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Subfossil peatland trees as proxies for Holocene palaeohydrology and palaeoclimate

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1   **Abstract:**

2   Due to the scarcity of reliable and highly resolved moisture proxies covering much of the

3   Holocene, there has been increased interest in the study of living and subfossil peatland trees

4   sensitive to gradual and extreme changes in hydrology, precipitation, and related environmental

5   processes. Peatland development and the associated carbon accumulation, which are strongly

6   influenced by hydrological fluctuations, are also of prime importance as peatlands represent long-

7   term sinks of atmospheric carbon. Improved knowledge of peatland development and soil

8   moisture variability during the Holocene is therefore essential to our understanding of long-term

9   hydroclimate changes, the terrestrial carbon cycle, and to enable more robust predictions of

10   peatland response to future climate changes.

11   Here, we review the existing mid- to late Holocene peatland tree-ring chronologies that

12   have been used to study climate variability on (sub-)annual to centennial scales with a primary

13   focus on northern Europe. Since the 1970s, absolutely dated tree-ring chronologies covering

14   substantial parts of the Holocene have been developed from excavated remains of oak (*Quercus*

15   spp.) and pine (*Pinus sylvestris* L.). The annual tree-ring patterns of these trees are often

16   characterized by periods of depressed growth reflecting annual to decadal hydroclimatic changes.

17   In addition, changes in the spatio-temporal distribution of trees throughout the Holocene are often

18   found to reflect decadal to centennial climate and hydrological changes. Moreover, synchronicity

19   between tree-ring chronologies and tree-population dynamics over larger geographical areas

20   show periods of coherent regional climate forcing, especially during the mid-Holocene.

21   This review (i) provides an overview of pioneering and recent studies presenting tree-ring

22   chronologies developed from subfossil peatland trees, and (ii) presents recent developments in the

23   fields of dendroecology (i.e. the response of tree growth and changes in vitality as a result of

24   changes in climatic variables) and dendroclimatology (i.e. the reconstruction of climate

25   fluctuations based on tree-ring analyses) in peatland regions. Moreover, we (iii) use long-term

26   climate reconstructions based on alternative proxies for comparison, and (iv) present different

27   ways to analyse tree-ring records to generate novel information on annual to centennial

28   timescales. This analysis is based on an unprecedented network of tree-ring chronologies from

29   Denmark, Finland, Germany, Great Britain, Ireland, Lithuania, the Netherlands, Poland, Sweden,

30   and Canada, as well as a wealth of old and previously (un) published literature from Scandinavia

31   and Germany, which has not been accessible to a wider audience in the past due to inaccessibility

32   or linguistic barriers. Finally, a map of possible hotspots for the assessment of continuous

33   peatland-tree studies is presented, along with suggestions for new research directions in the field.

34

35   **Keywords**: Peatland; Raised bog; Palaeohydrology; Palaeoclimatology; Dendrochronology;

36   Subfossil trees; *Quercus robur*; *Pinus sylvestris*.

37

38   **Highlights**

39   • We review extensive peatland tree-ring chronologies from northern Europe covering

40   major parts of the Holocene.

41   • Long distance cross-matches (correlograms) and significant positive correlation point to

42   larger-scale climate signals.

43   • Subfossil peatland trees can be used for detailed palaeoclimatic and palaeohydrological

44   reconstructions.

45   • Warm/dry conditions are favourable for peatland tree growth, but may turn peatlands from

46   carbon sinks to carbon sources.

47

48

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 km^2 across Eurasia and North

73 America (Lappalainen, 1996; MacDonald et al., 2006), they also constitute an important sink for

74 atmospheric carbon dioxide (CO_2) and a considerable source of methane (CH_4) (MacDonald et

75 al., 2006; Yu et al., 2010; Limpens et al., 2011). In fact, peatlands store twice as much carbon (C)

76 as forests (Joosten and Couwenberg, 2008). Spatio-temporal dynamics of CO_2 and CH_4 fluxes in

77 peatlands are mainly driven by hydrological conditions, which can be expressed by water-table

78 levels (Mitsch et al., 2013). In addition to driving the carbon flux, water-table fluctuations in

79 peatland ecosystems also influence a wide range of environmental processes such as vegetation

80 patterns, the fixation of nitrogen, and the chemical composition of water passing through

81 peatlands (Limpens et al., 2011; Waddington et al., 2014). Consequently, reconstructions of past

82 water-table variations based on tree-ring records are of prime importance not only to improve our

83 understanding of climate variability, but also to the assessment of the functioning of peatlands in

84 a context of changing climatic conditions and under increasing levels of greenhouse gases.

85

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

87   (1) Synthesize current knowledge on relationships between tree growth, hydrology, and

88   climate changes in peatlands from both an ecophysiological and dendroecological

89   perspective, to evaluate and document the potential of peatland trees as a proxy for water

90   table and/or regional hydroclimatic reconstructions;

91   (2) Review and map past work on peatland tree-ring chronologies across the Northern

92   Hemisphere. We include studies from e.g. Germany and Scandinavia, written in languages

93   other than English, to make them accessible to a wider audience;

94   (3) Compare the spatial and temporal distribution of peatland forests at regional to

95   hemispheric scales, to remove site effects and to interpret results in a longer-term climatic

96   context;

97   (4) Compare regional patterns of change with hydrological proxies covering the same period

98   to test how the tree-ring records capture changes in (hydro)climatic variables;

99   (5) Discuss the potential of tree-ring records derived from peatland trees for palaeoclimatic

100   and palaeohydrological reconstructions over the course of the Holocene, and to illustrate

101   related possibilities, benefits, and limitations of subfossil peatland trees in achieving these

102   goals;

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

104   regions.

105

106 **2. Peatlands, peat, structure and development**

107 Peat can be defined as a natural substance that is formed by partially decomposed remains of

108 plants and contains less than 20-30% of minerals (= ash content) (Warner, 2003). The chemical

109 and physical properties of peat are highly variable in space and time, depending on the type of

110 plant species contributing to its formation, the degree of decomposition, and the geochemistry of

111 water supply. In an undisturbed peatland, peat is primarily composed of water (88-97%), dry

112 matter (2-10%), and gas (1-7%). Peat changes in composition over time with very slow

113 decomposition, compaction, and geochemical alteration, such that it eventually forms coal after

114 several million years. Based on the dominant botanical composition and degree of decomposition,

115 four main categories of peat can be described: moss, herbaceous, wood, and humified peat

116 (Charman, 2002; Loisel et al., 2014). In humified peat, the plant remains are so decomposed that

117 the bulk of plants are no longer identifiable.

118   A peatland can be defined as an area covered by at least 30 cm of peat (Joosten and Clark,

119 2002; Charman, 2002). Peatlands, in a broader context, are a type of wetland characterized by

120 organic soil. The term "mire" is sometimes used to indicate a peatland with active accumulation

121 of peat, but for our purposes the two terms are equivalent. On a global scale, three main regions

122 of peatland development can be distinguished; northern peatlands, primarily distributed in boreal

123 and subarctic climate in the Northern Hemisphere (Fig. 1), tropical peatlands (primarily

124 distributed in Southeast Asia, but also in South America and Africa), and Southern peatlands

125 (primarily distributed in Patagonia, but also in temperate Australasia) (Yu, 2011). Estimates of

126 the global peatland area are highly variable due to the different wetland classification systems and

127 insufficient survey data (Lappalainen, 1996; Rydin and Jeglum, 2006), but it is generally agreed

128 that total peatland area is approximately 4 million km^2, corresponding to c. 2.7% of the Earth's

129 land surface (Lappalainen, 1996; MacDonald et al., 2006). Estimates for tropical regions are

130 subject to much greater error than those for northern peatlands. Of the total peatland area, 1.5% is

131 found in Africa, 28% in Asia, 0.4% in Australia and Oceania, 2.6% in Central and South

132 America, 24% in Europe, and 44% in North America (Lappalainen, 1996).

133 Peatland initiation patterns differ for the three main regions because of different histories

134 of ice cover recession and climate change over the glacial-interglacial transition (Fig. 2).

135 Northern peatlands show an initiation peak around 9050-7050 BCE (11,000-9000 years before

136 present, BP), South American peatlands around 15,050-12,550 BCE (17,000-14,500 years BP),

137 and many tropical peatlands started to form more than 18,050 BCE (20,000 years BP; Yu et al.,

138 2010). The average peat accumulation rate is c. 13 g C m^{-2} yr^{-1} in tropical peatlands and c. 19-22

139 g C m^{-2} yr^{-1} in northern and southern peatlands (Yu et al., 2010; Loisel et al., 2014). A

140 conservative estimate of overall peat C pool indicates that world peatlands store c. 610 GtC,

141 primarily in northern peatlands (c. 89%) with a small amount in tropical (c. 8%) and southern (c.

142 3%) peatlands (Yu et al., 2010). Overall, although covering only c. 2.7% of the Earth's land

143 surface, peatlands store at least 25% of global soil organic C (Hiederer and Köchy, 2012).

144   On the basis of vegetation composition, hydrology, peat, and water chemistry, northern

145   peatlands (which are the focus of this review) can be distinguished into two major types:

146   minerotrophic peatlands (= fens) and ombrotrophic peatlands (= bogs). Minerotrophic peatlands

147   receive their water and nutrient input from both atmospheric deposition and surrounding

148   groundwater, whereas ombrotrophic peatlands are fed entirely from atmospheric deposition

149   (Rydin and Jeglum, 2006). The main consequence of such different hydrological pathways is that

150   fens are richer in dissolved minerals and have a higher water pH than bogs. These geochemical

151   differences are reflected in the floristic composition; fens are typically dominated by vascular

152   plants (particularly sedges) and brown mosses (Amblystegiaceae family), whereas bogs are

153   usually dominated by peat mosses (Sphagnaceae family) and a smaller vascular plant component.

154   The role of vascular plants, such as dwarf shrubs, has however gained increased interest recently

155   because they seem to have competitive advantages in response to climate warming (Breeuwer et

156   al., 2010; Buttler et al., 2015). In both fens and bogs, tree cover is often limited, but there are

157   densely tree-covered peatlands in the boreal region (Fig. 3). Under natural conditions, the most

158   common tree species colonizing peatlands in Eurasia are Scots pine (*Pinus sylvestris* L.),

159   Mountain pine (*Pinus uncinata* Ramond ex DC.), Dwarf mountain pine (*Pinus mugo* Turra), and

160   Siberian pine (*Pinus sibirica* Du Tour), whereas Mountain birch (*Betula pubescens* Ehrh.),

161   willow (*Salix* spp), and black alder (*Alnus glutinosa* L.) often colonize fens. Other tree species on

162   northern peatlands include black spruce (*Picea mariana* (Mill.) Britton, Sterns and Poggenb.),

163   whereas Tamarack (*Larix laricina* (Du Roi) K.Koch) sometimes colonizes fens. In this review,

164   Scots pine and oak (*Quercus robur* L. and *Q. petraea* L.) will be in primary focus, as these

165   species are commonly excavated in northern peatlands and are suitable for dendrochronological

166   studies (Table 1). Excavated trunks and plant macrofossils show that oak trees once colonized

167   significant peatland areas in northwest Europe (Pilcher et al., 1984; Leuschner et al., 2002).

168   However, analogous peatland ecosystems do not appear to exist any longer (Sass-Klaassen and

169   Hanraets, 2006).

170   The presence of *Sphagnum* is particularly important for peat accumulation in

171   ombrotrophic peatlands. *Sphagnum* plants have the capacity to acidify the surrounding water as a

172   result of an extremely efficient cation exchange capacity (van Breemen, 1995; Rydin and Jeglum,

173   2006). This enables *Sphagnum* to absorb nutrients from very low concentrations in the water

174   source, and produces a litter that is resistant to decay. *Sphagnum* also increases soil anoxia by

175   storing water in empty cells (hyalocysts). Because Sphagna, like all bryophytes, cannot regulate

176   their water balance, their development is possible whenever there is a surplus of water. In

177   addition, because they are most competitive under acidic conditions (pH < 4-5), most *Sphagnum*

178   species benefit from the presence of low mineral content. This combination of hydrological and

179   geochemical conditions is prevalent on ombrotrophic peatlands (van Breemen, 1995). The

180   physiological requirements of *Sphagnum* are one of the key determinant of the global distribution

181   of northern ombrotrophic peatlands, which are typically located north of 45° N, in particular at

182   50°–70° N (Yu et al., 2011), under climatic conditions and landscape morphology that promote a

183   surplus of water and low mineral availability. However, whilst *Sphagnum* is a key taxon for

184   northern peatland formation, the presence of *Sphagnum* is not a pre-requisite for peat

185   accumulation and some extraordinary examples exist where peat forms from plants such as e.g.,

186   Poaceae (Smith and Clymo, 1984). Peat can be formed by a range of other vascular plants as

187   well, particularly sedges in fens and wood in peatlands with shrub and tree cover. Peat derived

188   from woody plants is especially important in the tropics. Specific taxa, such as the restiad rushes

189   in Australasia, are also important peat formers in some regions (Clarkson, 2004). Peat

190   accumulation can be equally fast in these peat types (Loisel et al., 2014) and prevailing climate

191   appears to be a more important driver of peat accumulation rates over millennial timescales than

192 botanical composition (Charman et al., 2013, 2015). The presence of waterlogged conditions

193 (persistent soil anoxia), low chemical quality of peat moss litter, and low pH, all hamper the

194 microbial decomposition of plant remains, thereby favouring the long-term accumulation of peat

195 (a sink of atmospheric C) and the preservation of plant macro- and micro-fossils creating an

196 archive of past environmental conditions, especially in ombrotrophic northern peatlands

197 (Chambers and Charman, 2004; Chambers et al., 2012).

