Yang, Qiannan, Li, Hongkai, Zhao, Hongyan, Chambers, Frank M ORCID logoORCID: https://orcid.org/0000-0002-0998-2093, Bu, Zhaojun, Bai, Edith and Xu, Guangyuan (2022) Plant assemblages-based quantitative reconstruction of past mire surface wetness: A case study in the Changbai Mountains region, Northeast China. Catena, 216 (Part B). Art 106412. doi:10.1016/j.catena.2022.106412

Official URL: http://dx.doi.org/10.1016/j.catena.2022.106412
DOI: http://dx.doi.org/10.1016/j.catena.2022.106412
EPrint URI: https://eprints.glos.ac.uk/id/eprint/11185

Plant assemblages-based quantitative reconstruction of past mire surface wetness: A case study in the Changbai Mountains region, Northeast China

Qiannan Yang [a, b, 1], Hongkai Li [a, b, c, 1], Hongyan Zhao [a, b, c], Frank M. Chambers [d], Zhaojun Bu [a, b, c], Edith Bai [a, b, c], Guangyuan Xu [a, b, c]

[a] Key Laboratory of Geographical Processes and Ecological Security in Changbai Mountains, Ministry of Education, School of Geographical Science, Northeast Normal University, Changchun 130024, Jilin, China

[b] Institute for Peat & Mire Research, Northeast Normal University, Changchun 130024, Jilin, China

[c] State Environmental Protection Key Laboratory of Wetland Ecology and Vegetation Restoration, Northeast Normal University, Changchun 130024, Jilin, China

[d] Centre for Environmental Change and Quaternary Research, School of Natural and Social Sciences, University of Gloucestershire, Cheltenham GL50 4AZ, Gloucestershire, UK

Abstract

Quantitative relationships between mire plant assemblages and environmental variables have been investigated widely in Europe and North America, but hitherto insufficiently addressed in the East Asian monsoon region. In this study, the plant assemblages of 274 plots along hydrological gradients in five peatlands from the Changbai Mountains region, Northeast China were investigated during the growing seasons (from May to October) from 2014 to 2016. Seven environmental variables of surface water including depth to water table (DWT), pH, electrical conductivity (EC), total nitrogen (TN), total phosphorus (TP), calcium (Ca) and magnesium (Mg) were measured. Canonical correspondence analysis (CCA) indicated that DWT was the principal environmental variable determining the plant assemblages. A transfer function for inferring DWT based on plant assemblages was developed and refined using four models. The transfer function was shown to have strong predictive power following thorough statistical and ecological tests. When the plant assemblages-based transfer function was applied to a 41 cm peat sequence from Laobaishan bog in the Changbai Mountains region, the reconstructed DWTs were essentially consistent, in the trend and vital details of mire surface wetness, with those inferred from a testate amoebae-transfer function, which has been verified to be robust for reconstructing water table in peatlands in the same region. This study suggests that the mire plant assemblages-based transfer function has great potential for quantitative reconstruction of past mire surface wetness, and allows for further research into palaeoclimatology, palaeohydrology and palaeoecology in the East Asian monsoon region using multi-proxy methods.

Keywords: Mire surface wetness, Transfer function, Plant macrofossils, Northeast China, Hydroclimate

1. Introduction

Quantitative reconstruction of palaeoclimate and environmental change has been a priority in palaeoclimatological and palaeoecological research (Turner et al., 2013; Seddon et al., 2014). A practical tool for quantitative reconstruction of past climate and environmental variability is the transfer function (Väliranta et al., 2007; Ghosh et al., 2017). Transfer functions model empirical relationships between contemporary taxa and environmental variables (Wen et al., 2013; Krashevska et al., 2020). Based on uniformitarian principles of the relationships, the developed transfer functions are applied to reconstruct past climate and environment variability quantitatively from palaeoecological taxa (Amesbury et al., 2013; Swindles et al., 2015a) and even predict the trends of taxa shifts in the context of global warming (Mitchell et al., 2008; Tierney et al., 2020). Thus, transfer functions have been viewed to revolutionize palaeoecology (Payne et al., 2012). More advanced statistical techniques have been applied to evaluate the predictive power of transfer functions in extended geographical regions since the first transfer model was developed (Telford and Birks, 2009; Swindles et al., 2015b; Kurina and Li, 2019). Transfer functions are now commonly applied to quantitative reconstruction of past environment and climate changes from different proxies in various archives, especially from fossil data of plants, such as pollen (Cao et al., 2014; Ghosh et al., 2017), phytoliths (Lu et al., 2006) and plant macrofossils (Va¨liranta et al., 2007).

Peatlands are unique and valuable ecosystems owing to their various functions such as storage of carbon, regulation of catchment hydrology, and archives of environmental change (Dise, 2009; Yu et al., 2010). Peatlands hold the equivalent of half the atmospheric carbon and approximately one-tenth global freshwater although they only cover about 3% of the Earth’s land area (Dise, 2009; Xu et al., 2018). The carbon stored in peatlands originated predominantly from incompletely decomposed mire plants, which accumulate sequentially in situ. Thus, peatlands record a wealth of information pertaining to the development of the mire plant assemblages and environmental changes over time, and have become an important archive used to record past and contemporary environmental changes (Chambers and Charman, 2004; H´edl et al., 2017; Kapfer et al., 2017; Zhang et al., 2020). The vegetation succession of

[1] This author contributed equally to this work.

peatlands depends on individual mire plant responses to changes in regional and local conditions (Rydin and Jeglum, 2013). Different types of mire plants grow in different habitats according to variations in wetness, acidity and nutrition (Laine et al., 2018). The plant assemblages may be regulated by climate changes and anthropogenic land-use transformation (Mitchell et al., 2013). These indications of mire plant habitats are recorded by means of plant remains, especially plant macrofossils (＞125 μm) in peatlands. If plant macrofossils are found in a peat sequence, it is probable that their parent plants were growing in situ or very close by (Birks, 2007). In peat sequences, plant macrofossils, which often can be identified to species level, provide precise data on historical vegetation dynamics at a relatively high taxonomic resolution (Mauquoy and Barber, 2002; Väliranta et al., 2012; Mitchell et al. 2013; Piilo et al., 2020).

Researchers have demonstrated the close ecological coupling relationship between plant macrofossils and hydrological factors, for example surface wetness described by depth to water table (DWT), although acidity (pH) and trophic status of peatlands also influence growth of mire plants (Väliranta et al., 2007; Rydin and Jeglum, 2013; Castro et al., 2015). Mire surface wetness had been reconstructed using plant macrofossils in peatlands using qualitative (Barber, 1981) and semi-quantitative technique (Barber, 1994) before the 20th century. Later, several transfer functions between mire plant assemblages and surface wetness were generated and applied to reconstruct past surface wetness quantitatively using a modern calibration dataset mostly in Europe (Väliranta et al., 2007; Birks and van Dinter, 2010; Väliranta et al., 2012; Mitchell et al., 2013) and North America (Thompson et al., 2008). These transfer function models of local or regional scales have provided robust quantitative reconstruction of palaeoenvironment and palaeoclimate based on a sound ecological basis, for example the relationship between living plants and DWT (Väliranta et al., 2012). Nevertheless, different plant species from the same genus might grow in different geographical regions and respond to different environmental variables or have different optima for the same environmental variable, for example DWT (Mauquoy and van Geel, 2010; Yang et al., 2019). The reconstructed environmental variable may have a large deviation when regional-scale plant species not included in their training set are applied (Turner et al., 2013). Hence, the plant-based transfer functions need to be developed and strengthened to be applied at local and regional scales outside of Europe and North America. Furthermore, the performance of transfer functions should be thoroughly tested with statistical and ecological methods before application to fossil data. The need to estimate quantitatively past hydrological and climatic conditions from plant macrofossils with higher precision is becoming increasingly important. In this paper, we aim to (1) investigate whether DWT is the principal environmental variable determining coverage of mire plants in the Changbai Mountains region, Northeast China; (2) develop a transfer function between modern mire plant assemblages and the principal environmental variable; and (3) assess the potential application of a plant-based transfer function in the context of climatic change.

