lageard et al., 1999), Thorne (2475 BCE; Boswijk, 1998), and Hatfield (2445 BCE; Boswijk and Whitehouse, 2002) all terminate at 2507 ± 62 BCE (4456 ± 62 BP).

5.3. The late Holocene

The unfavourable conditions recorded towards the very end of the HTM continued in a similar manner between 2200 and 2160 BCE (4150–4110 BP; Fig. 10), and resulted in abrupt dying-off phases at various sites in northwestern Germany (Eckstein et al., 2010; Bauerochse et al., 2015), the Netherlands (Leuschner et al., 2002), and Finland (Helama et al., 2004). The similarities between continental and Irish mean-age records, which were present during the entire HTM, also start to disappear at about 2000 BCE (4000 BP; Leuschner et al., 2002). The effects of a large-scale shift in climatic conditions are also obvious in northern Finland where the replication of the subfossil pine chronology collapses around 2200–2000 BCE. Moreover, indications of pine germination are clearly missing at the high elevation sites in Finland as of 2400 BCE (4350 BP), and are followed by a gradual decline in pine populations until 600 BCE (2550 BP; Helama et al., 2004). Since about 1500 BCE (3450 BP), following yet another dying-off phase recorded across northwestern European peatlands, fewer dated peatland pines have been found in Germany (Achterberg et al., 2015) and Ireland (Pilcher et al., 1995). Most of these observations can be linked to the onset of a widespread climatic transition, sometimes referred to as the Neoglacial phase (Nesje et al., 1991; Wanner et al., 2008).

The climatic change about 2250 BCE (4200 cal. BP and often referred to as the 4.2 ka event; Roland et al., 2014) is evident at the hemispheric scale in numerous proxy records and was most likely driven by changes in orbital insolation patterns (Bradley, 2003; Booth et al., 2005; Morley et al., 2014), but changes in tree populations do not appear abruptly or synchronously between different sites (Fig. 10). Instead, a multi-proxy study from Sweden points to a stepwise transition phase dated to between c. 2650 and 1450 BCE (4600 and 3400 cal. BP; Jessen et al., 2005). In a similar way, several dying-off events have been recorded among Swedish peatland trees (Edvardsson, 2016), whereas a two-stage temperature decrease with an onset c. 3050–2550 BCE (5000–4500 cal. BP) and a termination c. 2350–1350 BCE (4300–3300 cal. BP) has been described around the Baltic Sea (Borzenkova et al., 2015). Moreover, testate amoebae in Irish peatlands do not provide

any compelling evidence for a rapid transition about 2250 BCE (4200 cal. BP; Roland et al., 2014), whereas records from Great Britain and Denmark suggest a system shift at about 2150 BCE (4100 cal. BP; Mauquoy et al., 2008). These results show that the origin and impact of the 4.2 ka event is spatially complex and was probably less marked towards low latitudes, and may also explain why the drop in tree replication in Ireland and Sweden started 200 years later than in Germany and the Netherlands (Fig. 10). These results also confirm the need for climate reconstructions with high spatio-temporal resolution to improve our understanding of complex climate transitions. Pollen-based temperature reconstructions from Scandinavia show that the annual mean temperature was reduced by almost 2 °C during this transition phase (Seppä et al., 2005; Heikkilä and Seppä, 2010), whereas lake-level reconstructions suggest wetter conditions with rising lake levels between 3000 and 500 BCE (5000–2500 cal. BP; Digerfeldt, 1988; Magny, 2004, 2013; Sohar and Kalm, 2008). Indications of rising water levels after the termination of the HTM also exist for northern Finland in the form of submerged pines with their root systems anchored in the palaeo-shoreline, two meters below the current water level (Eronen et al., 1999). The rising water tables and wetter peatland surface conditions are therefore also believed to have caused widespread dying-off phases, leading to the termination of most Swedish and German pine records at about 1100 BCE (3050 BP; Eckstein et al., 2011; Edvardsson, 2016). Together, these observations indicate that the widespread transition towards wetter and colder conditions continued for at least a millennium after the end of the HTM. These findings are also confirmed by radiocarbon-dated recurrence surfaces detected in several Swedish peat sequences, for which the wet shift is synchronous with the final dying-off phases in the German and Swedish pine chronologies (Borgmark and Wastegård, 2008; Rundgren, 2008) and peat records from northern Britain (Charman et al., 2006).