198 A complex microtopography often develops on the surface of ombrotrophic peatlands,

199 created by a process of differential growth and decay, sometimes enhanced by physical processes

200 such as freezing. Microhabitats of pools, hollows, lawns, and hummocks are formed in relation

201 to a water table gradient, which in turn drives vegetation composition and the spatial distribution

202 of plants (Bragazza and Gerdol, 1999). Pools form in the wettest areas of peatlands (Fig. 3),

203 characterized by standing water with only free-floating peat mosses and vascular plants. Hollows,

204 lawns, and hummocks occur along a gradient of decreasing wetness and are often characterized

205 by a continuous and dense layer of *Sphagnum* plants, and a sparse cover of vascular plants. Along

206 the gradient from hollows to hummocks, *Sphagnum* species become more drought-adapted and

207 vascular plants become more shrubby and abundant. In the driest locations, *Sphagnum* is absent

208 and may be replaced by more drought tolerant mosses. In such a typical sequence of

209 microhabitats on ombrotrophic peatlands, the presence of trees is determined by the moisture

210 content of the peat due to the sensitivity of tree roots to anoxic conditions (Boggie, 1972; Vitas

211 and Erlickytë, 2007).

212 Where hydrological conditions are stable, tree distribution is limited to the hummocks and

213 individual trees tend to be small and slow growing. Where changes in hydrological conditions

214 occur, the expansion of trees is favoured by any reduction in soil water content, such as decreased

215 precipitation or increased evapotranspiration (Boggie, 1972; Edvardsson et al., 2015a). Peatlands

216 with consistently dry surface conditions can be heavily forested with relatively large trees,

217 especially in boreal environments. The dominant hydrological control on tree growth means that

218 the direct effect of temperature is less important, whereas lowering of the water table will

219 promote expansion of tree cover and increased tree growth rates (Smiljanić et al., 2014;

220 Edvardsson et al., 2015a, b). This theoretical concept has been confirmed by observations of tree

221 growth following peatland drainage (Dang and Lieffers, 1989; MacDonald and Yin, 1999;

222 Freléchoux et al., 2000). Lowering of the water table increases soil temperature, improves soil

223 aeration, and increases nutrient availability through organic matter mineralization (Grootjans et

224 al., 1985; Choi et al., 2007; Weedon et al., 2012), with positive effects on tree growth.

225   Although success of tree seed germination does not differ between lawns (wet

226 microhabitats) and hummocks (drier microhabitats), the performance of tree seedlings and the

227 probability of maturation is greater on hummocks (Holmgren et al., 2015). Positive feedbacks

228 have also been shown between tree recruitment and dwarf shrubs on hummocks (Holmgren et al.,

229 2015). Once they are established, trees can cause a further drying of the peat due to enhanced

230 transpiration (Moir et al., 2010; Limpens et al., 2014a), promoting even greater tree

231 encroachment.

232   Peatland development over time is driven primarily by successional processes and climate

233 dynamics (Fig. 2; Hughes, 2003). Historically, the conventional successional sequence is via

234 terrestrialisation of aquatic systems and fen peat formation to bog peat (Walker, 1970), but it is

235 now commonly accepted that a wide variety of successional sequences can occur in different

236 peatlands. Paludification (i.e. the gradual spread of peatland through waterlogging of previously

237 dry ground) is the other main process leading to peat formation particularly in many boreal

238 peatlands and blanket bogs. The occurrence and preservation of trees is influenced by

239 successional stages, with tree growth occurring most likely in the later stages of succession, when

240 drier surfaces are more prevalent. In paludified peatlands, tree remains typically occur at the base

241 of the sequence, as they were growing on the drier surfaces prior to peat formation. Moreover,

242 trees can be preserved in peatlands even if they were not growing on the surface. For example,

243 trees can fall into the margins of ponds or fens and may therefore be preserved in peat and

244 sediment formed during the early aquatic stages of peatland growth.

245

246 **3. Historical background: Pioneering to recent studies**

247 Since the late nineteenth century, palaeobotanic and climatic research has been performed in

248 peatlands, initially with a focus on Nordic countries (Dau 1829; Vaupell 1851; Blytt, 1876;

249 Sernander, 1890, 1893; von Post 1924, 1930), and later in other regions of the northern

250 hemisphere (Lewis, 1906, van Geel, 1978; Barber et al., 1994; Yu et al., 2014; Loisel et al.,

251 2014). Most often, such studies have been based on plant macrofossils, pollen grains or peat

252 decomposition, but the attention of many pioneer researchers was attracted by the presence of

253 subfossil trees (Fig. 2 and 4) in peat stratigraphy (Dau 1829; Vaupell 1851; Blytt 1876; see also

254 Birks and Seppä, 2010; Nielsen and Helama, 2012).

255   For example, Dau (1829) presented pioneering studies where he described the

256 stratigraphic distribution of tree trunks in Danish peat bogs, and Vaupell (1851) studied buried

257 trees and their relationship with soil nutrients, sunlight, and moisture conditions (Nielsen and

258 Helama, 2012). Steenstrup (1842) classified tree horizons on the basis of species composition and

259 interpreted tree population shifts as environmental changes associated with temperature and

260 hydrological shifts during the postglacial period (Birks and Seppä, 2010; Nielsen and Helama,

261 2012). For these observations, Steenstrup can be considered as one of the founders of Holocene

262 palaeoecology and climate research (Birks and Seppä, 2010). In Norway, Blytt (1876)

263 investigated tree horizons in relation to variations in peat decomposition, and interpreted

264 synchronous changes as shifts controlled by climate. The Swedish researcher Sernander thereafter

265 improved the methods introduced by Blytt (1876) and associated dark peat layers containing

266 wood material with periods of relatively dry continental climate, whereas less humified peat

267 layers without fossil trees were interpreted as humid climatic periods (Sernander, 1890, 1893).

268 Sernander also developed a schematic model of postglacial climate change, known as the Blytt-

269 Sernander scheme, which has been used by many generations of Quaternary geologists and

270 palaeobotanists (e.g., Smith and Pilcher, 1973; Blackford and Chambers, 1991; Birks and Seppä,

271 2010). Outside Scandinavia, pine trees exposed in erosion scars in blanket peats across the

272 Scottish Highlands (Lewis, 1906, 1908) were interpreted as evidence of constant changes in the

273 character of the vegetation covering the Scottish peatlands.

274   During the early twentieth century, palaeoclimatological research was improved

275 significantly by pollen analysis, introduced by von Post (1924, 1930). Moreover, stratigraphic

276 studies by Granlund (1932) showed that abrupt peat humification shifts, referred to as "recurrence

277 surfaces" (Fig. 2), were associated with rapid climatic shifts towards colder and wetter

278 conditions. Following the introduction of radiocarbon dating, the studies by e.g., Aaby (1976) and

279 Barber (1981) were able to link peat humification shifts to actual climate changes. Currently,

280 climate reconstructions based on peatlands are common in the palaeoclimatic literature (e.g.,

281 Langdon and Barber, 2005; Mauquoy et al., 2008) and generally based upon several parameters

282 such as peat humification, pollen data, plant macrofossils, and testate amoebae (e.g., Hughes et

283 al., 2006; Swindles et al., 2013).

284   Even though tree horizons in peat deposits were discovered over a century ago and their

285 potential role as indicators of environmental changes was rapidly realized, subfossil trees in

286 peatlands remained an underutilized source of palaeoclimatic information for a long time. Then,

287 in the late 1960s, a number of projects were initiated with the aim of developing tree-ring

288   chronologies using subfossil trees excavated from peatlands in northwest Europe (Pilcher, 1973;

289   Pilcher et al., 1977). This approach was made possible by the large number of well-preserved tree

290   remains that have been exposed by peat extraction for fuel and horticulture (Fig. 4-5, Joosten and

291   Clarke, 2002). During the 1970s and 1980s, oak samples from such peatlands in Ireland and

292   Germany were used for the establishment of the first multi-millennial peatland tree-ring

293   chronologies (Pilcher 1973; Pilcher et al., 1977, 1984; Leuschner and Delorme, 1984). At a very

294   early stage, dendrochronological studies proved that subfossil wood material originating from

295   different Irish peatlands could be cross-dated (Pilcher, 1973; Pilcher et al., 1977), which

296   encouraged further work. Cross-dating is a standard procedure in dendrochronology in which

297   individual tree-ring width (TRW) series are statistically and visually compared (Douglass, 1941;

298   Fritts, 1976; Wigley et al., 1987). Several statistical parameters are normally tested, of which the

299   t-test (Baillie and Pilcher, 1973) is the most commonly used (Table 1) and referred to when cross-

300   dating statistics are presented (Fig. 6-7).

301   During the 1970s, floating tree-ring chronologies were developed from oaks found in

302   multiple peatlands across Ireland (Pilcher, 1973; Pilcher et al., 1977). In parallel, an Irish oak

303   chronology from living and archaeologically excavated trees was developed by Baillie (1973,

304   1995), which would later enable absolute dating of some of the floating chronologies to obtain a

305   continuous tree-ring chronology spanning 7272 years (Pilcher et al., 1984). The chronology

306   proved to be a valuable calendric climate record and provided a standard for the radiocarbon

307   calibration curve (Pilcher et al., 1984; Pearson et al., 1986; Reimer et al., 2013). As the Holocene

308   record of subfossil peatland trees is of significance to both palaeoclimatologists and archeologists

309   the literature contains a mixture of chronologies that quote ages as both BP and CE/BCE.

310   Although, for the purposes of a review it may seem appropriate to adopt one scheme or the other,

311   however, this has inherent problems for both of the relevant communities. Consequently, in this

312   study where we refer to an absolute age we quote the age in CE/BCE with the BP alternative in

313   brackets, but where an event is known by a BP age, we quote the cal. BP age (calibrated years

314   before AD 1950) and refer to an approximate BCE age in brackets.

315   Meanwhile, tree-ring chronologies for environment and climatic reconstructions were also

316   constructed in Germany (Bauerochse et al., 2015). In this case, thousands of trees preserved in

317   central and north German riverine sediments (Becker and Schirmer, 1977; Becker, 1983;

318   Friedrich et al., 2004) and in north German peatlands (Leuschner and Delorme, 1984) were used.

319   Due to stepwise and long-distance cross-dating it was possible to age determine previously

320   undated material and to correct problematic and falsely dated sections (Fig. 6-7; Pilcher et al.,

321   1984; Brown and Baillie 2012). Ever since then, the use of stepwise cross-dating has given an

322   absolute age to tree-ring chronologies from England (Chambers et al., 1997; Lageard et al. 1999;

323   Boswijk and Whitehouse, 2002), Scotland (Moir et al., 2010; Moir, 2012) the Netherlands

324   (Jansma, 1996; Sass-Klaassen and Hanraets, 2006), Denmark (Christensen, 2007) and Sweden

325   (Edvardsson et al., 2012a, 2014b).

326   In the late 1960s, Munaut (1967) and Smith et al. (1972) successfully developed the first

327   tree-ring chronologies from subfossil peatland pines. However, pine trees were often considered

328   as unreliable for chronology construction due to problems such as missing and wedging rings

329   (Fig. 5). Attempts in Scotland during the 1980s, for example, failed to cross-date approximately

330   200 samples (Bridge et al., 1990). Radiocarbon dates later showed that the samples had a large

331   temporal range, which explained parts of the problems with cross-dating. By contrast, more

332   recent studies focusing on Irish, Scottish, and British peatland pine chronologies have been

333   successful in cross-dating tree-ring records (Pilcher et al., 1995; Lageard et al., 2000; Moir et al.,

334   2010).

335   The interest in peatland pines increased, especially as they were found to have the

336   potential to extend further back in time than the Irish oak chronology (then at 5452 BCE or 7401

337   BP; Pilcher et al., 1995). In the Lower Saxony area, northwest Germany, extensive work was

338   initiated on peatland pines (Leuschner et al., 2007; Eckstein et al., 2009, 2011; Achterberg et al.,

339   2015, 2016). The German pine chronologies have been constructed from some 4000 peatland

340   trees (Bauerochse et al., 2015) and show a temporal spread over the period 6703-1165 BCE

341   (8652-3114 BP; Achterberg et al., 2016). Scots pine has been shown to represent by far the most

342   common tree species in Scandinavian (Gunnarson, 1999; Edvardsson et al., 2012a) and Baltic

343   (Pukienė, 1997; Edvardsson et al., 2016a) peatlands and in northern Sweden, pine remains in

344   peaty environments have been used for treeline reconstructions during the Holocene (Kullman,

345   1987). However, these trees have proved to be unsuitable for chronology development due to of

346   the smaller sample number and wide temporal range. In central and southern Sweden, by contrast,

347   peatland pines have been used successfully for the development of multi-millennial tree-ring

348   chronologies (Gunnarson 1999; 2008; Edvardsson et al., 2012a, b). In northern Finland, subfossil

349   pine remains have been recovered from peatlands and lacustrine sediments of lakes with thick

350   layers of organogenic riparian substrate (Eronen et al., 1999). Dendrochronological analyses of

351   this material yielded a continuous tree-ring chronology over the mid- and late-Holocene (from

352   5634 BCE, Eronen et al., 2002; Helama et al., 2008), with indications that pine population

353   density and hydrologic conditions varied over time (Helama et al., 2005). The suitability of

354   subfossil peatland pines for long-term climate and palaeohydrology reconstructions has now been

355   shown in a range of studies (Pilcher et al., 1995; Lageard et al., 2000; Boswijk and Whitehouse,

356   2002; Leuschner et al., 2007; Eckstein et al., 2009; Moir et al., 2010; Edvardsson et al., 2012a;

357   Achterberg et al., 2016).

358

359

4. General interpretations of peatland tree-growth dynamics

361

4.1. Tree growth, climate and hydrology

363

High water levels in peatlands have profound effects on seed germination and seedling development (Kozlowski, 1997; Holmgren et al., 2015). Indeed, the activation of the physiological processes required for seed germination depends on oxygen (O_2) supply. A water table located close to the peat surface will restrict O_2 availability to the embryo and thereby prevent or postpone seed germination (Dang et al., 1991; Kozlowski and Pallardy, 1997; Fragnière et al., 2015; Kozlowski 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 (Kozlowski and Pallardy, 1984). By contrast, the uptake of iron

383   (Fe) and manganese (Mn) is increased because of an increase in soluble ferric and manganic

384   forms. Yet, abundant ferrous and manganous ions in wet soils may be toxic to some tree species

385   (Crawford, 1989). Moist conditions reduce root growth of most woody plants by inhibiting root

386   formation and branching, repressing growth of existing roots and mycorrhizae, and by promoting

387   root decay (DeBell et al., 1984; Kozlowski, 1984; Kozlowski and Pallardy, 1997; Eckstein et al.,

388   2011). Tree growth is inhibited by the lack of O_2 (Dang et al., 1991; Kozlowski and Pallardy,

389   1997) and in particular, reduced macronutrients uptake (especially nitrogen, phosphorus, and

390   potassium) driven by a reduction in O_2 supply to the roots (e.g., Osundina and Osonubi, 1989).