2. Regional setting and study sites

Changbai Mountains in Northeast China are located at the southern edge of temperate peatlands (Fig. 1). Climate in this region is primarily controlled by the East Asian monsoon. Mean annual temperature ranges from 2 to 6 ◦C. Mean monthly temperature ranges from -20 to -15 ◦C in January, and from 17 to 24 ◦C in July, respectively. Mean annual precipitation decreases from 900 to 700 mm from southeast to northwest. More than 60% of precipitation occurs in the growing season (from May to October). With the joint influence of the East Asian monsoon, frozen and volcanic activities, peatlands have developed widely since the Last Glacial Maximum in various landforms, varying from lava platforms, crater lakes to alpine valleys (Xing et al., 2015). The Changbai Mountains region has become one of the key regions for the reconstruction of peat-based palaeoclimate and palaeoenvironment since the Last Glacial Maximum (Hong et al., 2009; Zhou et al., 2010; Zhang et al., 2019, 2020).

Five peatlands, namely Hani (HN), Hanlongwan (HLW), Jinchuan (JC), Xinglong (XL) and Dongfanghong (DFH) in the Changbai Mountains region, were selected for this research. They represent a range of trophic status in peatlands from different latitudes, longitudes and altitudes in the Changbai Mountains region (Fig. 1, Table 1). HN mire is in a meso- to oligotrophic condition with differentiated vegetation zones from the margin to the centre of the mire (Schröder et al., 2007). The forest dominated by *Larix olgensis* at the margin becomes thinner with increasing distance from the mire edge, when shrubs including *Betula ovalifolia*, *Vaccinium uliginosum* and *Ledum palustre* take over. This latter zone is followed by species-rich sedge reeds that again merge into *L. olgensis* forest. The stands close to the river are dominated by *Cornus alba*-shrub or open sedge reed with high tussocks. HLW mire originated from a small marr lake with a diameter of about 500 m. Now the mire surface is occupied by *Carex lasiocarpa, C. limosa, Phragmites australis* and *Sphagnum amblyphyllum*.JC mire and XL mire are open rich fen with various plants species. The dominant plant communities are *B. ovalifolia–C. schmidtii–S. subsecundum*, *C. limosa* and *P. australis–C. pseudocuraica* from the edge of mire to the centre (Ma et al., 2020). DFH mire is in a mesotrophic–oligotrophic state. The vegetation is dominated by *L. olgensis*, *V. uliginosum*, *Eriophorum polystachion*, *C. schmidtii*, *S. magellanicum*, *S. fuscum* and *S. angustifolium*, but is also rich in vascular plants, such as *B. ovalifolia*, *L. palustre*, and *P. australis*. (Liu et al., 2020).

3. Materials and methods

3.1. Investigation of plant assemblages and determination of environmental variables

The investigation plots were selected along hydrological gradients in the above-mentioned five peatlands (HN, JC, HLW, XL and DFH) to ensure dominant mire plant species occur in at least three plots (Fig. 1). The longitude, latitude and altitude of the plot were recorded using a GPS. Investigation of extant plant assemblages was conducted in July or August once every year from 2014 to 2016. An area of 4 m x 4 m quadrats was investigated for woody plants, with 1 m x 1 m quadrat for herbaceous plants and 50 cm x 50 cm quadrats for mosses. The average coverage and height of each plant species in a quadrat and habitat types of each quadrat (hummocks, lawns and hollows) were mainly recorded in situ. More precise species identification was conducted in the laboratory under a stereomicroscope in detail if the plant species was not identified on site. DWT was measured in each quadrat by inserting a 3 cm-diameter plastic tube (with holes at different depths) and then a dry rod was inserted into the tube after 30 min to record the depth. Electrical conductivity (EC) and pH of mire surface water (0–10 cm) were measured using a

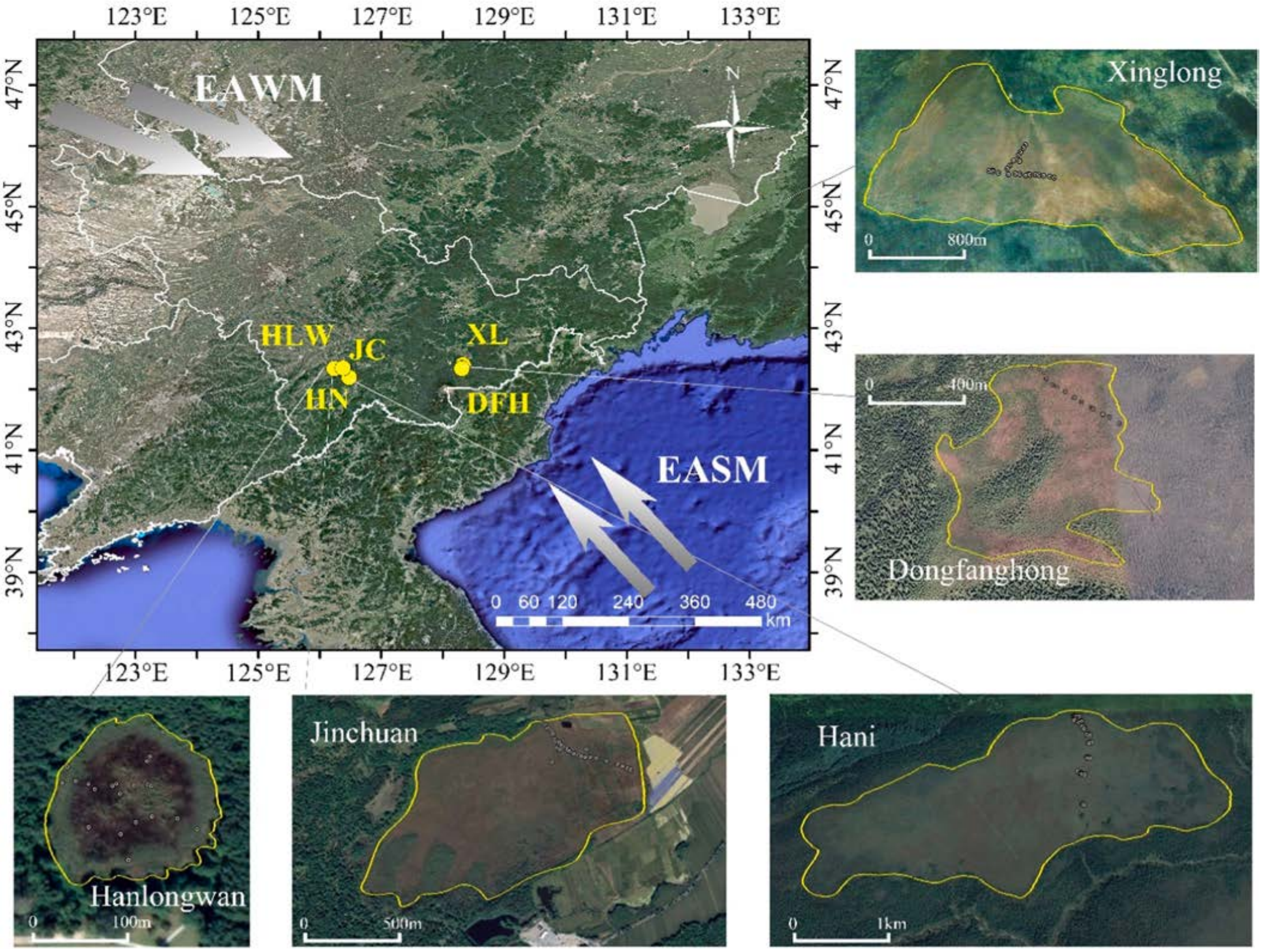

Fig. 1. Location of five peatlands (Hani, Jinchuan, Hanlongwan, Xinglong, Dongfanghong) and investigation plots in each peatland in the Changbai Mountains region. EASM: East Asian summer monsoon, EAWM: East Asian winter monsoon.