Although the period 2250–1100 BCE (4200–3050 BP) is in general associated with increasingly wetter and colder conditions, some short and regional colonization events were still taking place. The German pine colonization phase at around 1900 BCE (3850 BP), described by Bauerochse et al. (2015), is also visible in records from Sweden, the Netherlands, and Scotland (Fig. 10). Over the last 3000 years, however, relatively few tree establishment phases have been recorded in German and Irish peatlands, whereas trees appear to be close to absent at all known Swedish sites (Fig. 10). Despite this fact, tree colonization has been recorded at peatlands in the Netherlands (Sass-Klaassen and Hanraets, 2006), Poland (Barniak et al., 2014), Lithuania (Pukienė, 1997; Edvardsson et al., 2016a), and in one of the few regions documented in North America (Québec; Arseneault and Payette, 1997). With the exception of the Canadian records, these phases are relatively short, which may also explain why only the Dutch chronologies have been cross-dated successfully over long distances (Figs. 6–7). It is therefore difficult to judge to what extent these tree colonization phases are related to site-specific variations or are linked to regional climate dynamics.

About 850 BCE (2800 cal. BP), yet another shift towards cooler, wetter, and windier conditions has been recorded in European peatlands (referred to as the 2.8 ka event; van Geel et al., 1996, 2014; Mauquoy et al., 2008; Mellström et al., 2015). Observations made in peatlands are confirmed by other proxy records, which suggest rising lake levels (Magny, 2004, 2013) and more drift ice in the North Atlantic (Bond et al., 1997). The nature and causes of this cold and wet event have been subject to debate, but the shift broadly coincides with an increase of the atmospheric ¹⁴C concentration due to reduced solar activity (Kilian et al., 1995; Swindles et al., 2013; Mellström et al., 2015). The Irish replication and mean-age records indicate dying-off phases or generation shifts, whereas the German and Dutch series point to a decline in replication records (Fig. 10). A dying-off phase about 850 BCE has also been detected in the Polish tree-ring chronologies (Barniak et al., 2014). Despite the general absence of dated peatland pine chronologies from Sweden, macrofossil analysis from a southwest Swedish peat bog

shows that pine must have been present locally at the site prior to 910 BCE (2860 cal. BP), but was absent after 740 BCE (2690 cal. BP; Mellström et al., 2015). Gaps also exist in Lithuanian (Edvardsson et al., 2016a) and Canadian (Arseneault and Payette, 1997) tree records during the same period, which may strengthen the hypothesis that the 2.8 ka event did indeed significantly influence large parts of the northern Hemisphere.

Between c. 500 BCE and 300 CE (2500 and 1600 BP), tree replication records from Ireland, Germany, and the Netherlands again show some tree colonization phases, but of minor importance (Fig. 10). These colonizations coincide with somewhat warmer and drier climatic conditions during the period often referred to as the Roman Warm Period (RWP; Seneviratne et al., 2010; Büntgen et al., 2011). Partial agreements between the Irish and continental mean-age records presumably indicate changes between relatively similar and diverse forcing mechanisms between the two regions over the period (Leuschner et al., 2002). In the Netherlands, a shift in tree population dynamics with establishment of both oak and ash trees has been recorded as late as 300 CE (1600 cal. BP) followed by striking changes in site hydrology and a dying-off phase at about 530 CE (Sass-Klaassen and Hanraets, 2006).

Dying-off phases recorded at several peatlands in Lithuania (Pukienė, 1997; Edvardsson et al., 2016a), by contrast, coincide with the well-known cooling at about 300–600 CE (1650–1350 BP), which is commonly referred to as the Dark Age or Migration Period (Wanner et al., 2011). At about 800 CE (1200 cal. BP), massive tree establishment has been recorded in Lithuanian peatlands (Pukienė, 1997; Edvardsson et al., 2016a) and at the same time, peat records from both Great Britain and Denmark point to a dry phase (Mauquoy et al., 2008). These changes coincide with the onset of the Medieval Warm Period (MWP) and indicate yet another change towards drier conditions in peatlands. Furthermore, Arseneault and Payette (1997) have reported strong radial tree growth over the corresponding period, which indicates relatively favourable conditions for tree growth at Canadian peatlands as well.