391   Finally, a variety of toxic compounds such as aldehydes, organic acids, and ethanol accumulated

392   in wet soils have been demonstrated to variously contribute to injury, growth reduction, and

393   mortality of woody plants (Kozlowski, 1997; Vitas and Erlickytë, 2007).

394   Consequently, a change toward wetter climatic conditions would lead to rising water

395   tables, causing shallower unsaturated zones (Schouwenaars, 1988; Hunt et al., 1999), and thereby

396   reduce recruitment of new trees and growth reductions in trees already growing at the peat

397   surface (Boggie, 1972; Linderholm et al., 2002; Edvardsson et al., 2015a). Soil moisture is

398   therefore a key driver of both radial tree growth and tree population dynamics in peatlands.

399   Growth depressions and dying-off phases in subfossil chronologies are therefore an expression of

400   unfavourable growth conditions, linked to changes in site hydrology towards moister conditions

401   (Leuschner et al., 2002; Edvardsson et al., 2012b; Scharnweber et al., 2015). Lowered water

402   tables, on the other hand, are typically associated with enhanced radial growth or the colonization

403   of peatland trees (Freléchoux et al., 2000; Eckstein et al., 2009; Edvardsson et al., 2015b). This

404   hypothesis is supported by a comparison of climate-growth relationships obtained for pine trees

405   growing on peat and adjacent mineral soils (Fig. 8). This comparison also clearly demonstrates

406   that tree growth on mineral soils is significantly correlated with winter and early summer

407 temperatures, whereas a more complex, weaker and clearly site-dependent response to monthly

408 temperature and precipitation is detected in peatland trees. The latter presumably reflects the

409 multiannual synthesis of moisture variability and changing hydrology (Fig. 9), which could be

410 further complicated by a hydrological lag and/or feedback response in peatlands (Linderholm et

411 al., 2002; Edvardsson et al., 2015a; Edvardsson and Hansson, 2015).

412   Studies exploring climate-growth relationships have not been realized for subfossil

413 peatland oaks so far. Indeed, during extended periods of the Holocene, deciduous oaks have

414 established in peatlands across northwestern Europe (Pilcher et al., 1984; Leuschner et al., 2002),

415 but any detailed interpretation of the subfossil oak data has long been problematic due to the

416 absence of modern peatlands with oak tree cover (Sass-Klaassen, 2004). In a study by

417 Scharnweber et al. (2015), however, a catastrophic rewetting of a drained, oak covered peatland

418 in northeast Germany has provided the opportunity to study growth responses in oaks following

419 well-documented hydrological changes. Similar to the work on pine, moisture is also shown to be

420 the main growth-limiting factor in peatland oak trees.

421

422 *4.2. Hydrological lag effects*

423 Several studies show that a hydrological lag response to changing precipitation in peatlands

424 exists, meaning that some delay can be observed between actual climate changes and related

425 hydrological shifts in the peatlands (Kilian et al., 1995; Waddington et al., 2014). Such delayed

426 responses have in the past been attributed to (i) water transport in soils towards the peatlands

427 (e.g., Cowan, 1965; Hillel, 1971), (ii) water interception or accumulation in plants (Shukla and

428 Mintz, 1982; Seneviratne et al., 2010), (iii) delays between snowfall and associated snowmelt

429 (Price and Schlotzhauer, 1999), and (iv) the process by which water is replacing air in the

430 relatively large pore spaces of the unsaturated zone of peat (Ingram, 1983; Almendinger et al.,

431   1986). In addition, it is known that (v) peat soils are compressible such that changes in water

432   content may result in volumetric fluctuations and thereby variations in surface elevation, which in

433   turn can vary depending on the amount of water stored in the peat (Almendinger et al., 1986;

434   Price and Schlotzhauer, 1999). These slow hydrological changes may therefore result in monthly

435   to multiannual lags between climate and tree growth responses, as observed and discussed in

436   studies by Linderholm et al. (2002), Edvardsson et al. (2014a, 2015a), or Edvardsson and

437   Hansson (2015). Knowledge about such delays is important for our understanding of relations

438   between hydrological variability and tree growth, and for all studies aiming at; (i) reconstructing

439   past and future hydroclimate changes, (ii) long-term carbon storage capacity of northern

440   peatlands, (iii) the prediction of future peatland vegetation dynamics, and (iv) an improved

441   understanding of peatland vulnerability to changing climate (Waddington et al., 2014).

442

443   *4.3. The influence of trees on peatland hydrology*

444   As discussed, surface moisture in peatlands is the most important factor governing tree growth

445   and colonization (Boggie, 1972; Edvardsson et al., 2015b). Tree density may in turn influence

446   surface moisture and ultimately carbon sequestration in the peatlands, as a result of feedback

447   effects (Limpens et al., 2014a; Holmgren et al., 2015). Trees can affect the moisture status of

448   peatland environments through transpiration and interception (Limpens et al., 2014b).

449   Colonisation by trees therefore has the potential to cause a positive drying feedback, whereby

450   increased root uptake for transpiration demand causes a lowering of the water table, in turn

451   promoting improved tree growth and seedling recruitment and/or shrubification as root

452   oxygenation and root zone thickness increase (Limpens et al., 2014b). This positive feedback is

453   amplified further by; (i) increased soil nutrient availability by litter fall, (ii) increased levels of

454   interception with increased canopy (Dubé et al., 1995), and (iii) reduced aerodynamic resistance

455 (by e.g., wind) favoured by higher stand density which increases evaporation (Kellner, 2001).

456 The change in hydrology may also lead to increased decay rates in the upper peat profile due to a

457 deepening of the aerobic zone. Changes in tree cover can therefore be a fundamental shift in the

458 peatland carbon cycle and it is possible that tree-covered peatlands could become net sources of

459 carbon if increased net photosynthetic rates and carbon fixation are lower than increased peat

460 decomposition rates (Juutinen et al., 2010). The effects that tree density has on water loss have

461 important implications for the structure and functioning of peatlands but the relation between

462 evapotranspiration and tree density is non-linear (Limpens et al., 2014b). This is because

463 increasing density of tree stands can result in shading of the peat surface, thereby reducing the

464 energy available for evaporation (Ohlson et al., 2001; Strakova et al., 2012).

465

466

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

468

469 The present interglacial, the Holocene, started about 11,700 cal BP (calibrated years before AD

470 1950) with a rapid transition from the cold Younger Dryas to subsequent conditions characterized

471 by significantly warmer and more stable conditions (Bond et al., 2001; Wanner et al., 2008;

472 Marcott et al., 2013). At the millennial timescale, the climate of the Holocene has been influenced

473 strongly by hemispheric trends in solar insolation, but was also interrupted by shorter centennial

474 events related to other drivers such as solar and volcanic forcing (Dansgaard et al., 1989; Bond et

475 al., 2001; Wanner et al., 2011). High spatial and temporal variability temperature and moisture

476 records covering the Holocene have been reconstructed from archives such as ice cores, ocean,

477 lake, and peat sediment cores, speleothems and glacier fluctuations (Wanner et al., 2011).

478 Climatic and environmental mismatches or delays between different geographical regions,

479   however, underline the importance of multiple site studies and call for high-resolution

480   reconstructions using proxies such as tree rings, which remain the most widespread source of

481   annual resolution, precisely dated palaeoclimatic data. In the following discussion, the Holocene

482   is subdivided into the early (c. 9750-6250 BCE or 11,700–8200 cal. BP), mid (c. 6250-2250 BCE

483   or 8200–4200 cal. BP), and late (c. 2250 BCE or 4200 cal. BP to present) Holocene as suggested

484   by Walker et al. (2012).

485

486   *5.1. The early Holocene*

487   Subfossil peatland trees from the early Holocene are scarce for obvious reasons, primarily due to

488   the fact that most northern peatlands were not ombrotrophic until later periods of the Holocene

489   due to slow peat formation and accumulation (Barber et al., 2003; Yu et al., 2010). Despite this

490   limitation, radiocarbon dated pine trees as old as c. 9050 BCE (11,000 cal. BP) have been

491   discovered in northwestern German peatlands (Achterberg et al., 2016). The formation of raised

492   bogs in this region, however, only began about 2000 years later (Petzelberger et al., 1999;

493   Eckstein et al., 2011), which suggests that the material consists of mineral soil pines overgrown

494   by and preserved in expanding peatlands. Tree colonization directly on peat soils of northwestern

495   Germany has, however, been recorded about c. 6750 BCE (8700 cal. BP), evident from peatland

496   pines dated to 6703 BCE (8652 BP; Achterberg et al., 2015) and oaks dated to 6627 BCE (8576

497   BP; Leuschner et al., 2002; Achterberg et al., 2015). Oak trunks from this period, but dated by

498   radiocarbon, have also been discovered in Denmark (Christensen, 2007). Some centuries later,

499   about 6350 BCE (8300 cal. BP), minor periods of pine establishment have been noted in the Irish

500   and Scottish pine material (Bridge et al., 1990; Torbenson et al., 2015). Otherwise, few

501   establishment phases have been recorded prior to the 8200 cal. BP cold event (referred to as the

502   8.2 ka event, c. 6250 BCE; Alley et al., 1997), which may have generated moist and unfavourable

503   conditions for tree colonization at the peatlands. The 8.2 ka event is recorded on a hemispheric

504   scale in a broad range of proxy records (Alley et al., 1997; Veski et al., 2004; Nicolussi and

505   Scüchter, 2012). The number of German pines recorded (replication in Fig. 10) drops during (or

506   slightly after) the 8.2 ka event and a 108-year gap has been documented in the German bog oak

507   record (Achterberg et al., 2016), indicating a shift towards unfavourable conditions for peatland

508   tree growth (Fig. 10). Although from a different context, the lowest tree replication in the Alpine

509   tree-ring chronology by Nicolussi et al. (2009) is observed around 6100 BCE, very close to the

510   8.2 ka event. In a similar way, Helama et al. (2008) also suspect that the lack of subfossil trees in

511   Finnish Lapland was caused by the same climatic effect and that it would likely have decelerated

512   pine colonization in the region.

513   *5.2. The mid-Holocene*

514   About 8100 years ago, following the cold 8.2 ka event (Alley et al., 1997), tree establishment has

515   been recorded in various peatlands in northwestern Europe, namely in Ireland (Pilcher et al.,

516   1995; Torbenson et al., 2015), Germany (Leuschner et al., 2002; Eckstein et al., 2009; Achterberg

517   et al., 2015), Denmark (Christensen, 2007), and Sweden (Edvardsson et al., 2012b). These initial

518   pulses of tree establishment were followed by continuous and fluctuating mid-Holocene tree

519   colonization across northwest European peatlands (Fig. 8).

520   During the mid-Holocene, cross-dating between series from different regions yields

521   statistically significant results and points to striking similarities in annual growth and tree

522   population dynamics over substantial parts of northwestern Europe, especially for the period 5300

523   to 2500 BCE (7250-4550 BP; Fig. 6-7). The successful cross-dating between various sites,

524   sometimes separated by hundreds of kilometres, also indicates that similar year-by-year climate

525   variability has influenced environmental conditions at these peatlands, and thereby radial growth

526   of trees (Pilcher et al., 1977, 1984; Leuschner et al., 2002; Eckstein et al., 2009; Edvardsson et

527   al., 2012a). Similarities in tree replication records on the other hand, show coinciding

528   regeneration and later life stages, whereas mean-age records indicate changes in the age structure

529   of tree populations. The German pines, for instance, were not randomly distributed over time.

530   Instead, woodland establishment and dying-off phases were periodic, as detected in pine

531   populations from 36 different German peatlands (Eckstein et al., 2009). Together, the significant

532   cross-dating statistics and similarities in tree population dynamics imply similar high- (i.e. annual

533   to decadal scale) and low-frequency variability (i.e. decadal to centennial scale) governed

534   hydroclimatic forcing mechanisms influencing peatland hydrology and associated tree growth

535   over a large geographic region (Fig. 6 and 10). Moreover, widespread colonization also points to

536   relatively dry and therefore favourable growth conditions for peatland trees, which is underlined

537   by the main woodland phases at German and Swedish peatlands between 5300 and 3700 BCE

538   (7250-5650 BP; Eckstein et al., 2009, 2011; Edvardsson et al., 2012a, b).

539   Pine records from the Alps show colonization at unusually high elevations (Tessier et al.,

540   1993) and strong replication (Nicolussi et al., 2009) during the same period. A combination of

541   high-altitude occurrence and an increased replication of subfossil pines is also evident in northern

542   Finland from 4200 to 2200 BCE (6150-4150 BP; Helama et al., 2004, 2010). The pine

543   colonisation of peatlands in northern Scotland occurred around 5000 years ago, and has been

544   interpreted as a regional phenomenon (Gear and Huntley, 1991; Charman, 1994; Daniell, 1997;

545   Huntley et al., 1997). By contrast, both oak and pine trees colonized Baltic peatlands during the

546   mid-Holocene (Pukienė, 2003; Vitas, 2010; Edvardsson et al., 2016a), and therefore add further

547   evidence of widespread impacts of favourable climatic conditions.