Table 1 Details of investigation sites with the ranges of environmental parameters

Site	Hani	Hanlongwan	Jinchuan	Xinglong	Dongfanghong
Code	HN	HLW	JC	XL	DFH
Latitude (°N)	42°11′43″	42°20′18″	42°20′56″	42°24′09″	
	42°20′31″ Longitude (°E)	126°28′44″	126°13′55″	126°22′51″	
	128°19′50″	128°18′45″ Elevation (m a.s.l.)	882	782	616
	694		1146		
Sample number	96	29	58	30	61
DWT (cm)	−3.3-46.8	3.0-25.7	−12.3-21.2	−6.5-30.0	−2.5-58.5
pH	5.20-6.51	4.86-6.38	5.41-6.06	5.50-6.45	4.14-5.81
Conductivity (μS cm^{-1})	13-314	39-431	34-558	24-87	6-82
TN (mg L^{-1})	0.37-10.35	0.52-8.52	0.64-9.25	0.78-4.78	1.33-15.23
TP (mg L^{-1})	0.01-0.29	0.03-0.37	0.03-0.41	0.02-1.83	0.04-2.86
Ca (mg L^{-1})	2.41-30.99	4.14-15.66	5.38-18.84	7.47-30.17	4.10-36.40
Mg (mg L^{-1})	0.40-8.32	0.56-2.75	1.02-5.17	1.41-4.86	0.68-8.76

portable multi-parameter water quality analyzer (YSI 6600, Yellow Spring Instruments, USA). Two extra plastic bottles of surface water samples (100 ml each) were collected nearby each plant quadrat to measure physio-chemical properties, such as total nitrogen (TN), total phosphorus (TP), calcium (Ca) and magnesium (Mg). The concentrations of TN and TP were measured using a SmartChem 140 analyzer (AMS-Westco Scientific Instruments, Inc., Rome, Italy), and the concentrations of Ca and Mg were analyzed using ICP-OES in the Key Laboratory of Geographical Processes and Ecological Security in Changbai Mountains, Ministry of Education, Northeast Normal University. Each environmental variable was measured at least three times during every growing season (from May to October) between 2014 and 2016.

3.2. Data processing and statistical analysis

Two datasets of plant assemblages and environmental variables obtained from the investigation were compiled to explore the relationships between plant composition and seven environmental variables (DWT, pH, EC, TN, TP, Ca, Mg) using canonical correspondence analysis (CCA) with CANOCO 5 (ter Braak and Šmilauer, 2012). Rare species in plant assemblages were downweighted. A Monte Carlo test with 999 permutations was used to test the significance of the environmental variables and ordination axis (Lepš and Šmilauer, 2003).

The transfer function was developed using weighted averaging (WA), weighted averaging partial least squares (WAPLS), modern analogue technique (MAT) and maximum likelihood (ML) with a R (R Development Core Team, 2020) package, the rioja (Juggins, 2013). The weighted averaging model was further divided into weighted averaging with inverse deshrinking (WA-inv), weighted averaging with classical deshrinking (WA-cla), tolerance downweighted weighted averaging with inverse deshrinking (WATOL-inv) and downweighted weighted averaging with classical deshrinking (WATOL-cla). The transfer function performance was assessed in term of R^2, the root mean square error of prediction (RMSEP), average bias and maximum bias. The leave-one-out (LOO) method was used to cross-validate the transfer function performance, and leave-one-site-out (LOSO) method was used to evaluate the impact of clustered sampling (Payne et al., 2012). Segment-wise RMSEPs were calculated to test the potential effect of uneven sampling along the DWT gradient (Telford and Birks, 2011). To identify spatial autocorrelation beyond the scale of inter-site differences, the random neighbourhood exclusion test was used to compare the effect of deleting geographically proximal versus random samples on model performance (Telford and Birks, 2009).

3.3. Quantitative reconstruction and comparison of past mire surface wetness

A 41 cm peat sequence from Laobaishan (LBS) bog (44º06′13″N, 128º02′37″E, 1691 m a.s.l.), located at the top of Zhangguangcai Mountain in the Changbai Mountains region, was applied to assess the potential of the plant assemblages-based transfer function for quantitative reconstruction of past mire surface wetness. Detrended correspondence analysis (DCA) was conducted on fossil plant assemblages of the LBS peat sequence. DWTs of the LBS peat sequence were quantitatively reconstructed applying the transfer function developed in this study. For comparison, DWTs in this sequence were also inferred with a well-developed transfer function between testate amoebae and DWT suitable for this region (Qin et al., 2021).

4. Results

4.1. The environmental variables

The details of investigation sites with the ranges of the environmental variables are shown in Table 1. The 55 kinds of mire plants that were investigated responded widely to seven physiochemical variables of mire surface water (Fig. 2; Table 2). In total, the DWT ranged from -12.3 cm to 58.5 cm, while the mire plants were adapted to acid to neutral water environments. Concentrations of Ca and Mg, as well as EC of mire surface water fluctuated from one to two orders of magnitude. Concentrations of TN changed from 0.37 mg L^{-1} to 15.23 mg L^{-1} while concentrations of TP ranged from 0.01 mg L^{-1} to 2.86 mg L^{-1}. Large changes in TN and TP concentrations indicates these peatlands are in different trophic level from oligotrophic, mesotrophic to eutrophic status. The relatively great fluctuation ranges of the environmental variables (such as DWT, TN, TP) may be related not only to various habitats involved in investigation from hummocks, lawns and hollows within a peatland and among peatlands with different trophic types, but also to various weather and climatic conditions at the time of sampling from May to October each year from 2014 to 2016.

4.2. Ordination analysis

Canonical correspondence analysis showed relatively even distribution of the investigated sites and considerable representativeness of different peatlands (Fig. 2A). In addition, CCA illustrated at least two groups of environmental gradients strongly determined plant assemblages (Fig. 2B). One was strongly correlated with surface wetness (DWT) as axis 1 indicated. Different types of plants were primarily separated along axis 1 among and within different peatlands. For example, species commonly inhabiting dry conditions with higher DWTs, such as *L. palustre*, *S. fuscum*, *S.* sect. *Acutifolia*, *Polytrichum strictum*, were on the right, whereas species in wet conditions, including *Menyanthes trifoliata* and *Scheuchzeria palustris* were toward the left end of axis 1 (Fig. 2B). The other group of environmental gradients, pointed out by axis 2, was a combination of pH, the concentrations of Ca and Mg, and to some extent correlated with nutrient availability (TN, TP). The CCA results showed that DWT had greater marginal

Table 2 Full names and abbreviation of investigated mire plant taxa.