By contrast, an almost complete absence of subfossil peatland trees has been recorded during the Little Ice Age (LIA; 1350–1850 CE), which clearly indicates colder and moister conditions compared to the preceding periods (Wanner et al., 2008) and a widespread lack of tree establishment at peatland sites (Fig. 10). Widespread wet shifts have also been reported in European peat stratigraphic records at about 1350 CE and 1600 (600 and 350 cal. BP; Mauquoy et al., 2008). Apparently these conditions generated growth conditions that were too harsh for peatland trees as the final dying-off phases, recorded at about 1400 CE (550 cal. BP), coincide with a shift towards colder (Wanner et al., 2011) and wetter (Charman et al., 2006) climatic conditions. These observations are also supported by the fact that finding recent peatland pines older than 200 years has proven very difficult (Linderholm et al., 2002; Cedro and Lamentowicz, 2011; Edvardsson et al., 2015a), confirming the likely absence of peatland trees during the LIA. As the LIA came to an end, widespread pine colonization occurred in peatlands across Estonia (Smiljanic et al., 2014), Lithuania (Edvardsson et al., 2015a), Poland (Cedro and Lamentowicz, 2011), and Sweden (Linderholm and Leine, 2004; Edvardsson and Hansson, 2015). Observed tree establishment in recent periods is likely to result from a combination of climatic and land-use changes. Nevertheless, changing climatic conditions over the twentieth century have, at least in some cases, been regarded to be the most important driver of increasing tree establishment rates (Edvardsson et al., 2015b).

6. Target areas for future research

There is still a need for improved understanding of the relations between peatland tree growth, moisture variability, and climate dynamics, to enable more robust hydrology and climate interpretation from peatland tree-ring, replication, and mean-age records. For example, there is a clear need for new methods to isolate the temperature and precipitation signals in tree-growth patterns. Here, we address several

suggestions for future studies, which will help to advance our understanding of peatland tree-growth variability, as well as of the connections between tree growth, peatland hydrology, and climate dynamics. We also discuss potential new research fields using subfossil peatland trees.

6.1. Isolating and amplifying the climate signal

6.1.1. Long-term reconstructions using multiple proxy records

To understand the basic functions of peatland tree growth and colonization, tree growth and population dynamics data need to be compared and coupled with climate-moisture proxies. Studies using peat stratigraphic records have been carried out to detect large-scale hydrological shifts to put the subfossil tree record into a long-term environmental context (Gunnarson et al., 2003; Eckstein et al., 2010, 2011; Edvardsson et al., 2012b, 2014b). To advance these interpretations further, comparisons using pollen (Gear and Huntley, 1991; Eckstein et al., 2010, 2011; Edvardsson et al., 2014b), plant macrofossils (Edvardsson et al., 2014b), and peat humification (Edvardsson et al., 2012b) have been undertaken. The disadvantage of such proxy records is their multi-annual temporal resolution and lower temporal precision that radiocarbon ages offer compared to trees. To improve comparative long-term studies further, proxy records of higher, preferably annual resolution are required. Such records can sometimes be obtained from laminated lake sediments (Veski et al., 2004; Tylmann et al., 2013), ice cores (Vinther et al., 2006), speleothems (Labuhn et al., 2015), corals (Zinke et al., 2014), and highly resolved peat stratigraphic records (Gear and Huntley, 1991; Amesbury et al., 2012). The disadvantage of most annually resolved data sources is that they do not record peat hydrological changes directly, although they do provide an independent record of hydroclimate variability against which to test the dendroecological time series.

Further in-depth comparison between multi-millennial tree-ring chronologies representing different environments and soil types is another approach that is generating valuable paleoenvironmental information. Such comparative studies have been performed using living pine trees (Linderholm et al., 2002; Cedro and Lamentowicz, 2011; Edvardsson et al., 2015a), but Bauerochse et al. (2015) recently started to compare subfossil Hohenheim oaks conserved in river sediments and gravel pits (Spurk et al., 2002; Friedrich et al., 2004) to peatland oaks from Lower Saxony (Leuschner et al., 2002). Although comparisons showed promising potential, it would be premature to draw any conclusions as the focus was on a relatively short period of the past (2500–2000 BCE or 4450–3950 BP). We call for further comparisons of continuous material such as the German oak chronologies or attempts to correlate Scandinavian peatland tree-ring reconstructions with the Torneträsk (Grudd et al., 2002) or Jämtland (Gunnarson et al., 2003) chronologies, as moisture and temperature sensitive records would then be compared over multi-millennial time scales.