548   These favourable growth conditions for peatland trees during the mid-Holocene were

549   probably closely linked to a relatively warm and dry climate regime, which commonly is referred

550   to as the Holocene Thermal Maximum (HTM; Seppä et al., 2005; Renssen et al., 2009). The onset

551   and termination of the HTM varies clearly between different geographical regions and studies,

552   but is generally dated to the period c. 6850-2450 BCE (8000–4400 cal. BP) across northern

553   Europe (Jessen et al., 2005; Seppä et al., 2005; Renssen et al., 2009; De Jong et al., 2009). The

554   comparably high air temperatures and dry conditions in northwestern Europe were probably

555   caused by (i) an orbitally-forced increase in summer insolation, and (ii) a stronger meridional

556   overturning circulation and intensified northward ocean heat transport after the Laurentide Ice

557   Sheet had vanished (Snowball et al., 2004; Renssen et al., 2009; Wanner et al., 2011).

558   Temperature reconstructions based on stable isotopes from ice-cores as well as pollen data from

559   lake sediments and peat cores all point to summer temperatures which would have been

560   approximately 2-3°C above present values across most parts of northwestern Europe and

561   Scandinavia (Huntley and Prentice, 1988; Seppä et al., 2005; Brown et al., 2011; Helama et al.,

562   2012). At the same time, moisture records indicate a dry phase at about 5250 to 3750 BCE (7200-

563   5700 BP; Wanner et al., 2011), which is confirmed indirectly by lake level proxies pointing to

564   generally low water levels (Digerfeldt, 1988; Hammarlund et al., 2003; Magny, 2004, 2013;

565   Sohar and Kalm, 2008).

566   The annual resolution and accurate dating of the tree-ring chronologies allow detailed

567   studies of rapid climatic events during the HTM, which may be missed in lower resolution

568   proxies. Several peaks in the Irish replication records have, for instance, been recorded about

569   6050, 5350, 4250, and 1250 BCE (8000, 7300, 6200 and 3200 BP; Turney et al., 2006), and are

570   consistent with peaks and establishment phases detected in replication records from Germany, the

571   Netherlands, and Sweden (Fig. 10). Moreover, many dying-off phases described in the German

572   records (Leuschner et al., 2002; Eckstein et al., 2009; Bauerochse et al., 2015; Achterberg et al.,

573   2015) can be found in other records from northwestern Europe. For instance, the dying-off phase

574   between 4600-4550 BCE (6550-6500 BP) described by Achterberg et al. (2015) is also visible in

575   the oak records from Germany and the Netherlands (Leuschner et al., 2002), as well as in the

576   Scottish (Bridge et al., 1990) and Swedish (Edvardsson et al., 2012a) pine records.

577   Towards the end of the HTM, shifts towards wetter conditions about 3250 BCE and 2250

578   BCE (5200 and 4200 cal. BP) have been described in the literature (referred to as the 5.2 and 4.2

579   ka events; Roland et al., 2014, 2015). The 5.2 ka event (c. 3250 BCE) has been identified as a

580   coherent shift towards wetter conditions caused by prolonged positive North Atlantic Oscillation

581   conditions, and was found in stable isotope, testate amoebae, plant macrofossil, and humification

582   records from peatlands in Northern Ireland (Roland et al., 2015). Evidence for such a wet shift is

583   lacking in the Irish oak replication records, whereas a decrease in German peatland pines and a

584   dying-off phase in Lithuanian pines can be observed (Fig. 10). Moreover, a coincident phase of

585   lowered replication of subfossil pines is evident in northern Finland (Helama et al., 2004, 2010).

586   Several synchronous and massive dying-off phases can also be detected about 2500 BCE (4450

587   BP) in Scotland (Gear and Huntley, 1991; Charman, 1994; Daniell, 1997), Ireland (Pilcher et al.,

588   1995), Great Britain (Lageard et al., 1999; Boswijk and Whitehouse, 2002), Germany (Eckstein

589   et al., 2011; Bauerochse et al., 2015), and Sweden (Edvardsson et al., 2014b), and thus point to a

590   spatially structured, regional environmental change. By way of example, the British peatland pine

591   chronologies from Garry Bog (2569 BCE; Pilcher et al., 1995), White Moss (2559 BCE; Lageard

592   et al., 1999), Thorne (2475 BCE; Boswijk, 1998), and Hatfield (2445 BCE; Boswijk and

593   Whitehouse, 2002) all terminate at 2507±62 BCE (4456±62 BP).

594

595   *5.3. The late Holocene*

596   The unfavourable conditions recorded towards the very end of the HTM continued in a similar

597   manner between 2200 and 2160 BCE (4150-4110 BP; Fig. 10), and resulted in abrupt dying-off

598 phases at various sites in northwestern Germany (Eckstein et al., 2010; Bauerochse et al., 2015),

599 the Netherlands (Leuschner et al., 2002), and Finland (Helama et al., 2004). The similarities

600 between continental and Irish mean-age records, which were present during the entire HTM, also

601 start to disappear at about 2000 BCE (4000 BP; Leuschner et al., 2002). The effects of a large-

602 scale shift in climatic conditions are also obvious in northern Finland where the replication of the

603 subfossil pine chronology collapses around 2200-2000 BCE. Moreover, indications of pine

604 germination are clearly missing at the high elevation sites in Finland as of 2400 BCE (4350 BP),

605 and are followed by a gradual decline in pine populations until 600 BCE (2550 BP; Helama et al.,

606 2004). Since about 1500 BCE (3450 BP), following yet another dying-off phase recorded across

607 northwestern European peatlands, fewer dated peatland pines have been found in Germany

608 (Achterberg et al., 2015) and Ireland (Pilcher et al., 1973). Most of these observations can be

609 linked to the onset of a widespread climatic transition, sometimes referred to as the Neoglacial

610 phase (Nesje et al., 1991; Wanner et al., 2008).

611   The climatic change about 2250 BCE (4200 cal. BP and often refered to as the 4.2 ka

612 event; Roland et al., 2014) is evident at the hemispheric scale in numerous proxy records and was

613 most likely driven by changes in orbital insolation patterns (Bradley, 2003; Booth et al., 2005;

614 Morley et al., 2014), but changes in tree populations do not appear abruptly or synchronously

615 between different sites (Fig. 10). Instead, a multi-proxy study from Sweden points to a stepwise

616 transition phase dated to between c. 2650 and 1450 BCE (4600 and 3400 cal. BP; Jessen et al.,

617 2005). In a similar way, several dying-off events have been recorded among Swedish peatland

618 trees (Edvardsson, 2016), whereas a two-stage temperature decrease with an onset c. 3050-2550

619 BCE (5000-4500 cal. BP) and a termination c. 2350-1350 BCE (4300-3300 cal. BP) has been

620 described around the Baltic Sea (Borzenkova et al., 2015). Moreover, testate amoebae in Irish

621 peatlands do not provide any compelling evidence for a rapid transition about 2250 BCE (4200

622   cal. BP; Roland et al., 2014), whereas records from Great Britain and Denmark suggest a system

623   shift at about 2150 BCE (4100 cal. BP; Mauquoy et al., 2008). These results show that the origin

624   and impact of the 4.2 ka event is spatially complex and was probably less marked than in low

625   latitudes, and may also explain why the drop in tree replication in Ireland and Sweden started 200

626   years later than in Germany and the Netherlands (Fig. 10). These results also confirm the need for

627   climate reconstructions with high spatio-temporal resolution to improve our understanding of

628   complex climate transitions. Pollen-based temperature reconstructions from Scandinavia show

629   that the annual mean temperature was reduced by almost 2 °C during this transition phase (Seppä

630   et al., 2005; Heikkila and Seppä, 2010), whereas lake-level reconstructions suggest wetter

631   conditions with rising lake levels between 3000 and 500 BCE (5000-2500 cal. BP; Digerfeldt,

632   1988; Magny, 2004, 2013; Sohar and Kalm, 2008). Indications of rising water levels after the

633   termination of the HTM also exist for northern Finland in the form of submerged pines with their

634   root systems anchored in the palaeo-shoreline, two meters below the current water level (Eronen

635   et al., 1999). The rising water tables and wetter peatland surface conditions are therefore also

636   believed to have caused widespread dying-off phases, leading to the termination of most Swedish

637   and German pine records at about 1100 BCE (3050 BP; Eckstein et al., 2011; Edvardsson, 2016).

638   Together, these observations indicate that the widespread transition towards wetter and colder

639   conditions continued for at least a millennium after the end of the HTM. These findings are also

640   confirmed by radiocarbon-dated recurrence surfaces detected in several Swedish peat sequences,

641   for which the wet shift is synchronous with the final dying-off phases in the German and Swedish

642   pine chronologies (Borgmark and Wastegård, 2008; Rundgren, 2008) and peat records from

643   northern Britain (Charman et al., 2006).

644   Although the period 2250-1100 BCE (4200-3050 BP) is in general associated with

645   increasingly wetter and colder conditions, some short and regional colonization events were still

646   taking place. The German pine colonization phase at around 1900 BCE (3850 BP), described by

647   Bauerochse et al. (2015), is also visible in records from Sweden, the Netherlands, and Scotland

648   (Fig. 10). Over the last 3000 years, however, relatively few tree establishment phases have been

649   recorded in German and Irish peatlands, whereas trees appear to be close to absent at all known

650   Swedish sites (Fig. 10). Despite this fact, tree colonization has been recorded at peatlands in the

651   Netherlands (Sass-Klaassen and Hanraets, 2006), Poland (Barniak et al., 2014), Lithuania

652   (Pukienė, 1997; Edvardsson et al., 2016a), and in one of the few regions documented in North

653   America (Québec; Arseneault and Payette, 1997). With the exception of the Canadian records,

654   these phases are relatively short, which may also explain why only the Dutch chronologies have

655   been cross-dated successfully over long distances (Fig. 6-7). It is therefore difficult to judge to

656   what extent these tree colonization phases are related to site-specific variations or are linked to

657   regional climate dynamics.

658   About 850 BCE (2800 cal. BP), yet another shift towards cooler, wetter, and windier

659   conditions has been recorded in European peatlands (referred to as the 2.8 ka event; van Geel et

660   al., 1996, 2014; Mauquoy et al., 2008; Mellström et al., 2015). Observations made in peatlands

661   are confirmed by other proxy records, which suggest rising lake levels (Magny, 2004, 2013) and

662   more drift ice in the North Atlantic (Bond et al., 1997). The nature and causes of this cold and

663   wet event have been subject to debate, but the shift broadly coincides with an increase of the

664   atmospheric ^{14}C concentration due to reduced solar activity (Kilian et al., 1995; Swindles et al.,

665   2013; Mellström et al., 2015). The Irish replication and mean-age records indicate dying-off

666   phases or generation shifts, whereas the German and Dutch series point to a decline in replication

667   records (Fig. 10). A dying-off phase about 850 BCE has also been detected in the Polish tree-ring

668   chronologies (Barniak et al., 2014). Despite the general absence of dated peatland pine

669   chronologies from Sweden, macrofossil analysis from a southwest Swedish peat bog shows that

670   pine must have been present locally at the site prior to 910 BCE (2860 cal. BP), but was absent

671   after 740 BCE (2690 cal. BP; Mellström et al., 2015). Gaps also exist in Lithuanian (Edvardsson

672   et al., 2016a) and Canadian (Arseneault and Payette, 1997) tree records during the same period,

673   which may strengthen the hypothesis that the 2.8 ka event did indeed significantly influence large

674   parts of the northern Hemisphere.

675   Between c. 500 BCE and CE 300 (2500 and 1600 BP), tree replication records from

676   Ireland, Germany, and the Netherlands again show some tree colonization phases, but of minor

677   importance (Fig. 10). These colonizations coincide with somewhat warmer and drier climatic

678   conditions during the period often referred to as the Roman Warm Period (RWP; Seneviratne et

679   al., 2010; Büntgen et al., 2011). Partial agreements between the Irish and continental mean-age

680   records presumably indicate changes between relatively similar and diverse forcing mechanisms

681   between the two regions over the period (Leuschner et al., 2002). In the Netherlands, a shift in

682   tree population dynamics with establishment of both oak and ash trees has been recorded as late

683   as AD 300 (1600 cal. BP) followed by striking changes in site hydrology and a dying-off phase at

684   about AD 530 (Sass-Klaassen and Hanraets, 2006).

685   Dying-off phases recorded at several peatlands in Lithuania (Pukienė, 1997; Edvardsson

686   et al., 2016a), by contrast, coincide with the well-known cooling at about 300-600 AD (1650-

687   1350 BP), which is commonly referred to as the Dark Age or Migration Period (Wanner et al.,

688   2011). At about AD 800 (1200 cal. BP), massive tree establishment has been recorded in

689   Lithuanian peatlands (Pukienė, 1997; Edvardsson et al., 2016a) and at the same time, peat records

690   from both Great Britain and Denmark point to a dry phase (Mauquoy et al., 2008). These changes

691   coincide with the onset of the Medieval Warm Period (MWP) and indicate yet another change

692   towards drier conditions in peatlands. Furthermore, Arseneault and Payette (1997) have reported

31

693   strong radial tree growth over the corresponding period, which indicates relatively favourable

694   conditions for tree growth at Canadian peatlands as well.

695   By contrast, an almost complete absence of subfossil peatland trees has been recorded

696   during the Little Ice Age (LIA; AD 1350-1850), which clearly indicates colder and moister

697   conditions compared to the preceding periods (Wanner et al., 2008) and a widespread lack of tree

698   establishment at peatland sites (Fig. 10). Widespread wet shifts have also been reported in

699   European peat stratigraphic records at about CE 1350 and 1600 (600 and 350 cal. BP; Mauquoy

700   et al., 2008). Apparently these conditions generated growth conditions that were too harsh for

701   peatland trees as the final dying-off phases, recorded at about AD 1400 (550 cal. BP), coincide

702   with a shift towards colder (Wanner et al., 2011) and wetter (Charman et al., 2006) climatic

703   conditions. These observations are also supported by the fact that finding recent peatland pines

704   older than 200 years has proven very difficult (Linderholm et al., 2002; Cedro and Lamentowicz,

705   2011; Edvardsson et al., 2015a), confirming the likely absence of peatland trees during the LIA.