Full name	Abbreviation	Full name	Abbreviation
Aulacomnium palustre	*Aul. pal*	*Oxycoccus palustris*	*O. pal*
Betula ovalifolia	*B. ova*	*Phragmites australis*	*P. aus*
Calamagrostis angustifolia	*C. ang*	*Polygonum* spp.	*Polygonum*
Calliergonella cuspidata	*C. cus*	*Polytrichum strictum*	*P. str*
Caltha palustris	*Cal. pal*	*Potentilla fruticosa*	*P. fru*
Carex lasiocarpa	*C. las*	*Rhododendron parvifolium*	*R. par*
Carex limosa	*C. lim*	*S. amblyphyllum*	*S. amb*
Carex meyeriana	*C. mey*	*S. fallax*	*S. fal*
Carex pseudocuraica	*C. pse*	*S. fuscum*	*S. fus*
Carex rhynchophysa	*C. rhy*	*S. imbricatum*	*S. imb*
Carex schmidtii	*C. sch*	*S. magellanicum*	*S. mag*
Carex spp.	*Carex*	*S. palustre*	*S. palu*
Carex tenuiflora	*C. ten*	*S. sect. Acutifolia*	*S. sect. Acu*
Chamaedaphne calyculata	*C. cal*	*S. sect. Cuspidata*	*S. sect. Cus*
Comarum palustre	*Com. pal*	*S. sect. Subsecunda*	*S. sect. Sub*
Dicranum scoparium	*D. sco*	*Salix myrtilloides*	*S. myr*
Drepanocladus aduncus	*D. adu*	*Salix rosmarinifolia*	*S. ros*
Equisetum hyemale	*E. hye*	*Sanguisorba tenuifolia*	*S. ten*
Eriophorum polystachion	*E. pol*	*Saussurea* spp.	*Saussurea*
Eriophorum vaginatum	*E. vag*	*Scheuchzeria palustris*	*Sch. pal*
Gentiana spp.	*Gentiana*	*Scirpus* spp.	*Scirpus*
Iris spp.	*Iris*	*Smilacina trifolia*	*S. tri*
Juncus effusus	*J. eff*	*Sphagnum* spp.	*Spha*
Larix olgensis	*L. olg*	*Spiraea salicifolia*	*S. sal*
Ledum palustre	*L. pal*	*Thelypteris palustris*	*T. pal*
Lonicera edulis	*L. edu*	*Typha angustifolia*	*T. ang*
Lythrum salicaria	*Lythrum*	*Vaccinium uliginosum*	*V. uli*
Menyanthes trifoliata	*M. tri*		

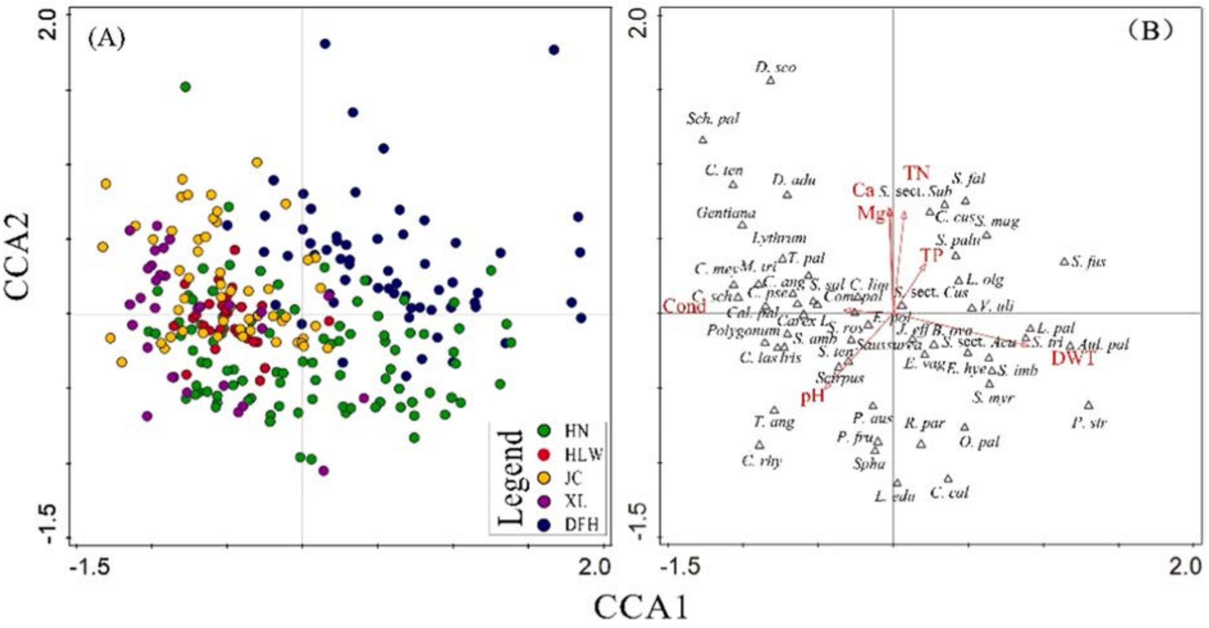

Fig. 2. Samples (Fig. 2A) / Species (Fig. 2B) -environmental variables ordination plot of canonical correspondence analysis (CCA) based on all samples. Different colors represented different peatlands (Fig. 2A). Full species names (Fig. 2B) were given in Table 2.

effects than other six environmental variables (Table 3). Although axis 1 (eigenvalue = 0.355) and axis 2 (eigenvalue = 0.174) explained 11.6% of the variance in total (Table 3), DWT alone explained 3.6% of variability in total species, while other individual variables contributed less of the variance (<2.5% individually). The Monte Carlo permutation test showed that CCA axis 1 has a significant effect on the plant assemblages (p = 0.001, 999 random permutations). Ordination analysis provides a basis for the development of transfer functions between plant assemblages and DWT.

4.3. Transfer function development and performance

The performance and cross-validation results of four types of models are shown in Table 4. All of the models with the full dataset had relatively large RMSEP with relatively small R^2 when LOO cross validation or LOSO cross validation was applied. After model optimization by removing the outliers greater than one-fifth of the measured DWT range in the training set, all transfer function models performed better with a considerable increase in R^2 (14.27%–37.39%) and decrease in RMSEP (24.37%–42.89%), especially with reduction of maximum bias (Table 4; Fig. 3). The optimized models showed better predictive power in term of R^2 (almost greater than 0.5), RMSEP as well as average and maximum biases, especially with LOO cross validation. The WATOL-inv model performed best among four WA models and was therefore selected to further statistical test. The four types of transfer function models (WATOL-inv, WAPLS, ML and MAT) performed differently in terms of alternative performance measures. For R^2, the order of best performance was MAT > ML > WAPLS ≈WATOL-inv, but the difference was relatively small. For RMSEP, the order changed into MAT > WATOL-inv > WAPLS > ML. In terms of the average and maximum biases, the WATOL- inv model generally performed best.

4.4. Mire surface wetness of the LBS peat sequence

The plant macrofossils diagram of the LBS peat sequence is shown in Fig. 4. Significant correlation between axis 1 scores obtained from DCA on fossil plant assemblages (Fig. 5A) and inferred DWTs from the plant assemblages-based transfer function (Fig. 5B) ($r^2 = 0.58$, $p < 0.01$, n = 41) provided good analogues for the plants in the contemporary training sets and fossil assemblages. This indicated that the plant assemblages- based function can be used on the LBS peat sequence. This was also shown by the significant correlation ($r^2 = 0.63$, $p < 0.01$, n = 41) between the inferred DWTs from the plant assemblages-based transfer function and the testate amoebae-based transfer function (Fig. 5C).

5. Discussion

5.1. The principal environmental variables determining growth of mire plants

The selected 55 mire plants (11 species of trees and shrubs, 29 species of graminoids and other herbs, and 15 species of mosses from genus to species) from five peatlands represent the common mire plant taxa in the Changbai Mountains region (Fig. 2; Table 2). It is noteworthy that most species in this region are the same as those that grow in the Greater Khingan Mountains and Lesser Khingan Mountains, which are representative of temperate montane peatlands, Northeast China, with woody plant *V. oxycoccus*, herbcaeous assemblages composed of *E. vaginatum, M. trifoliata,* and mosses *(S. palustre, Aulacomnium palustre,* and *S. fuscum)* (Lou et al., 2018). Although some plants are different at the level of species, they may be the same at the level of genus with mire plants in North America (Goud et al., 2018) or Europe under the control of continental climate (Mauquoy and Barber, 2002; Bragazza, 2006). Moreover, some mire plants in the Changbai Mountains region are also comparable to those in boreal peatlands in the regions influenced by oceanic climate (Mauquoy and van Geel, 2010; Jiroušek et al., 2013). This suggests most taxa have broad geographic distribution.