6.1.2. Assessment of hydroclimate and tree growth relationships

Dendroclimatic studies using living peatland trees and meteorological data represent yet another field, which has remained largely underexplored (Cedro and Lamentowicz, 2011; Smiljanic et al., 2014), but which has potential to increase our understanding of relations between peatland tree growth and climate variables. In addition, previous work may not have been conclusive due to hydrological lag effects and poorly understood feedback mechanisms in peatlands (Linderholm et al., 2002; Edvardsson et al., 2015a; Edvardsson and Hansson, 2015). Most studies have consistently reported a negative correlation between annual tree growth and precipitation records, yet correlation statistics have mostly been insignificant (Fig. 8). The use of continuous growth monitoring devices (such as manual or automated dendrometers), micro-meteorological stations and local hydrological stations (i.e. piezometers) could be a valuable way to address relations between meteorological events, water-table fluctuations, and tree growth in more

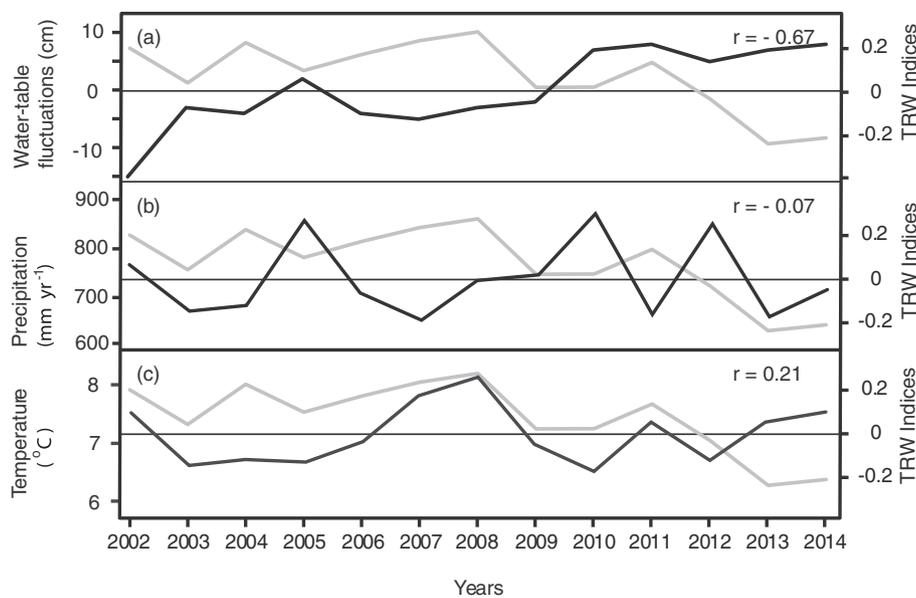


Fig. 11. Correlation tests between dimensionless TRW indices (grey) from the peatland Čepkeliai, Lithuania and (a) water-table fluctuations (cm) in relation to the average level, (b) total annual precipitation (mm), and (c) annual mean temperature ($^{\circ}\text{C}$).