706   As the LIA came to an end, widespread pine colonization occurred in peatlands across Estonia

707   (Smiljanić et al., 2014), Lithuania (Edvardsson et al., 2015a), Poland (Cedro and Lamentowicz,

708   2011), and Sweden (Linderholm and Leine, 2004; Edvardsson and Hansson, 2015). Observed tree

709   establishment in recent periods is likely to result from a combination of climatic and land-use

710   changes. Nevertheless, changing climatic conditions over the twentieth century have, at least in

711   some cases, been regarded to be the most important driver of increasing tree establishment rates

712   (Edvardsson et al., 2015b).

713

714

715   **6. Target areas for future research**

716

717   There is still a need for improved understanding of the relations between peatland tree growth,

718   moisture variability, and climate dynamics, to enable more robust hydrology and climate

719   interpretation from peatland tree-ring, replication, and mean-age records. For example, there is a

720   clear need for new methods to isolate the temperature and precipitation signals in tree-growth

721   patterns. Here, we address several suggestions for future studies, which will help to advance our

722   understanding of peatland tree-growth variability, as well as of the connections between tree

723   growth, peatland hydrology, and climate dynamics. We also discuss potential new research fields

724   using subfossil peatland trees.

725

726   **6.1. Isolating and amplifying the climate signal**

727

728   *6.1.1. Long-term reconstructions using multiple proxy records*

729   To understand the basic functions of peatland tree growth and colonization, tree growth and

730   population dynamics data need to be compared and coupled with climate-moisture proxies.

731   Studies using peat stratigraphic records have been carried out to detect large-scale hydrological

732   shifts to put the subfossil tree record into a long-term environmental context (Gunnarson et al.,

733   2003; Eckstein et al., 2010, 2011; Edvardsson et al., 2012b, 2014b). To advance these

734   interpretations further, comparisons using pollen (Gear and Huntley, 1991; Eckstein et al., 2010,

735   2011; Edvardsson et al., 2014b), plant macrofossils (Edvardsson et al., 2014b), and peat

736   humification (Edvardsson et al., 2012b) have been undertaken. The disadvantage of such proxy

737   records is their multi-annual temporal resolution and lower temporal precision that radiocarbon

738   ages offer compared to trees. To improve comparative long-term studies further, proxy records of

739   higher, preferably annual resolution are required. Such records can sometimes be obtained from

740   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; Smiljanić 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

765   hydrological lag effects and poorly understood feedback mechanisms in peatlands (Linderholm et

766   al., 2002; Edvardsson et al., 2015a; Edvardsson and Hansson, 2015). Most studies have

767   consistently reported a negative correlation between annual tree growth and precipitation records,

768   yet correlation statistics have mostly been insignificant (Fig. 8). The use of continuous growth

769   monitoring devices (such as manual or automated dendrometers), micro-meteorological stations

770   and local hydrological stations (i.e. piezometers) could be a valuable way to address relations

771   between meteorological events, water-table fluctuations, and tree growth in more detail and with

772   fewer uncertainties. The combination of such monitoring records may also provide key insights

773   into the hydrological functioning of peatland ecosystems, and especially into lag effects and their

774   impact on tree growth. This hypothesis of a lag effect is supported by unpublished data from

775   Čepkeliai peatland (southeastern Lithuania) where TRW records (AD 1848-2014) have been

776   correlated with hydrological and meteorological time series from the nearby Varėna station (AD

777   1951-2013). At Čepkeliai, bootstrap correlation functions between the TRW chronology and

778   monthly temperature and precipitation only show significant correlation (r=0.25, p<0.05) with

779   previous October precipitation (Fig. 8). At the same time, comparison between the TRW

780   chronology and a much shorter, but local peatland water-table record (AD 2001-2014) shows

781   significantly stronger negative correlation (r =-0.67, p<0.05; Fig. 11). Although the water-table

782   record only covers the last 13 years, these first correlation tests point to the potential of a

783   combined approach. At the same time, they suggest that peatland tree growth might be a valuable

784   direct measurement of moisture changes in peatlands, but a poorer proxy for direct precipitation

785   reconstructions. As long instrumental hydrological records do not exist for peatlands, we suggest

786   progress is made by: (i) testing for correlations between TRW series and hydrometeorological

787   variables, such as the ratio of actual to potential evapotranspiration (AET/PET) computed from

788   temperature and precipitation values; (ii) using tree-growth process models driven by climate and

789   other environmental factors (such as nutrient availability and soil moisture) as they might allow

790   better understanding of tree functioning and the effect which the interaction of different

791   environmental forcings has on tree growth (see Guiot et al., 2014 for a review); and (iii) deriving

792   longer-term water-table fluctuations series from locally-calibrated, process-based hydrological

793   models (see Gong et al., 2012 for a review on the topic) driven by local climatic parameters

794   (temperature, precipitation).

795

796   *6.1.3. Stationarity in tree growth–climate relationships?*

797   Dendroclimatology commonly assumes stationarity in the relationship between tree growth and

798   climate, and that trees are reacting to environmental changes in the same manner at present as

799   they have in the past (uniformitarian principle; Fritts, 1976). This principle has, however, been

800   challenged due to the divergence (Briffa et al., 1998a, b; Wilmking et al., 2005; D'Arrigo et al.,

801   2008) of tree growth at some Nordic sites which used to be temperature-limited in the past, but

802   show a weakening in their mean temperature response in recent decades as a result of global

803   warming. One should thus also assume changes in tree growth–climate relationships at longer

804   timescales as both climate and peatlands have undergone substantial changes over the course of

805   the Holocene. As a consequence, results and conclusions drawn from living material may not

806   therefore be directly transferable to subfossil trees. Trees in Swedish peatlands were shown to be

807   smaller and less long-lived under current conditions (average diameter 16 cm, age 105 yrs.) as

808   compared to the mid-Holocene when the same species produced significantly larger and older

809   trees (average diameter 25-30 cm and age 175 yrs.; Lindbladh et al., 2013). These differences can

810   be explained by more favourable climatic conditions and shallower peatlands in earlier periods,

811   but that may not be the only explanation. Further studies should specifically look into age, size,

812   and radial growth relations over various periods of the Holocene. Moreover, the development of

813   dedicated standardisation techniques, designed to remove internal, non-climatic growth trends in

814   ring-width series, with an aim to account for tree productivity-related biases needs further

815   evaluation. For example, the Signal-Free Regional Chronology Standardisation (Melvin and

816   Briffa, 2014) approach should be preferred for reconstructions if they contain both living and

817   subfossil peatland trees.

818

819   *6.1.4. What does tree replication mean?*

820   Tree replication data are often used as a climate proxy, but this has recently caused debate about

821   its value for climate inferences and on ways to interpret such records (Charman, 2010; Swindles

822   and Plunkett, 2010; Swindles et al., 2013; McGeever and Mitchell, 2015). Looking at the 2500

823   BCE–CE 1600 period, Swindles and Plunkett (2010) reported a lack of consistent relationship

824   between the Irish oak replication (Turney et al., 2005) and palaeohydrological records (Mauquoy

825   et al., 2008; Magny, 2004, 2013), changing solar activity (Hu et al., 2003; Muscheler et al.,

826   2005), or stacked drift ice records (Bond et al., 2001). However, Charman (2010) successfully

827   reconciled the Irish bog oak record with a large-scale compilation of peatland water table

828   reconstruction and other evidence from northern Britain, and showed the commencement of

829   declines in Irish oak populations were coincident with increased surface wetness in northern

830   British peatlands. This suggests that it is the direction of change in the population that is

831   sensitive to surface wetness, rather than the absolute numbers of trees in the record at any one

832   time. Disagreement between records in Swindles and Plunkett (2010) could be a consequence of

833   the mid-Holocene transition towards moister conditions about 2500 BCE (4450 BP; Wanner et

834   al., 2008), which caused divergent reactions between Irish and continental oak records

835   (Leuschner et al., 2002). It may also be a function of comparison with atypical surface wetness

836   records and the relatively small number of records after c. 2200 years ago (Pilcher et al., 1996).

837   McGeever and Mitchell (2015) looked into the temporal distribution of Irish peatland

838   pines dated by radiocarbon, and suggested that factors other than climate, such as the availability

839   of pine seeds and peatland surface area, may have influenced the presence of trees at Irish

840   peatlands and that this limitation might have disrupted the climate signal of the record during

841   certain periods. Despite this possible shortcoming, their pine record nevertheless shows a

842   significant peak during the late part of the HTM, a decline during the late-Holocene transition, an

843   absence of material during the 8.2 and 2.8 ka events, as well as during the LIA (Fig. 10).

844   Whilst there is a sound theoretical underpinning and increasing evidence for interpreting

845   tree records in terms of palaeoclimate, we acknowledge that tree replication will be influenced by

846   factors other than climatic wetness changes (Swindles and Plunkett, 2010; Swindles et al., 2013;

847   McGeever and Mitchell, 2015), such as natural succession and the transformation of a peatland

848   from a wetland to a raised bog (Fig. 2). Moreover, tree replication in different geographical

849   settings may not reflect the same environmental changes. Competition between tree species

850   colonizing peatlands in parallel is another possible factor influencing tree replication. In-depth

851   comparative studies between overlapping records from *in-situ* pine and oak trees from common

852   study sites may generate valuable information on competition between species, habitat

853   preferences and tree population dynamics. Furthermore, research on processes governing

854   peatland tree colonization in different geographical regions might help us to understand if

855   establishment and dying-off phases reflect similar environmental processes or if local controls are

856   more important.

857

858   **6.2 New study areas and research fields**

859

860   *6.2.1. New study areas*

861   This review provides a literature-based overview of geographical areas for which tree-ring

862   analyses have been performed with subfossil peatland trees (Fig. 1 and Table 1). The distribution

863   of peatland regions in the Northern Hemisphere (Fig. 1) also enables us to identify new potential

864   study areas, at least for living peatland trees. In that sense, we hypothesize that Québec, Ontario,

865   and the Northern regions of Canada in more general terms, Southern Siberia (Russia), as well as

866   the Baltic countries clearly represent areas in which the potential of peatland dendrochronology

867   has been underutilized in the past, as shown by a series of very recent studies on Lithuanian

868   (Edvardsson et al., 2016b), Polish (Krąpiec and Szychowska-Krąpiec, 2016), and Romainian

869   (Árvai et al., 2016) peatland trees. Peat mining areas where there are likely to be exposed

870   subfossil trees can be detected easily on aerial photographs and satellite imagery. In some cases,

871   large wood deposits can also be observed on aerial photos of peat mining areas, but contacts with

872   peat mining companies are probably the best way of identifying which sites also have subfossil

873   wood remains.

874

875   *6.2.2. Potential new indicators for detection of moisture changes*

876   Stable isotopes in tree rings have proven to provide palaeoclimatic information with annual

877   resolution (see Loader and Switsur, 1996; McCarroll and Loader, 2004). Despite this, only two

878   studies exploring the potential of stable carbon ($\delta^{13}C$) and oxygen ($\delta^{18}O$) isotopes have been

879   performed so far with subfossil peatland tree material (Sass-Klaassen et al., 2005; Edvardsson et

880   al., 2014a). When considered together, these isotopes have been shown to be sensitive to the

881   variability in growing season moisture regimes experienced by trees. Based on the correlation

882   analysis between TRW and isotope series, Edvardsson et al (2014a) demonstrated a three-year lag

883   between a decline in $\delta^{13}C$ and $\delta^{18}O$ values in trees and the corresponding tree-ring response,

884   possibly reflecting a relatively slow rise in local water table in response to wetter climate. Despite

885   the fact that isotopic records generate much additional information compared to TRW records

886   alone, no further attempts have been performed to date, possibly as these methods are still

887   expensive and time consuming.

888   Despite the fact that roots will be the first to experience any changes in water-table

889   fluctuations, root morphology has been used only rarely to detect possible water table changes in

890   peatland ecosystems (Lageard et al., 1995; Eckstein et al., 2010). For example, a substantial water

891   table lowering may cause the formation of adventitous roots (Stoffel and Bollschweiler, 2008).

892   Dendrochronological dating of roots (Stoffel et al., 2013), in combination with field

893   measurements of their depth and morphological features, may generate detailed information

894   about the timing and magnitude of hydrological shifts (Eckstein et al., 2010). Such information

895   cannot be obtained without a detailed assessment of root morphology in the field and the

896   sampling of second-generation, adventitious roots. We therefore recommend systematic field

897   measurements and sampling of adventitous roots to test their response to a decline in water table,

898   and to evaluate whether this can lead to instability of moist surfaces and subsequent formation of

899   reaction wood (Stoffel and Bollschweiler, 2008) in trees (Fig. 5).

900   Another important aspect of peatland ecosystems and environmental changes is their

901   response to fire, which can be studied through absolutely dated fire scars in subfossil or living

902   trees (Arseneault and Payette, 1997; Lageard et al., 2000; Eckstein et al., 2009; Edvardsson et al.,

903   2012a). The age and frequency of fires may not be sufficient to estimate the loss of burned carbon

904   from peatlands, but periods showing an increase in fire activity may be indicative of phases with

905   relatively dry surface conditions. The fire scar records cannot be compared yet, as they do not

906   originate from continuous records and do not overlap sufficiently in time. Further studies are

907   therefore required to evaluate if increased fire frequency in tree-ring records does indeed

908   correspond to periods of relatively dry peatland surface conditions. In addition, fire-scar records

909   can be compared to existing charcoal records, which often represent continuous records and thus

910   can provide clear evidence of fire frequency and intensity at local to regional scale (Patterson and

911   Backman, 1988). If combined, the two approaches clearly have the potential to generate long-

912   term data from charcoal and more detailed (i.e. annual to intra-annual) records for those periods

913   for which tree-ring data are available.