The relationship of mire plants and environmental variables suggested that DWT was the principal environmental variable determining compositions and distribution of plant assemblages (Fig. 2B). This was also evidenced by the highest marginal effect and the lowest variance inflation factor (VIF) of DWT among seven environmental variables (Table 3). It is reasonable that among three environmental gradients (wetness, acidity and nutrition) DWT is overriding in determining compositions of mire plant assemblages (Jiroušek et al., 2013; Potvin et al., 2015). Peatlands are kinds of transitional, amphibious ecosystems with special habitat between open water and terrestrial ecosystems (Rydin and Jeglum, 2013). The waterlogged, often poorly aerated condition is a key feature of peatlands. Thus, DWT directly influences colonization and growth of mire plant species, further compositions and succession of mire plant communities, as well as accumulation and decomposition of peat (Malhotra et al., 2016; Kokkonen et al., 2019). Following DWT, acidity (pH, Ca and Mg) and nutrient availability were subordinately responsible for the growth of mire plants (Fig. 2B, Table 3). The results are consistent with previous studies conducted in the peatlands of Europe and North America (Rydin and Jeglum, 2013; Mitchell et al., 2013).

Table 3 Variance inflation factors and marginal effect of seven environmental variables in CCA.

Variables	DWT	pH	Cond	TN	TP	Ca	Mg
Variance inflation factor	1.0620	1.1781	1.2653	1.7366	1.7673	8.0022	7.7524
Percentage variance	3.6%	2.3%	1.5%	1.7%	1.2%	1.4%	1.4%
Significance level	0.002	0.002	0.002	0.002	0.002	0.002	0.002

Table 4 Comparison of prediction performance of different models for DWT in cross validation. Data in normal are from all samples included in training sets; Data in parentheses are outliers filtered out. LOO: leave-one-out cross validation; LOSO: leave-one-site-out cross validation. WA-inv: weighted averaging inverse deshrinking; WA-cla: weighted averaging with classical deshrinking; WATOL-inv: tolerance downweighted weighted averaging inverse deshrinking; WATOL-cla: downweighted weighted averaging with classical deshrinking; WAPLS: weighted averaging partial least squares; ML: maximum likelihood; MAT: modern analogue technique.

	RMSEP$_{LOO}$	R^2_{LOO}	Average Bias$_{LOO}$	Maximum Bias$_{LOO}$	RMSEP$_{LOSO}$	R^2_{LOSO}	Average Bias$_{LOSO}$	Maximum Bias$_{LOSO}$
WA-inv	10.08	0.45	0.01	28.68	11.34	0.35	0.46	30.29
	(7.06)	(0.63)	(-0.01)	(10.47)	(8.22)	(0.54)	(0.19)	(11.96)
WA-cla	14.02	0.46	0.02	25.62	17.27	0.37	0.23	27.06
	(8.49)	(0.64)	(0.00)	(5.69)	(10.86)	(0.57)	(0.03)	(8.24)
WATOL-inv	10.13	0.45	0.06	28.15	11.86	0.32	0.32	30.53
	(6.99)	(0.64)	(0.05)	(10.69)	(8.41)	(0.51)	(0.20)	(12.71)
WATOL-cla	13.40	0.45	0.08	24.67	17.60	0.34	0.72	27.84
	(8.26)	(0.64)	(0.07)	(6.41)	(11.10)	(0.53)	(-0.18)	(8.70)
WAPLS	10.14	0.45	−0.86	27.70	11.43	0.35	−0.63	29.41
	(7.43)	(0.66)	(-0.49)	(14.70)	(8.61)	(0.57)	(-0.36)	(16.40)
ML	13.47	0.46	1.28	27.08	17.75	0.24	−1.58	26.81
	(7.77)	(0.74)	(0.96)	(5.77)	(12.05)	(0.45)	(-1.26)	(5.38)
MAT	9.25	0.54	0.68	23.06	11.64	0.36	2.15	29.56
	(6.08)	(0.77)	(0.46)	(16.8)	(7.92)	(0.59)	(1.91)	(22.93)

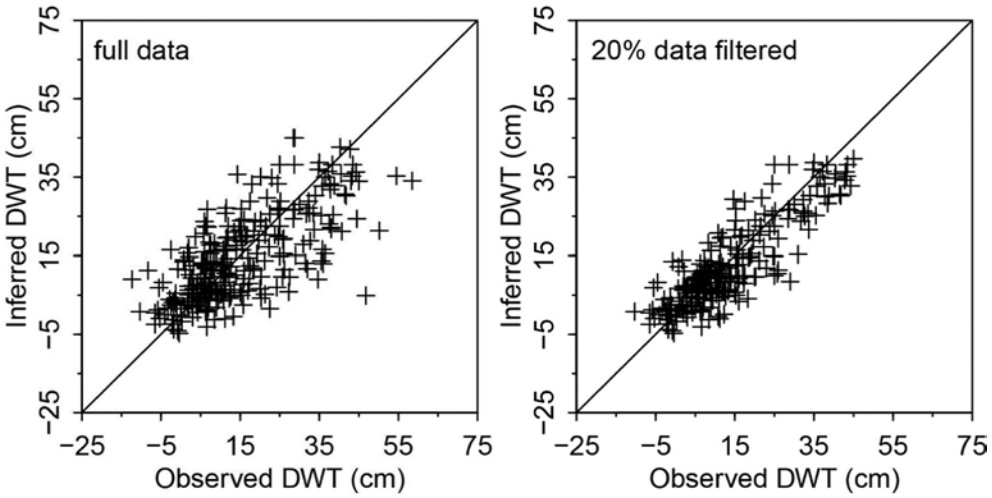

Fig. 3. Comparison of observed DWT and inferred DWT by the MAT model between full data and 20% filtered data. The 1:1 line was plotted for reference.

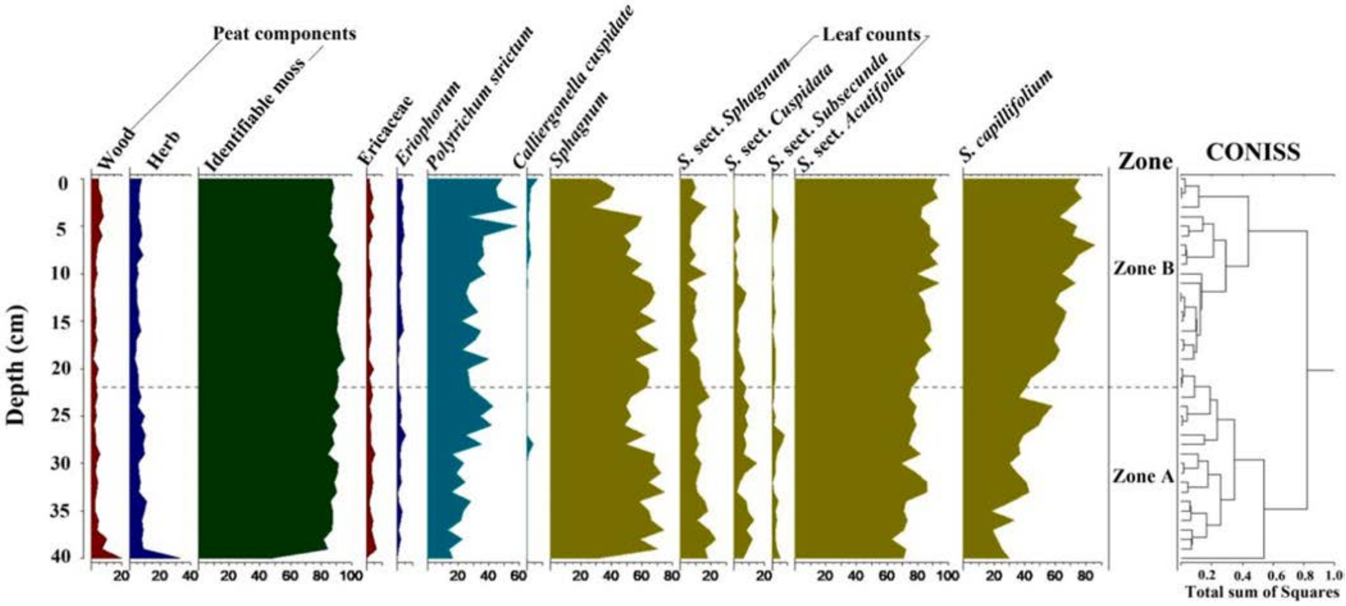

Fig. 4. Diagram for the plant macrofossils in the LBS peat sequence.