detail and with fewer uncertainties. The combination of such monitoring records may also provide key insights into the hydrological functioning of peatland ecosystems, and especially into lag effects and their impact on tree growth. This hypothesis of a lag effect is supported by unpublished data from Čepkeliai peatland (southeastern Lithuania) where TRW records (1848–2014 CE) have been correlated with hydrological and meteorological time series from the nearby Varėna station (1951–2013 CE). At Čepkeliai, bootstrap correlation functions between the TRW chronology and monthly temperature and precipitation only show significant correlation ($r = 0.25$, $p < 0.05$) with previous October precipitation (Fig. 8). At the same time, comparison between the TRW chronology and a much shorter, but local peatland water-table record (2001–2014 CE) shows significantly stronger negative correlation ($r = -0.67$, $p < 0.05$; Fig. 11). Although the water-table record only covers the last 13 years, these first correlation tests point to the potential of a combined approach. At the same time, they suggest that peatland tree growth might be a valuable direct measurement of moisture changes in peatlands, but a poorer proxy for direct precipitation reconstructions. As long instrumental hydrological records do not exist for peatlands, we suggest progress is made by: (i) testing for correlations between TRW series and hydrometeorological variables, such as the ratio of actual to potential evapotranspiration (AET/PET) computed from temperature and precipitation values; (ii) using tree-growth process models driven by climate and other environmental factors (such as nutrient availability and soil moisture) as they might allow better understanding of tree functioning and the effect which the interaction of different environmental forcings has on tree growth (see Guiot et al., 2014 for a review); and (iii) deriving longer-term water-table fluctuations series from locally-calibrated, process-based hydrological models (see Gong et al., 2012 for a review on the topic) driven by local climatic parameters (temperature, precipitation).

6.1.3. Stationarity in tree growth–climate relationships?

Dendroclimatology commonly assumes stationarity in the relationship between tree growth and climate, and that trees are reacting to environmental changes in the same manner at present as they have in the past (uniformitarian principle; Fritts, 1976). This principle has, however, been challenged due to the divergence (Briffa et al., 1998a, 1998b; Wilmsking et al., 2005; D'Arrigo et al., 2008) of tree growth at some Nordic sites which used to be temperature-limited in the past, but show a

weakening in their mean temperature response in recent decades as a result of global warming. One should thus also assume changes in tree growth–climate relationships at longer timescales as both climate and peatlands have undergone substantial changes over the course of the Holocene. As a consequence, results and conclusions drawn from living material may not therefore be directly transferable to subfossil trees. Trees in Swedish peatlands were shown to be smaller and less long-lived under current conditions (average diameter 16 cm, age 105 yrs.) as compared to the mid-Holocene when the same species produced significantly larger and older trees (average diameter 25–30 cm and age 175 yrs.; Lindbladh et al., 2013). These differences can be explained by more favourable climatic conditions and shallower peatlands in earlier periods, but that may not be the only explanation. Further studies should specifically look into age, size, and radial growth relations over various periods of the Holocene. Moreover, the development of dedicated standardisation techniques, designed to remove internal, non-climatic growth trends in ring-width series, with an aim to account for tree productivity-related biases needs further evaluation. For example, the Signal-Free Regional Chronology Standardisation (Melvin and Briffa, 2014) approach should be preferred for reconstructions if they contain both living and subfossil peatland trees.

6.1.4. What does tree replication mean?

Tree replication data are often used as a climate proxy, but this has recently caused debate about its value for climate inferences and on ways to interpret such records (Charman, 2010; Swindles and Plunkett, 2010; Swindles et al., 2013; McGeever and Mitchell, 2015). Looking at the 2500 BCE–1600 CE period, Swindles and Plunkett (2010) reported a lack of consistent relationship between the Irish oak replication (Turney et al., 2005) and palaeohydrological records (Mauquoy et al., 2008; Magny, 2004, 2013), changing solar activity (Hu et al., 2003; Muscheler et al., 2005), or stacked drift ice records (Bond et al., 2001). However, Charman (2010) successfully reconciled the Irish bog oak record with a large-scale compilation of peatland water table reconstruction and other evidence from northern Britain, and showed the commencement of declines in Irish oak populations were coincident with increased surface wetness in northern British peatlands. This suggests that it is the direction of change in the population that is sensitive to surface wetness, rather than the absolute numbers of trees in the record at any one time. Disagreement between

records in Swindles and Plunkett (2010) could be a consequence of the mid-Holocene transition towards moister conditions about 2500 BCE (4450 BP; Wanner et al., 2008), which caused divergent reactions between Irish and continental oak records (Leuschner et al., 2002). It may also be a function of comparison with atypical surface wetness records and the relatively small number of records after c. 2200 years ago (Pilcher et al., 1996).

McGeever and Mitchell (2015) looked into the temporal distribution of Irish peatland pines dated by radiocarbon, and suggested that factors other than climate, such as the availability of pine seeds and peatland surface area, may have influenced the presence of trees at Irish peatlands and that this limitation might have disrupted the climate signal of the record during certain periods. Despite this possible shortcoming, their pine record nevertheless shows a significant peak during the late part of the HTM, a decline during the late-Holocene transition, an absence of material during the 8.2 and 2.8 ka events, as well as during the LIA (Fig. 10).