914   The anaerobic conditions in saturated peat soils generate exceptional preservation

915   conditions for organic material (Fig. 4). Rapid wet shifts usually cause increased vertical rates of

916   peat growth, which can be identified in the form of recurrence surfaces in stratigraphic records

917   (Granlund, 1932; Rundgren, 2008). The same environmental changes will also result in quick

918   burial of dead peatland trees, and thereby improved preservation conditions for woody material

919   (Kokkonen, 1923; Leuschner et al., 2007). The degree of post-mortem degradation and stem

920   height can therefore be used as indicators of the moisture status following tree death. Excellent

921   preservation and conserved stem bark over distances greater than 30 cm above root level would

922   indicate fast burial due to moist conditions and rapidly growing peat, whereas conical and eroded

923   stumps lacking bark have been shown to be characteristic of slow burial and slow vertical peat

924   growth (Eckstein et al., 2009; Edvardsson et al., 2012a). A guide or strategy for a degradation

925   index for *in-situ* stumps would therefore be useful and would facilitate evaluation of peat

926   moisture conditions following dying-off phases.

927   By capitalizing on variable phenologies and tree growth responses to water-table

928   fluctuations, multispecies reconstructions may provide significantly more information about past

929   hydroclimatic variability than what we have today. In this context, *Picea*, *Fraxinus*, *Alnus*, *Taxus*

930   and *Betula* have repeatedly been observed in peat mining areas (Godwin, 1975; Arseneault and

931   Payette, 1997; Vitas, 2010; Edvardsson et al., 2014b), but to date, they have only rarely been used

932   as an additional source of information. Of course, the potential of developing multi-millennial

933   chronologies will be limited for many of these species, but they may provide additional

934   contextual evidence for the longer chronologies (Sass-Klaassen and Hanraets, 2006; Edvardsson

935   et al., 2014b).

936

937   *6.2.3. Carbon storage capacity*

938   The interaction between tree colonization, peatland surface moisture, and net carbon

939   sequestration is complex (Limpens et al., 2014a; Holmgren et al., 2015). Some authors have

940   suggested that peatlands may turn from carbon sinks into carbon sources during dry periods

941   (MacDonald et al., 2006; Yu et al., 2010; Limpens et al., 2011), and that dry surface conditions

942   will favour tree growth, tree colonization and increased standing biomass in peatland

943   environments (Freléchoux et al., 2000; Limpens et al., 2014a; Edvardsson et al., 2015b). Phases

944   with widespread peatland tree colonization may thus also represent periods of less important

945   peatland carbon accumulation, or even point to phases during which peatlands were indeed acting

946   as carbon sources. Although tree colonization is likely to increase productivity and litter input,

947   which may in turn increase peat accumulation rates, total peat accumulation and carbon

948   sequestration is believed to be reduced as soon as drier conditions start to turn open moss-

949   dominated peatlands into tree-covered conditions (Limpens et al., 2014a; Holmgren et al., 2015).

950   Further studies are, however, needed on the effects of tree colonization on the drying of

951   peatland surfaces due to increased water loss through tree evapotranspiration, and to determine

952   whether such scenarios have the potential to transform peatlands from net carbon sinks into

953   sources. The effects that tree stand density have on water loss are important and will have

954   implications for the structure and functioning of peatlands, especially as the relation between

955   evapotranspiration and tree stand density is non-linear (Limpens et al., 2014a). Systematic

956   measurements of surface peat moisture, water-table depths, and carbon fluxes to the atmosphere

957   between tree-covered and open peatland areas may give a first indication of the drying effect of

958   trees. Such studies would need to be performed on natural and managed peatlands representing

959   different geographical regions and to look into feedbacks and lag effects between climate,

960   peatland hydrology, and tree growth. To solve some of these remaining issues, we call for

961   continuous monitoring – over at least some years to decades – of; (i) tree growth in peatlands

962   with dendrometers, (ii) water table fluctuations, and (iii) carbon fluxes. To assess the overall

963   carbon balance in peatlands fully, more sophisticated multi-scale approaches will however, be

964   needed, such as those developed by e.g., Fox et al. (2008) and Hartley et al. (2015), as these will

965   also take account of the gaseous carbon components (i.e. CO_2 and CH_4 fluxes) as well as of the

966   dissolved carbon components (i.e. DOC, DIC, and POC). Moreover, such a monitoring setup

967   would enable calibration and validation of dynamic vegetation and ecosystem models such as the

968   modified version of LPJ-GUESS (Lund-Potsdam-Jena General Ecosystem Simulator; Smith et

969   al., 2014) named LPJ-GUESS Why-Me (Wetland Hydrology and Methane, Wania et al., 2009,

970   2010) and other models that are now including peatland carbon accumulation and methane

971   emission processes. Given the likelihood of significant shifts in treeline distribution across the

972   boreal and arctic, improved parameterisation of the interactions between peatland tree growth,

973   hydrology and carbon cycling is essential. A better understanding of the impact climate change

974   may have on tree cover, moisture variability and associated changes in the carbon balance in

975   peatland ecosystems, will advance the possibilities for reliable predictions for future climate

976   change.

977

978

979   **7. Conclusions**

980

981   Contemporary ecosystems can be used to study present-day conditions and to estimate historical

982   environmental changes, typically over timescales of decades. Palaeoecological techniques

983   provide much greater temporal depth (Jeffers et al., 2015), and allow assessments over periods

984   that have experienced significantly different climatic conditions compared to the present day.

985   Despite significant potential, subfossil wood has been identified as one of the most underutilized

986   sources of information in palaeoecology and forest conservation research (Lindbladh et al., 2013).

987   In this review, we have illustrated the origins and recent developments in the field of tree-ring

988   research in peatland environments, compiled the major datasets from Europe and North America,

989   but also identified thematic and geographic areas for which knowledge is still fragmentary. We

990   call for further studies using subfossil peatland trees for detailed reconstructions of long-term

991   hydroclimate dynamics and palaeoecological changes. Beyond palaeoclimate reconstruction and

992   palaeoenvironmental understanding, we expect such data to be important in conservation

993   planning and to determine restoration baselines for peatland management.

994   For more than a century, subfossil peatland trees have been used as a proxy record for

995   environmental changes (Dau 1829; Vaupell 1851; Nielsen and Helama, 2012). Over the last

996   decades, however, numerous studies have started to use the information contained in the annually

997   resolved tree-ring records in more detail to assess climatic changes during the Holocene in the

998   British Isles, Scandinavia, and throughout Central Europe (Table 1, Fig. 1). Through the

999   comparison between tree replication records, tree-ring width chronologies, climate and moisture

1000   proxies (i.e. ice cores, sediment records, pollen), as well as meteorological data, detection of

1001   climatic signals in peatland trees has been improved substantially. We conclude that:

1002   (1) Our current knowledge of the effects of (hydro-)climatic changes and anthropogenic

1003   activities on tree growth in peatland ecosystems is mainly based on ecophysiological,

1004   dendroclimatic, and dendroecological perspectives;

1005   (2) A majority of existing studies shows that excess moisture is a growth-limiting factor for

1006   peatland trees. Proxy records developed from subfossil peatland trees therefore have the

1007   potential to help in the reconstruction of (i) local water-table fluctuations, and (ii) regional

1008   hydroclimate dynamics. Annual tree-growth patterns can be used to assess changes at

1009   annual to decadal scales, whereas tree population dynamics reflect changes at decadal to

1010   centennial time scales;

1011   (3) Substantial work has been performed using subfossil trees from Germany, Great Britain,

1012   Ireland, the Netherlands, and parts of Scandinavia, whereas the vast majority of Canada,

1013   Russia, and the Baltic countries have significant under-exploited potential for the

1014   development of geographically widespread records;

1015   (4) Our data compilation showing temporal distribution of subfossil peatland forests confirms

1016   that relatively warm and dry periods – such as the HTM – offered conditions which were

1017   favourable for tree growth in peatlands and thereby allowed widespread tree colonization,

1018   whereas transitions towards moister and colder conditions (e.g., the mid-late Holocene

1019   transition and the LIA) are associated with widespread dying-off phases and/or depressed

1020   annual tree growth;

1021   (5) Further studies using e.g., stable isotopes, dendroclimatology, and field monitoring are

1022   critical to increase our knowledge about tree growth responses associated with

1023   hydroclimate changes, including understanding of hydrological lag and feedback effects

1024   detectable from lagging tree growth responses to climate on peatlands.

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Figure Caption

1798

1799   Fig. 1. (a) Location of the main peatlands referred to in Tables 1 and 2 (Id. No. 1-81). Sites from

1800   which subfossil trees have been sampled are shown by black squares while sites from which

1801   living trees have been sampled are shown by red triangles. (b) Map over peatlands outside

1802   northwest Europe. Peat coverage is based on Montanarella et al. (2006).

1803

1804   Fig. 2. (a) During the early Holocene, many topographic depressions were occupied by lakes in

1805   which organic layers consisting of e.g. gyttja (1) was deposited. In the shallow areas along the

1806   shores, reed or fen peat was developed (2). (b) During the mid-Holocene, relatively warm and dry

1807   conditions allowed trees to colonize many peatlands. (c) Accelerating peat growth following wet-

1808   shifts can often be observed as recurrence surfaces (RS) in stratigraphic records. Such

1809   hydrological changes may cause tree dying-off phases. Stumps and trunks from these trees can be

1810   preserved by the growing peat (3). (d) At present peatlands are valuable climate archives. Peat

1811   stratigraphic records (4) generate long-term information showing environmental changes,

1812   whereas tree-ring chronologies (5) can generate annually resolved information. The tree-ring

1813   chronologies (example from Edvardsson, 2016) can be developed from both living and subfossil

1814   trees (6). Tree growth is usually influenced by hydrological variations (7) related to climate (8).

1815   Moreover, climate, hydrology, and tree growth ultimately influence the carbon budget (9) of the

1816   peatlands.

1817

1818   Fig. 3. (a) The natural raised bog Fjällmossen (S. Sweden) is characterized by scattered

1819   populations of birch and pine trees. (b) Open water ponds at the raised bog Aukštumala

1820   (Lithuania) show how close the water table is to bog surface and the root systems of the pine

1821 trees. (c) Peatland pines growing at Saxnäs Mosse, Sweden. (d) A till hummock in

1822 Hästhultsmossen (S. Sweden) generates stable and dry conditions favoring colonization of trees.

1823 The area surrounding the mineral soil hummock, however, is relatively wet, unstable and

1824 supports significantly smaller pine trees even though the trees are of same age.

1825

1826 Fig. 4. (a) Several meters of peat have been harvested at the Rėkyva peat mining area (Lithuania)

1827 with the result that subfossil trees preserved in peat have been exposed. (b) Tree horizon at the

1828 Viss Mosse peatland (Sweden; Fig. 1, site 23) containing *in situ* pine stumps. These trees were

1829 growing at the bog surface between 7200 and 6500 years BP. (c) Field sampling of a c. 6000-

1830 years old pine tree at Hällarydsmossen (Sweden; Fig. 1, site 22b). (d) To enable continued peat

1831 mining, tree trunks and stumps are often stored in piles surrounding the peat mining area

1832 (Hällarydsmossen).

1833

1834 Fig. 5. Cross-sections and annual growth rings from subfossil trees exhibit different growth

1835 patterns and characteristics. (a) Two cross-sections from Scots pine (*Pinus sylvestris* L.)

1836 excavated at Viss Mosse (Fig. 1, site 23). The left hand sample contains a complete ring sequence

1837 from pith to bark corresponding to 5078–4970 BCE (7027-6919 BP). The right hand sample has

1838 degraded after death. The growth rings correspond to the period 4872–4716 BCE (6821-6665

1839 BP), but approximately 50–70 rings towards the center and another 10–20 of the outermost rings

1840 are expected but have eroded away. (b) Fire scar dated to 4420 BCE (6369 BP). (c) Abrupt

1841 growth depression visible in a pine tree from the peatland Åbuamossen (Fig. 1, site 24). The

1842 growth depression most likely resulted from a period of extremely wet conditions between 1288

1843 and 1270 BCE (3237-3219 BP) and is visible in all dated trees growing at the peatland. (d) Tree-

1844 ring sequence from a subfossil oak (*Quercus robur* L.). (e) Eccentric pine-stem cross-section

1845   characteristic for trees growing on unstable soils. The innermost 70 annual rings are circular,

1846   whereas about 4070 BCE (6020 BP) unstable conditions are evident having forced the tree to

1847   form reaction wood. (f) About 70 narrow annual rings (inside the circle) around the pith,

1848   indicating unfavourable conditions during establishment.

1849

1850   Fig. 6. Significant cross-dating statistics between continental and Irish peatland and oak

1851   chronologies have been described by Pilcher et al. (1984) and Leuschner et al. (2002; arrow a).

1852   German peatland-oaks also cross-date oaks from River Main (Friedrich et al., 2004, arrow b), the

1853   Netherlands (Sass-Klaassen and Hanraets, 2006; arrow c), Denmark (unpublished, see Fig. 7;

1854   arrow d), and Swedish pine (Edvardsson, 2013; arrow e), whereas the Irish chronologies (oak and

1855   pine) cross-date with the material from Great Britain and Scotland (e.g. Boswik and Woodhouse,

1856   2002; arrow f). Some of the Danish and Swedish oak chronologies also cross-date (Edvardsson et

1857   al., 2014b; arrow g). Furthermore, the Swedish and German pine chronologies generated strong

1858   cross-dating statistics (Edvardsson et al., 2012a; arrow e). Attempts to cross-date Baltic pine

1859   chronologies using material from Germany and Sweden have, however, failed (Edvardsson et al.,

1860   2016a; dashed arrows h). Tests to cross-date south Swedish pine chronologies with peatland pines

1861   described by Gunnarson (1999; dashed arrow i) and subfossil mineral soil pines from Torneträsk

1862   (Grudd et al., 2002; dashed arrow j) failed as well. By contrast, the north Swedish and Finnish

1863   chronologies (Helama et al., 2005; arrow k) indeed cross-date well. Peat coverage is based on

1864   Montanarella et al. (2006).

1865

1866   Fig. 7. Stepwise cross-dating of tree-ring chronologies from northwest Europe. The t-values

1867   between different chronologies are presented next to the arrows. Oak chronologies are shown in

1868   black, pine in grey, and dashed lines represent historical material anchored in present. The figures

1869 to the right correspond to the site IDs in Fig. 1 and Table 1. The River Main oak chronology (*,

1870 Friedrich et al., 2004) is also included in the figure.

1871

1872 Fig. 8. Comparisons between tree-ring width (TRW) and meteorological records (monthly

1873 temperature and precipitation data). Sites from which both tree growth at mineral soils (MS) and

1874 peat soils (PS) could be compared are presented. The identification numbers (Id. No.)