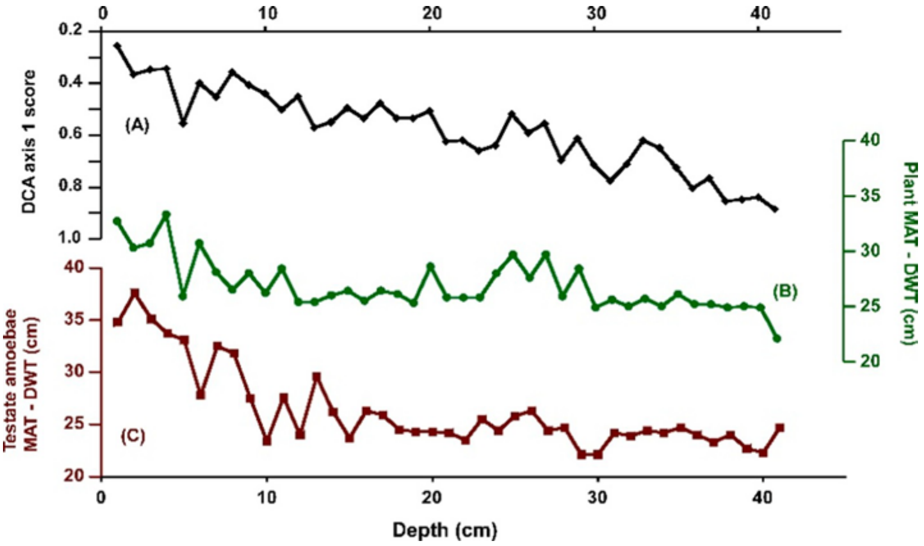

Fig. 5. (A) DCA axis 1 score: axis 1 score obtained from detrended correspondence analysis (DCA) on plant macrofossils; (B) Plant MAT - DWT: reconstructed DWT from plant macrofossils using the MAT model; (C) Testate amoebae MAT - DWT: reconstructed DWT from testate amoebae using the MAT model.

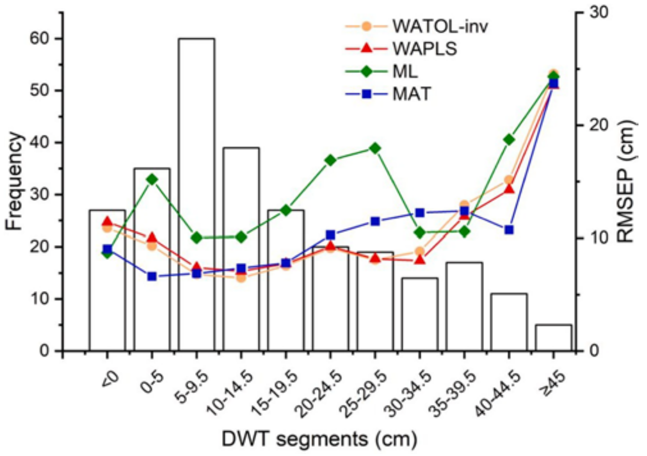

Fig. 6. Frequency and root mean square error of prediction (RMSEP) in different DWT segments of four types of models.

5.2. Statistical test of performance of mire plant assemblages-based function model

Statistical testing of transfer function models is fundamental to make the output of transfer functions meaningful (Payne et al., 2012). Segment analysis was applied to assess the effect of uneven sampling along the water table gradient on model performance (Telford and Birks, 2011). The segment-wise RMSEP (RMSEPSW) from testate amoebae-based transfer functions was also employed for comparison owing to less available segment analysis data from previous plant assemblages-based function models. After the removal of outliers with high residual values (Table 4), RMSEPSW in most DWT segments were 7–10 cm for the WATOL-inv and WAPLS models, 7–12 cm for the MAT model, and 10–17 cm for the ML model, respectively (Fig. 6). Although for all of the models, the RMSEPSW in most DWT segments were comparable to those in the published testate amoebae-based transfer functions (Amesbury et al., 2013; Li et al., 2015; Amesbury et al., 2016), the predictive power varied among models and in different DWT segments. The WATOL-inv and WAPLS models, which have almost the same curve, have the strongest predictive power owing to the lowest RMSEP_{SW}. Compared to the WATOL-inv and WAPLS models, the MAT model has quite similar RMSEP_{SW} at a DWT range of 5–20 cm, 35–40 cm and above 45 cm, and relatively high RMSEP_{SW} at a DWT range of 20–35 cm, as well as lower RMSEP_{SW} at DWT segments below 5 cm and 40–45 cm with relatively fewer samples. The ML model has the poorest predictive power because its RMSEP_{SW} exceeded the standard deviation of the water table (14.9 cm) in most DWT segments (Mitchell et al., 2013), particularly in the segment of DWT over 40 cm. Similarly, testate amoebae-based transfer functions also have relatively poor performance in dry conditions (Swindles et al., 2015b; van Bellen et al., 2014). This may be attributed to insufficient time for water equilibration in the driest sites with low saturated hydraulic conductivity, which may artificially induce the bias between real and measured DWTs (Swindles et al., 2015b; Zhang et al., 2017).

The LOSO test showed that the clustered sampling did overestimate the performance of these transfer function models (Telford and Birks, 2009). All of the models showed an apparent decrease in R^2_{loso} and increase in $\mathrm{RMSEP}_{\mathrm{loso}}$ when LOSO cross validation was used (Table 4), particularly for the ML model. This suggested that inter-site differences in plant assemblages have a considerable impact on performance of the transfer function (Telford and Birks, 2009). Another reason for performance deterioration in LOSO cross-validation might be that the large difference of sample number among five peatlands changed the size of the training set during the process of leave-one-site-out validation. For example, if the samples from Hani peatland were left out, around one-third of samples became excluded from the training set. Thus, the decrease of RMSEP would be unsurprising. However, in consideration that the $\mathrm{RMSEP}_{\mathrm{LOSO}}$ of all models were less than the standard deviation of measured DWT, all transfer function models built here still had their predictive power.

The effect of spatial autocorrelation on performance of the transfer function models is shown in Fig. 7. The results indicated that all models were robust to random sample deletion. The R^2 of all models remained stable, or only slightly decreased, even if more than half of samples were randomly deleted from the training set. When samples from geographical neighbourhoods were deleted, R^2 of all the models apparently decreased, but were still higher than when environmentally similar samples were deleted. This indicated that all the transfer models were affected, to different extents, by the spatial autocorrelation of the training set, which resulted from inter-site differences in plant assemblages rather than that the reconstructed DWTs were spatially autocorrelated. It is surprising that the MAT model, which is believed to be the most susceptible to spatial autocorrelation (Thompson et al., 2008), showed similar performance with WATOL-inv model in robust- ness to autocorrelation. This might be because that the results of spatial autocorrelation tests were complicated by the clustered nature of the training set (Amesbury et al, 2013). During the process of geographical neighbourhood deletion, it is always the case that all samples from certain sites within the geographical distance would be deleted. The resulting fewer samples in the training set can cause a decrease of R^2. However, since DWT of one site is independent of those from other sites, the remaining samples representing replicated microhabitats still had ability to model the ecological characteristics of most plant species.