Whilst there is a sound theoretical underpinning and increasing evidence for interpreting tree records in terms of palaeoclimate, we acknowledge that tree replication will be influenced by factors other than climatic wetness changes (Swindles and Plunkett, 2010; Swindles et al., 2013; McGeever and Mitchell, 2015), such as natural succession and the transformation of a peatland from a wetland to a raised bog (Fig. 2). Moreover, tree replication in different geographical settings may not reflect the same environmental changes. Competition between tree species colonizing peatlands in parallel is another possible factor influencing tree replication. In-depth comparative studies between overlapping records from in-situ pine and oak trees from common study sites may generate valuable information on competition between species, habitat preferences and tree population dynamics. Furthermore, research on processes governing peatland tree colonization in different geographical regions might help us to understand if establishment and dying-off phases reflect similar environmental processes or if local controls are more important.

6.2. New study areas and research fields

6.2.1. New study areas

This review provides a literature-based overview of geographical areas for which tree-ring analyses have been performed with subfossil peatland trees (Fig. 1 and Table 1). The distribution of peatland regions in the Northern Hemisphere (Fig. 1) also enables us to identify new potential study areas, at least for living peatland trees. In that sense, we hypothesize that Québec, Ontario, and the Northern regions of Canada in more general terms, Southern Siberia (Russia), as well as the Baltic countries clearly represent areas in which the potential of peatland dendrochronology has been underutilized in the past, as shown by a series of very recent studies on Lithuanian (Edvardsson et al., 2016b), Polish (Krapiec and Szychowska-Krapiec, 2016), and Romanian (Árvai et al., 2016) peatland trees. Peat mining areas where there are likely to be exposed subfossil trees can be detected easily on aerial photographs and satellite imagery. In some cases, large wood deposits can also be observed on aerial photos of peat mining areas, but contacts with peat mining companies are probably the best way of identifying which sites also have subfossil wood remains.

6.2.2. Potential new indicators for detection of moisture changes

Stable isotopes in tree rings have proven to provide palaeoclimatic information with annual resolution (see Loader and Switsur, 1996; McCarroll and Loader, 2004). Despite this, only two studies exploring the potential of stable carbon ($\delta^{13}\text{C}$) and oxygen ($\delta^{18}\text{O}$) isotopes have been performed so far with subfossil peatland tree material (Sass-Klaassen et al., 2005; Edvardsson et al., 2014a). When considered together, these isotopes have been shown to be sensitive to the variability in growing season moisture regimes experienced by trees. Based on the correlation analysis between TRW and isotope series, Edvardsson

et al. (2014a) demonstrated a three-year lag between a decline in $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values in trees and the corresponding tree-ring response, possibly reflecting a relatively slow rise in local water table in response to wetter climate. Despite the fact that isotopic records generate much additional information compared to TRW records alone, no further attempts have been performed to date, possibly as these methods are still expensive and time consuming.

Despite the fact that roots will be the first to experience any changes in water-table fluctuations, root morphology has been used only rarely to detect possible water table changes in peatland ecosystems (Lageard et al., 1995; Eckstein et al., 2010). For example, a substantial water table lowering may cause the formation of adventitious roots (Stoffel and Bollschweiler, 2008). Dendrochronological dating of roots (Stoffel et al., 2013), in combination with field measurements of their depth and morphological features, may generate detailed information about the timing and magnitude of hydrological shifts (Eckstein et al., 2010). Such information cannot be obtained without a detailed assessment of root morphology in the field and the sampling of second-generation, adventitious roots. We therefore recommend systematic field measurements and sampling of adventitious roots to test their response to a decline in water table, and to evaluate whether this can lead to instability of moist surfaces and subsequent formation of reaction wood (Stoffel and Bollschweiler, 2008) in trees (Fig. 5).