1875 corresponds to those presented in Fig. 1 and Table 2.

1876

1877 Fig. 9. (a–b) Examples of TRW chronologies from living trees growing at Aukštumala and

1878 Rėkyva (Edvardsson et al., 2015a). (c) Precipitation data from the meteorological station in

1879 Vilnius. (d) TRW chronologies from Buxabygds Mosse, Saxnäs Mosse and Store Mosse, Sweden

1880 (Edvardsson and Hansson, 2015). (e) Local precipitation data and (f) river discharge data. The

1881 blue bars emphasize moist periods associated with positive precipitation anomalies, grey lines

1882 represent average values. Growth depressions or trends towards narrower growth rings can often

1883 be observed during phases associated with positive precipitation/wet anomalies.

1884

1885 Fig. 10. Main data series compared in the discussion, oak in black, pine in green, and numbers in

1886 brackets correspond to those in Table 1. (a) Irish data series, in black Irish oak replication, in

1887 green pine establishments, and cumulative radiocarbon dated pine samples (green/black squares).

1888 (b) Cumulative weighted Scottish peatland trees dated by radiocarbon and coverage of peatland

1889 pines chronologies. (c) German peatland oaks. (d) Continental and Irish oak mean-age records.

1890 (e) German pine replication and woodland phases. (f) Replication and temporal spread of oak

1891 from the Netherlands. (g) Periods covered by Danish peatland oaks. (h) Swedish pine replication

1892 and periods covered by oak chronologies. (i) Polish pine chronologies. (j) Lithuanian pine

1893 replication as well as pine and oak coverage. (k) Pine replication from Finland. (l) Spruce

1894 coverage from Canada. (m) Dry and wet shifts highlighted in yellow and blue respectively

1895 (Wanner et al., 2011). (n) Wet shifts detected in peat bogs from northern Britain (Charman,

1896 2006). (o) Lake levels in the Baltic region (Sohar and Kalm, 2008). (p) High lake-level phases in

1897 mid-European lakes (Magny, 2004, 2013). (q) Wet shifts detected as recurrence surfaces in

1898 Swedish peat bogs (Borgmark and Wastegård, 2008). (r) In blue, temperature anomalies in

1899 relation to the average (Marcott et al., 2013) and in red, a pollen based temperature reconstruction

1900 by Heikkilä and Seppä (2008).

1901 Fig. 11. Correlation tests between dimensionless TRW indices (grey) from the peatland

1902 Čepkeliai, Lithuania and (a) water-table fluctuations (cm) in relation to the average level, (b) total

1903 annual precipitation (mm), and (c) annual mean temperature (°C).

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 *	P (b)	4629 BCE - CE 502
2. Achterberg et al. (2016)	DE / 52°50' N, 9°50' E *	P, Q (b)	6703 BCE - CE 931
3. Arseneaut & Payette (1997)	CA / 57°44' N, 76°10' W	Pi (b)	500 BCE - present
4. Baillie (1973)	IE / 54°50' N, 6°50' W *	Q (b)	5000-1380 CE
5. Baillie (1977)	IE / 54°50' N, 6°50' W *	Q (b)	5000-1001 CE
6. Baillie et al. (1983)	IE / 54°50' N, 6°50' W *	Q (b)	5000 – 1000 BCE
7. Baillie & Brown (1988)	IE / 54°50' N, 6°50' W *	Q (b)	5300 – 200 BCE
8. Barniak et al. (2014)	PL / 54°15' N, 19°44' E	P (b)	940-460 BCE **
9. Bauerochse et al. (2015)	DE / 52°50' N, 9°50' E *	P, Q (b)	2600-1500 BCE
10. Boswick & 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 *	P (b)	5900-1200 BCE ***
12. Brown et al. (1986)	IE / 54°50' N, 6°50' W *	Q (b)	5300-200 BCE
13. Brown & Baillie (1992)	IE / 54°50' N, 6°50' W *	P, Q (b)	3600-2600 BCE
14. Brown & Baillie (2012)	IE / 54°50' N, 6°50' W *	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 *	Q (b)	5000 BCE - present
17. Christensen (2007)	DK / 56°30' N, 9°50' E *	Q (m)	6000 – 200 BCE
18. Delorme et al. (1981)	DE / 52°50' N, 9°50' E *	Q (b)	350-150 BCE **
19. Eckstein et al. (2009)	DE / 52°50' N, 9°50' E *	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 *	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 *	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 **
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 *	P (b)	4000 BCE – CE 900 *
28. Gear & Huntley (1991)	GB / 58°24' N, 4°3' W	P (b)	2450-1900 BCE **
29. Grudd et al. (2000)	SE / 59°08' N, 17°55' E	P (b)	1700-1500 BCE **
30. Gunnarson (1999)	SE / 59°08' N, 17°55' E	P (b)	1686-1483 ± 23 BCE **
31. Gunnarson (2008)	SE / 63°16' N, 12°31' E	P (p)	5000-2000 BCE **
32. Hall et al. (1994)	IE / 55°05' N, 6°34' W	P, Q (b)	6000-0 BCE **
33. Helama et al. (2004)	FI / 67°50' N, 26°25' E *	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 *	P, Q (b)	3520-2462BCE **, 3228-1891 BCE
36. Lageard et al. (2000)	GB / 53°40' N, 2°20' W *	P (b)	2881-2639 BCE
37. Leuschner et al. (1987)	DE / 52°40' N, 8°20' E *	Q (b)	6000 BCE-500 CE
38. Leuschner & Delorme (1988)	DE / 52°40' N, 8°20' E*	Q (m)	6225 BCE - present
39. Leuschner (1992)	DE / 52°40' N, 8°20' E*	Q (b)	6000 BCE-500 CE
40. Leuschner et al. (2000)	DE, NL *	Q (b)	6000 BCE-500 CE (GE), 6000-4500 BCE, 3000 BCE-500 CE
41. Leuschner et al. (2002)	DE, IE, NL *	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 & Mitchell (2015)	IE / 53°00' N, 7°00' W *	P (b)	6000 BCE-1000CE ***
44. Moir et al. (2010)	GB / 58°90' N, 4°30' W *	P (b)	3200-3000 BCE
45. Moir (2005, 2012)	GB / 58°90' N, 4°30' W*	P (b)	3200-2800 BCE
46. Munaut (1967)	NL / 52°60' N, 6°30' E	P (b)	5000, 4000, 3000 BCE **
47. Munaut & Casparie (1971)	NL / 52°60' N, 6°30' E	P (b)	5000, 4000, 3000 BCE **

48. Nicolussi et al. (2005)	AU / 46°90' N, 10°70' E *	P (p)	7100-2100BCE
49. Nicolussi et al. (2009)	AU, IT, CH *	P, Pi, La (p)	7100BCE - present
50. Pilcher et al. (1973)	IE / 54°50'N, 6°50' W *	Q, P (b)	6000 BCE - present
51. Pilcher et al. (1977)	IE / 54°50'N, 6°50' W *	Q (b)	4000-1000 BCE
52. Pilcher et al. (1984)	IE, GB, DE *	Q (m)	5218-158 BCE (present)
53. Pilcher et al. (1995)	IE / 54°60' N, 5°90' W *	P (b)	3451-2569 BCE
54. Pilcher et al. (1996)	IE / 54°60' N, 6°50' W *	Q (m)	5218-158 BCE
55. Pukienė (1997, 2001)	LT / 56°05' N, 21°50' E	P (b)	200 BCE-present**
56. Pukienė (2003)	LT / 56°12' N, 24°44' E	Q (b)	4600-4400 BCE**
57. Sass-Klassen et al. (2005)	NL / 52°31' N, 6°02' E	Q (b)	200 BCE-150 CE
58. Sass-Klassen &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 *	Pi (b)	3200 BCE **
60. Tessier et al (1993)	FR / 45°05' N, 5°92' E	P (p)	6000 BCE - present **
61. Torbenson et al. (2015)	IR / 54°49' N, 6°30' W *	P (b)	6300-5600 BCE
62. Turney et al. (2005)	IE / 54°60'N, 6°40'W *	Q, P (m)	5000 BCE - present
63. Vitas (2009)	LT/ 55°50' N, 22°17' E	Q, F (b)	4700-1500 BCE **
64. Vitas (2010)	LT/ 55°48' N, 21°53' E	F, A, Q, B (b)	3800-1290 BCE **
65. Ward et al. (1987)	GB / 56°40′ N, 4°18′ W	P (b)	4500-1000 BCE **

*Approximate coordinates as the chronology/chronologies are based on material from several study sites
**Approximate ages as the chronology/chronologies are dated by radiocarbon
***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 Fig 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).

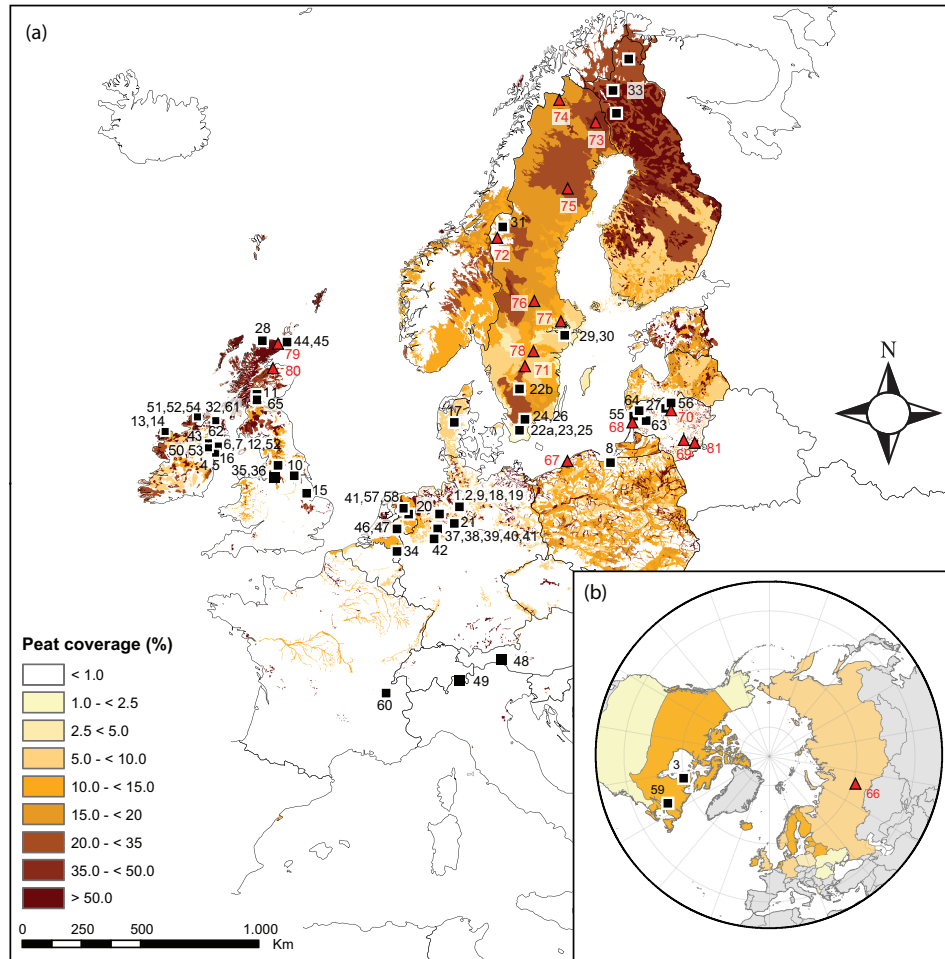| Id. No. and References	Country / Site name	Latitude, Longitude	Species
66. Blanchet et al. (2016)	RU / Mukhrino	60°54'N, 68°42'E	PiSy, PiSi
67. Cedro & Lamentowicz (2011)	PO / Słowinskie Błoto	54°21'N, 16°29'E	PiSy
68. Edvardsson et al. (2015a, b)	LT / Aukštumala	55°23'N, 21°22'E	PiSy
69. Edvardsson et al. (2015a, b)	LT / Kerėplis	54°27'N, 24°32'E	PiSy
70. Edvardsson et al. (2015a, b)	LT / Rėkyva	55°51'N, 23°15'E	PiSy
71. Edvardsson & 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

Fig. 1

Fig. 2

(a)
2.
1.

(b)

(c)
3.
RS
c.