5.3. Ecological assessment of mire plant assemblages-based function model

The potential of mire plant assemblages-based function for quantitative reconstruction of past mire surface wetness was assessed by comparing the DWTs of dominant mire plants in this study to the investigated DWTs in previous studies. The results from investigation on site (Fig. 8) and the model (Fig. 9) showed that most mire plants had similar DWT optima and tolerance to those in previous studies that were conducted in other temperate regions (Mauquoy and van Geel, 2010; Vicherová et al., 2017; Lou et al., 2018). For example, dwarf shrubs were generally found with DWT between 20 cm and 50 cm (Mauquoy and van Geel, 2010); *E. vaginatum*, with a wide range of moisture conditions (0–30 cm), inhabited most of the gradient; *S. palustre* settled at the sites (hollow or lawn) with lower DWT (～0 cm) (Bragazza, 2006); dry-preferring *Sphagnum* (for example *S.* section *Acutifolia*) and *P.* strictum preferred relatively dry conditions with greater DWT; wet-preferring *Sphagnum* (*S. fallax*, *S.* sect *Cuspidata* and *S.* sect *Subsecunda*) were in the hollow or lawn (Blaauw et al., 2004; Mauquoy and van Geel, 2010; Yang et al., 2019; Feurdean et al., 2019). However, several plant species had different adaptations to DWT compared to other research; for example, *Equisetum hyemale*, a variant species of *E. fluviatile*, investigated in this study grew on the hummocks with relatively high DWT. This is different from *E. fluviatile*, which usually inhabits hollow and lawn with relatively lower DWT (Mauquoy and van Geel, 2010).

In addition, different species of mire plants adapted to different fluctuation ranges of water table. The plant species (for example, *S. amblyphyllum*) that respond much more sensitively to variation in DWT have narrow fluctuation ranges of water table. Some species, including *E. vaginatum*, *V. oxycoccus*, *M. trifoliata*, have wider fluctuation ranges of water table than in previous research (Fig. 9) (Mauquoy and van Geel, 2010; Bu et al., 2011; Lou et al., 2018). This may be related to great fluctuation of DWT in the surface of the investigated peatlands during the growing season from 2014 to 2016 (Table 1). The relevant mechanism for this has been addressed by Lamentowicz et al. (2019), showing that the establishment of mire plants on peatlands may be a result of DWT extrema and their period of occurrence. Although absolute values and fluctuation ranges of DWTs may be much greater than in previous research, the optimal values of most mire plant species adapting to DWT were not significantly influenced. For example, *E. vaginatum* with a wide range of water table (0.2–41.5 cm) occupied most of the gradient from hollow through lawn to hummock; however, its optimum value (14.8 cm) was consistent with previous studies (14 cm) (Blaauw et al., 2004; Väliranta et al., 2012). The above analysis indicates that the mire plant assemblages-based function has great potential for reconstructing past surface wetness of mires in the Changbai Mountains region, and even to extend to peatlands with similar plant compositions in other regions.

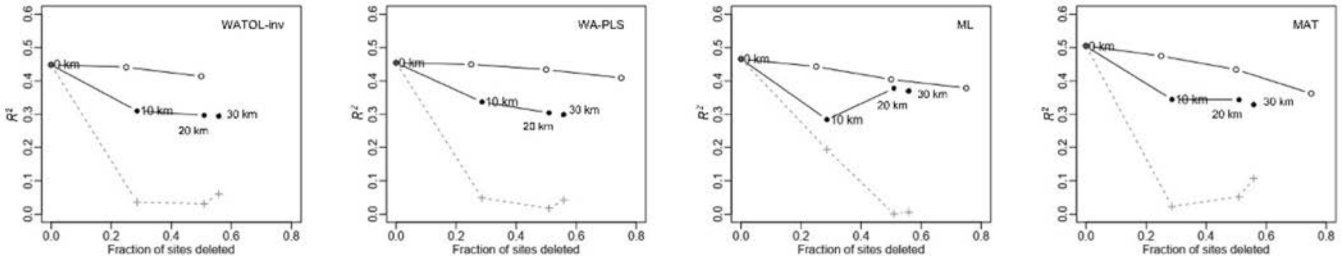

Fig. 7. The effect of spatial autocorrelation on performance (R^2) of four types of models.

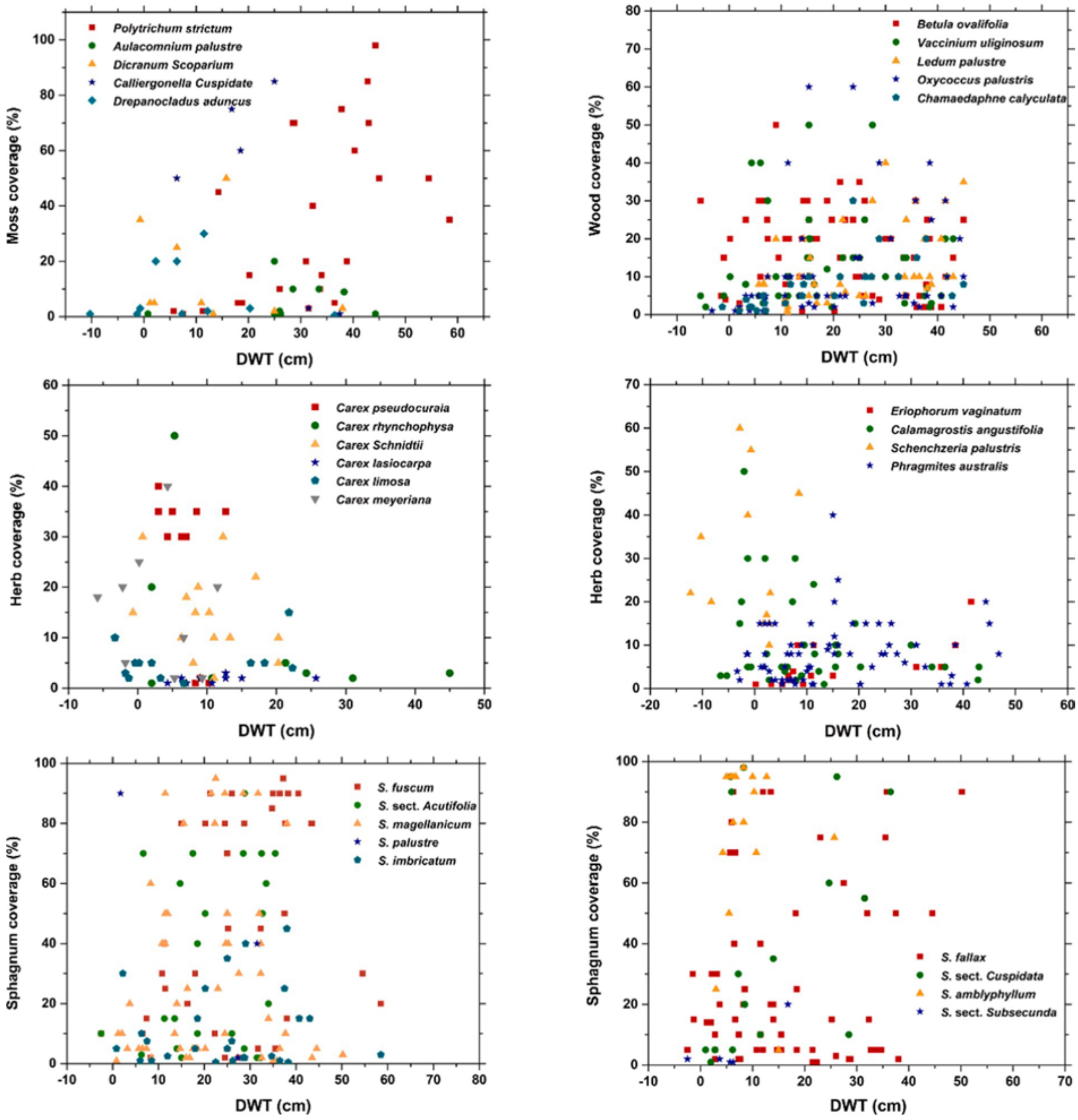

Fig. 8. Scatter plots of investigated DWT and coverage of selected moss, herb and wood species.