Another important aspect of peatland ecosystems and environmental changes is their response to fire, which can be studied through absolutely dated fire scars in subfossil or living trees (Arseneault and Payette, 1997; Lageard et al., 2000; Eckstein et al., 2009; Edvardsson et al., 2012a). The age and frequency of fires may not be sufficient to estimate the loss of burned carbon from peatlands, but periods showing an increase in fire activity may be indicative of phases with relatively dry surface conditions. The fire scar records cannot be compared yet, as they do not originate from continuous records and do not overlap sufficiently in time. Further studies are therefore required to evaluate if increased fire frequency in tree-ring records does indeed correspond to periods of relatively dry peatland surface conditions. In addition, fire-scar records can be compared to existing charcoal records, which often represent continuous records and thus can provide clear evidence of fire frequency and intensity at local to regional scale (Patterson and Backman, 1988). If combined, the two approaches clearly have the potential to generate long-term data from charcoal and more detailed (i.e. annual to intra-annual) records for those periods for which tree-ring data are available.

The anaerobic conditions in saturated peat soils generate exceptional preservation conditions for organic material (Fig. 4). Rapid wet shifts usually cause increased vertical rates of peat growth, which can be identified in the form of recurrence surfaces in stratigraphic records (Granlund, 1932; Rundgren, 2008). The same environmental changes will also result in quick burial of dead peatland trees, and thereby improved preservation conditions for woody material (Kokkonen, 1923; Leuschner et al., 2007). The degree of post-mortem degradation and stem height can therefore be used as indicators of the moisture status following tree death. Excellent preservation and conserved stem bark over distances >30 cm above root level would indicate fast burial due to moist conditions and rapidly growing peat, whereas conical and eroded stumps lacking bark have been shown to be characteristic of slow burial and slow vertical peat growth (Eckstein et al., 2009; Edvardsson et al., 2012a). A guide or strategy for a degradation index for in-situ stumps would therefore be useful and would facilitate evaluation of peat moisture conditions following dying-off phases.

By capitalizing on variable phenologies and tree growth responses to water-table fluctuations, multispecies reconstructions may provide significantly more information about past hydroclimatic variability than what we have today. In this context, *Picea*, *Fraxinus*, *Alnus*, *Taxus* and *Betula* have repeatedly been observed in peat mining areas (Godwin, 1975; Arseneault and Payette, 1997; Vitas, 2010; Edvardsson et al., 2014b), but to date, they have only rarely been used as an additional source of information. Of course, the potential of developing multi-

millennial chronologies will be limited for many of these species, but they may provide additional contextual evidence for the longer chronologies (Sass-Klaassen and Hanraets, 2006; Edvardsson et al., 2014b).

6.2.3. Carbon storage capacity

The interaction between tree colonization, peatland surface moisture, and net carbon sequestration is complex (Limpens et al., 2014a; Holmgren et al., 2015). Some authors have suggested that peatlands may turn from carbon sinks into carbon sources during dry periods (MacDonald et al., 2006; Yu et al., 2010; Limpens et al., 2011), and that dry surface conditions will favour tree growth, tree colonization and increased standing biomass in peatland environments (Freléchoux et al., 2000; Limpens et al., 2014a; Edvardsson et al., 2015b). Phases with widespread peatland tree colonization may thus also represent periods of less important peatland carbon accumulation, or even point to phases during which peatlands were indeed acting as carbon sources. Although tree colonization is likely to increase productivity and litter input, which may in turn increase peat accumulation rates, total peat accumulation and carbon sequestration is believed to be reduced as soon as drier conditions start to turn open moss-dominated peatlands into tree-covered conditions (Limpens et al., 2014a; Holmgren et al., 2015).