(d)
8.
8.
9. CH$_4$ & CO$_2$
6.
7.
RS
6.
4. Peat stratigraphic record
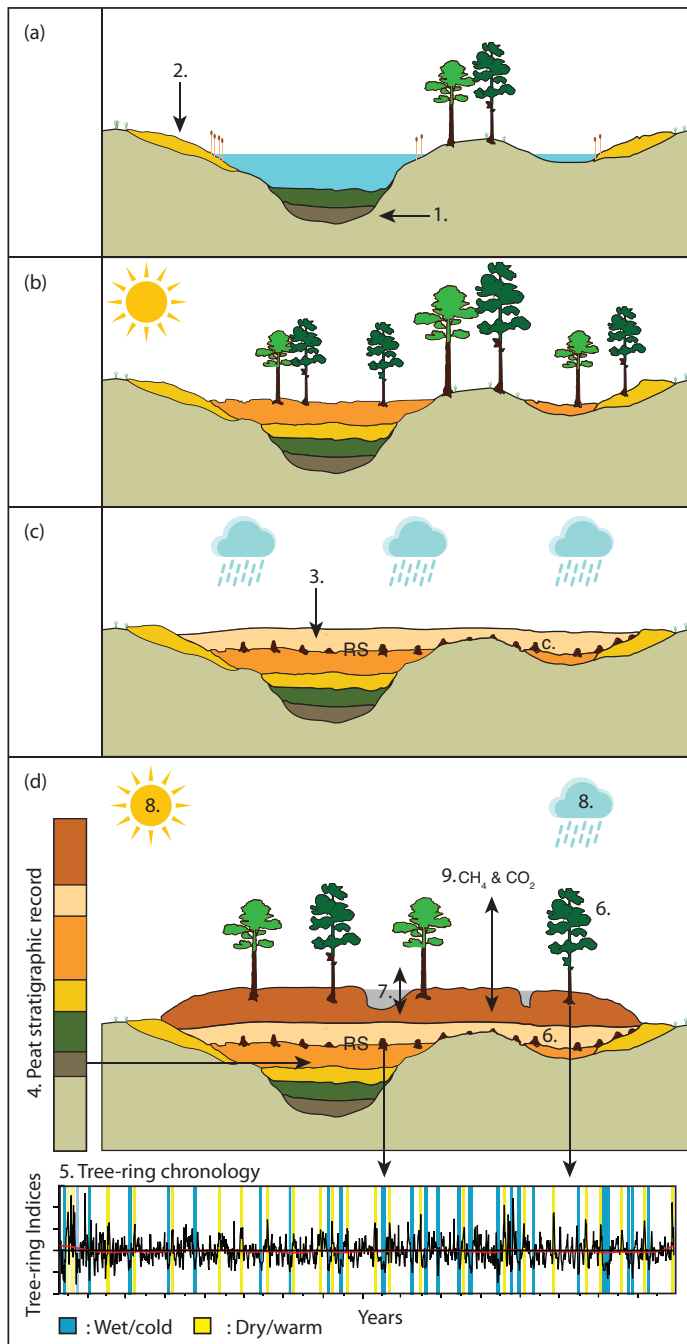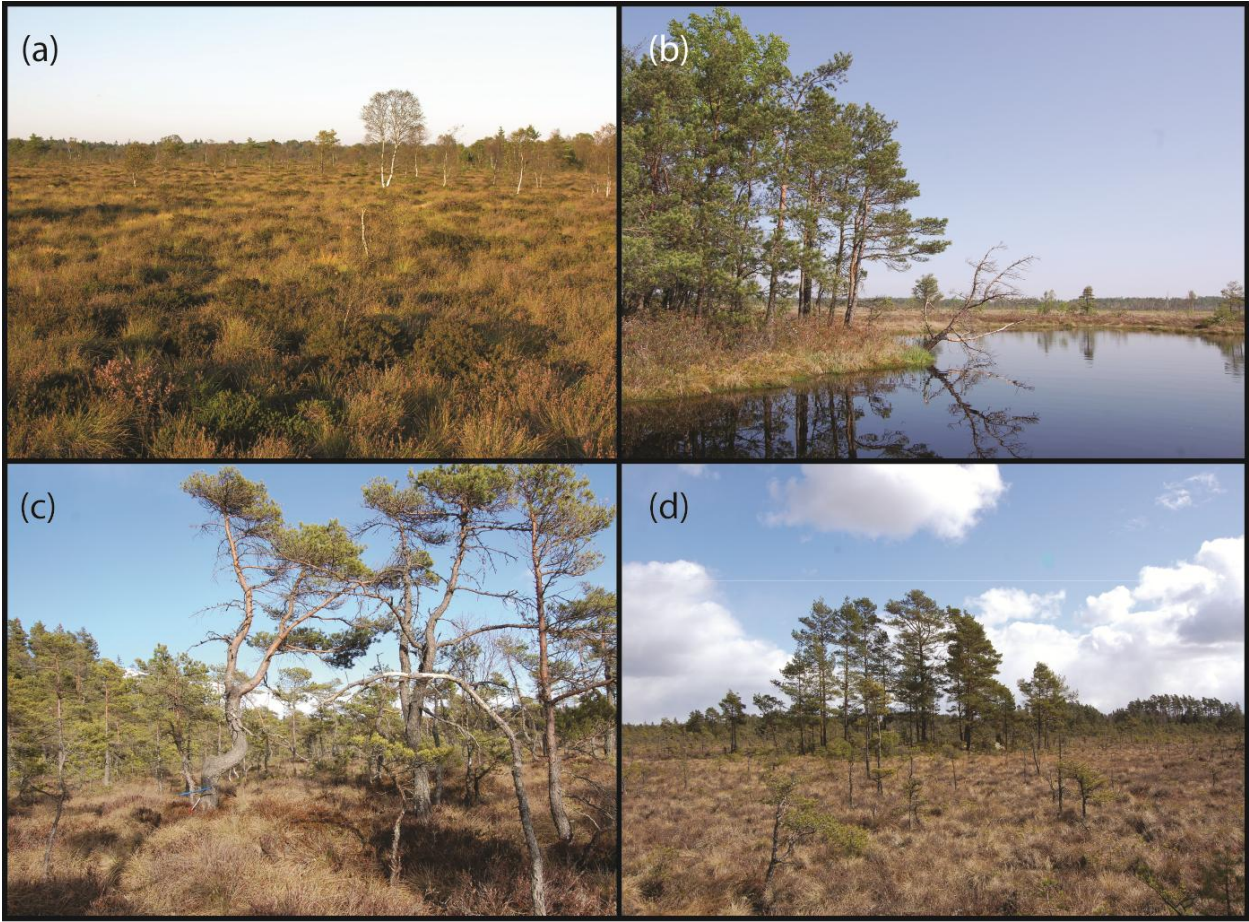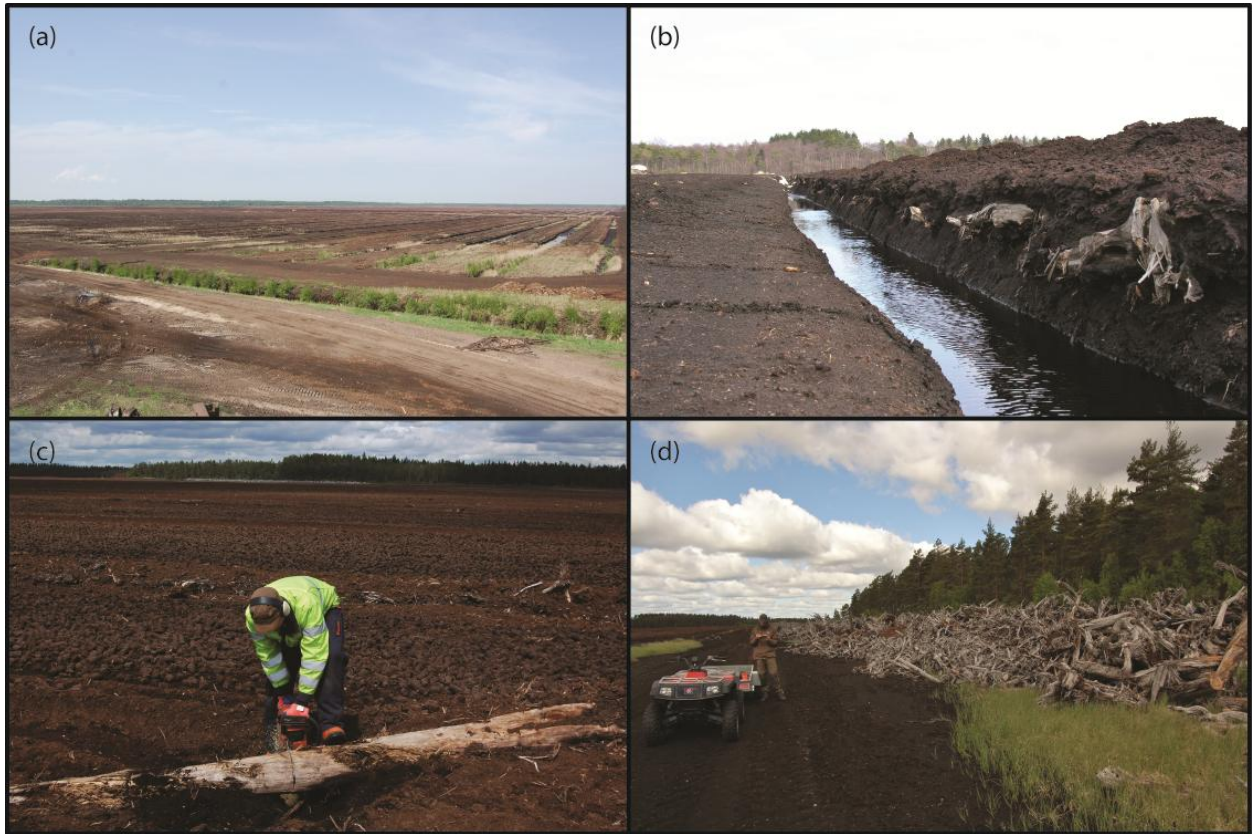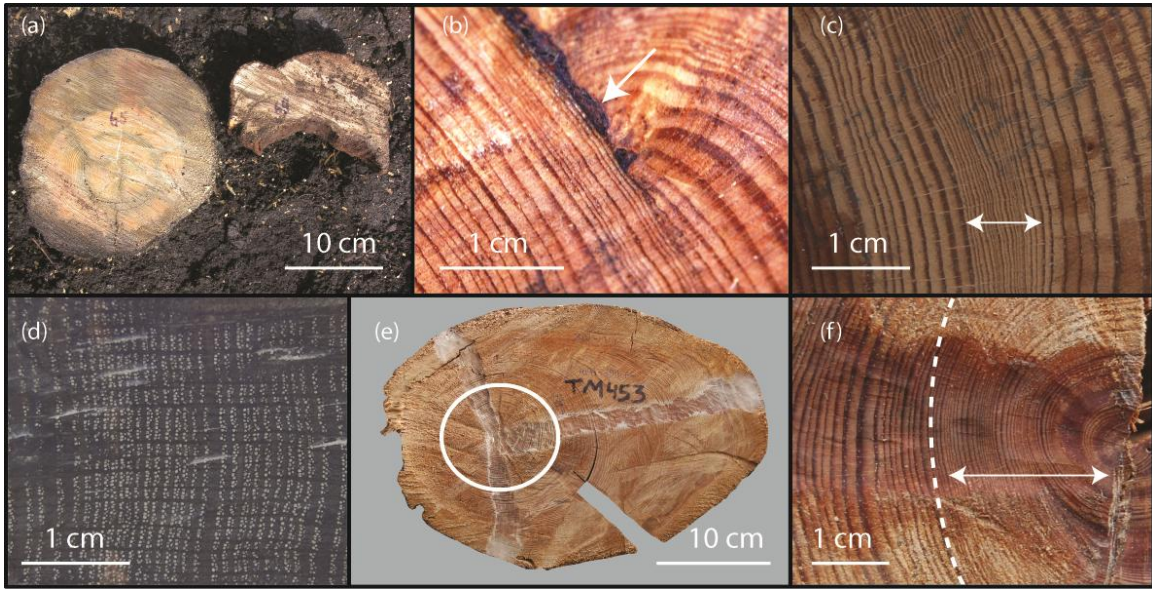5. Tree-ring chronology
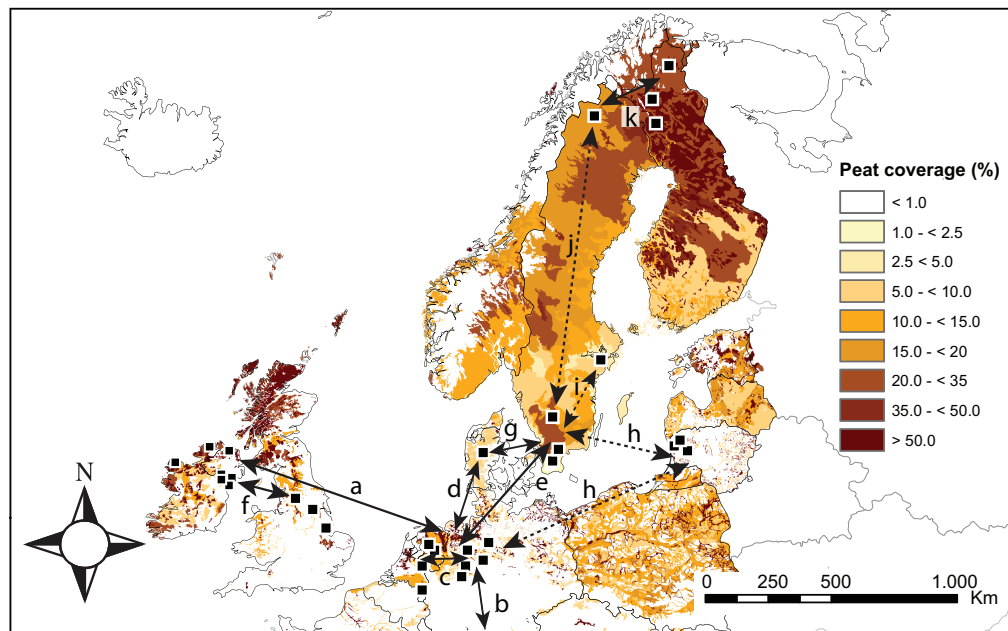Tree-ring Indices
: Wet/cold   : Dry/warm
Years

Fig. 3

Fig. 4

Fig. 5

Fig. 6

Fig. 7

Fig. 8

92

Fig. 9

Fig. 10

Fig. 11