Further studies are, however, needed on the effects of tree colonization on the drying of peatland surfaces due to increased water loss through tree evapotranspiration, and to determine whether such scenarios have the potential to transform peatlands from net carbon sinks into sources. The effects that tree stand density have on water loss are important and will have implications for the structure and functioning of peatlands, especially as the relation between evapotranspiration and tree stand density is non-linear (Limpens et al., 2014a). Systematic measurements of surface peat moisture, water-table depths, and carbon fluxes to the atmosphere between tree-covered and open peatland areas may give a first indication of the drying effect of trees. Such studies would need to be performed on natural and managed peatlands representing different geographical regions and to look into feedbacks and lag effects between climate, peatland hydrology, and tree growth. To solve some of these remaining issues, we call for continuous monitoring – over at least some years to decades – of; (i) tree growth in peatlands with dendrometers, (ii) water table fluctuations, and (iii) carbon fluxes. To assess the overall carbon balance in peatlands fully, more sophisticated multi-scale approaches will however, be needed, such as those developed by e.g., Fox et al. (2008) and Hartley et al. (2015), as these will also take account of the gaseous carbon components (i.e. CO₂ and CH₄ fluxes) as well as of the dissolved carbon components (i.e. DOC, DIC, and POC). Moreover, such a monitoring setup would enable calibration and validation of dynamic vegetation and ecosystem models such as the modified version of LPJ-GUESS (Lund-Potsdam-Jena General Ecosystem Simulator; Smith et al., 2014) named LPJ-GUESS Why-Me (Wetland Hydrology and Methane, Wania et al., 2009, 2010) and other models that are now including peatland carbon accumulation and methane emission processes. Given the likelihood of significant shifts in treeline distribution across the boreal and arctic, improved parameterisation of the interactions between peatland tree growth, hydrology and carbon cycling is essential. A better understanding of the impact climate change may have on tree cover, moisture variability and associated changes in the carbon balance in peatland ecosystems, will advance the possibilities for reliable predictions for future climate change.

7. Conclusions

Contemporary ecosystems can be used to study present-day conditions and to estimate historical environmental changes, typically over timescales of decades. Palaeoecological techniques provide much greater temporal depth (Jeffers et al., 2015), and allow assessments over

periods that have experienced significantly different climatic conditions compared to the present day. Despite significant potential, subfossil wood has been identified as one of the most underutilized sources of information in palaeoecology and forest conservation research (Lindbladh et al., 2013). In this review, we have illustrated the origins and recent developments in the field of tree-ring research in peatland environments, compiled the major datasets from Europe and North America, but also identified thematic and geographic areas for which knowledge is still fragmentary. We call for further studies using subfossil peatland trees for detailed reconstructions of long-term hydroclimate dynamics and palaeoecological changes. Beyond palaeoclimate reconstruction and palaeoenvironmental understanding, we expect such data to be important in conservation planning and to determine restoration baselines for peatland management.

For more than a century, subfossil peatland trees have been used as a proxy record for environmental changes (Dau, 1829; Vaupell, 1851; Nielsen and Helama, 2012). Over the last decades, however, numerous studies have started to use the information contained in the annually resolved tree-ring records in more detail to assess climatic changes during the Holocene in the British Isles, Scandinavia, and throughout Central Europe (Table 1; Fig. 1). Through the comparison between tree replication records, tree-ring width chronologies, climate and moisture proxies (i.e. ice cores, sediment records, pollen), as well as meteorological data, detection of climatic signals in peatland trees has been improved substantially. We conclude that:

- (1) Our current knowledge of the effects of (hydro-)climatic changes and anthropogenic activities on tree growth in peatland ecosystems is mainly based on ecophysiological, dendroclimatic, and dendroecological perspectives;
- (2) A majority of existing studies shows that excess moisture is a growth-limiting factor for peatland trees. Proxy records developed from subfossil peatland trees therefore have the potential to help in the reconstruction of (i) local water-table fluctuations, and (ii) regional hydroclimate dynamics. Annual tree-growth patterns can be used to assess changes at annual to decadal scales, whereas tree population dynamics reflect changes at decadal to centennial time scales;
- (3) Substantial work has been performed using subfossil trees from Germany, Great Britain, Ireland, the Netherlands, and parts of Scandinavia, whereas the vast majority of Canada, Russia, and the Baltic countries have significant under-exploited potential for the development of geographically widespread records;
- (4) Our data compilation showing temporal distribution of subfossil peatland forests confirms that relatively warm and dry periods – such as the HTM – offered conditions which were favourable for tree growth in peatlands and thereby allowed widespread tree colonization, whereas transitions towards moister and colder conditions (e.g., the mid-late Holocene transition and the LIA) are associated with widespread dying-off phases and/or depressed annual tree growth;
- (5) Further studies using e.g., stable isotopes, dendroclimatology, and field monitoring are critical to increase our knowledge about tree growth responses associated with hydroclimate changes, including understanding of hydrological lag and feedback effects detectable from lagging tree growth responses to climate on peatlands.

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