5.4. Quantitative reconstruction of past mire surface wetness by a mire plant assemblages-based function

The DWTs of LBS peat sequence from bottom to top reconstructed by the mire plant assemblages-based transfer function have shown a very similar trend ($r^2 = 0.63$, $p < 0.01$, $n = 41$) to increased DWTs from a testate amoebae-based transfer function (Fig. 5), which has been widely applied to reconstruct past water tables in peatlands with relatively high accuracy and precision (Mitchell et al., 2008; Amesbury et al., 2016; Zhang et al., 2017; Qin et al., 2021). This suggests that mire plant assemblages-based transfer function is comparable to the testate amoebae-based transfer function in terms of reconstructed DWT. However, there is still some inconsistency in the magnitude of reconstructed DWT between the two curves, especially for the top 8 cm. The inconsistency was also found in reported studies (Väliranta et al., 2012; Mitchell et al., 2013). The reasons for the divergence may be attributed to different ecological habits and physiological characteristics of mire plants and testate amoebae. Testate amoebae have a very rapid life cycle with ten generations a year as a group of unicellular shelled microorganisms (Charman et al., 2000; Mitchell et al., 2008). Accordingly, testate amoebae can record more rapid variability of mire surface wetness at a seasonal level. However, most mire plants response to variability in DWT lags behind testate amoebae because they are perennial and can tolerate a relatively wide range of DWT fluctuation. Thus, the DWT inferred from plant macrofossils may represent the average condition at an annual level. Swindles et al. (2015a) also pointed out that estimated DWT based on the testate amoebae community reflected directional changes, with poor representations of real mean or median water table magnitudes for the study sites. Amesbury et al. (2016) suggested that interpretation of transfer function models should focus on shifts of mire surface wetness, avoiding potentially inaccurate conclusions relating to specific DWT. Compared to testate amoebae, plant macrofossils have their own advantages in quantitively reconstructing past mire surface wetness based on total trend and major shifts in DWT, especially for long-term time scales, for example the DWTs since the last deglaciation. Just as mentioned above, plant macrofossils are indicators of original mire plant communities at the time of peat accumulation (Barber et al., 1994; Väliranta et al., 2012). Once the plant macrofossils in the peat sequences from this region are identified, the past surface wetness in the peatlands can be derived based on the quantitative relationship indicated by the transfer function between water table dynamics and compositions of the current mire flora. This allows for further research into past climate and hydrological changes since the last deglaciation.

6. Conclusions

(1) Datasets of mire plant assemblages and environmental variables were compiled from the Changbai Mountains region, Northeast China. Mire surface wetness (described as DWT) has been shown to be the principal variable that determined mire plant community composition, which provided a basis for the development of transfer functions between plant assemblages and DWT.
(2) The mire plant-DWT transfer function was successfully developed using four different types of models. The MAT model performed best although all of the models had their predictive power through a combination of statistical tests. The similar optima and tolerance of DWTs of dominant plant species to previous studies further indicated the potential of the plant assemblages-based function for reconstruction of mire surface wetness.
(3) Reconstructed DWTs of the LBS peat sequence by a plant assemblages-based transfer function showed high consistency in the trend and main shifts of surface wetness with those reconstructed by a testate amoebae-based transfer function. This demonstrated that the plant assemblages-based function has a great potential for quantitative reconstruction of past mire surface wetness.
(4) The modern calibration database built in this study fills a geographic gap with respect to quantitative relationships between mire plant assemblages and mire surface wetness in the temperate montane regions controlled by the East Asian monsoon. The quantitative reconstruction of past mire surface wetness is of great significance in vegetation science, community ecology, geographical modelling, global change biology, and especially in palaeoclimatology and palaeoecology.

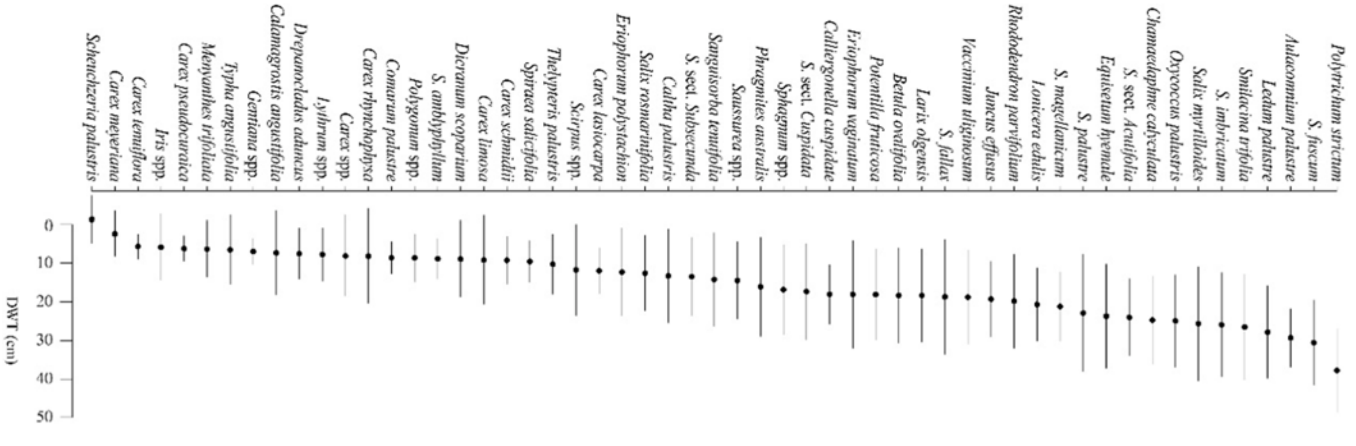

Fig. 9. Optima and tolerance of investigated species for DWT derived from the WA model.

Authorship contribution statement

Qiannan Yang: Investigation, Writing – original draft. Hongkai Li: Methodology. Hongyan Zhao: Conceptualization, Writing – review & editing. Frank M. Chambers: Writing – review & editing. Zhaojun Bu: Investigation. Edith Bai: Guangyuan Xu:

Investigation.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

The authors thank Chuantao Song, Sipeng Zhang, Hanxiang Liu, Fangyuan Chen, Zheng Han, Chenxi Duan, Xiaokang Zhou, Xuanqi Zhao, Yiwen Cao, and Cong Xu for their help in the fieldwork. We are grateful to Xinhua Zhou, Na Xu, Yanmin Dong, Jingjing Sun, Yangyang Xia, and Jicheng Ma for their assistance with laboratory chemical analysis.

Funding

This work was supported financially by National Natural Science Foundation of China (No. 41471165, 41771217), Ministry of Science and Technology of China (2016YFC0500407), Jilin Provincial Department of Science and Technology (20190101025JH) and Jilin Provincial Department of Education (2016506).

References

Amesbury, M.J., Mallon, G., Charman, D.J., Hughes, P.D.M., Booth, R.K., Daley, T.J., Garneau, M., 2013. Statistical testing of a new testate amoeba-based transfer function for water-table depth reconstruction on ombrotrophic peatlands in north-eastern Canada and Maine, United States. J. Quat. Sci. 28 (1), 27–39. https://doi. org/10.1002/jqs.2584.

Amesbury, M.J., Swindles, G.T., Bobrov, A., Charman, D.J., Holden, J., Lamentowicz, M., Mallom, G., Mazei, Y., Mitchell, E.A.D., Payne, R.J., Roland, T.P., Turner, T.E., Warner, B.G., 2016. Development of a new pan-European testate amoeba transfer function for reconstructing peatland palaeohydrology. Quat. Sci. Rev. 152, 132–151. https://doi.org/10.1016/j.quascirev. 2016.09.024.

Barber, K.E., 1981. Peat stratigraphy and climatic change: a palaeoecological test of the theory of cyclic peat bog regeneration. Cumbria England 219. https://doi.org/ 10.1016/j.quaint.2012.05.043.

Barber, K.E., Chambers, F.M., Maddy, D., Stoneman, R., Brew, J.S., 1994. A sensitive high-resolution record of late-Holocene climatic change from a raised bog in northern England. Holocene 4 (2), 198–205. https://doi.org/10.1177/095968369400400209.

Birks, H.H., 2007. Plant Macrofossil Introduction, in: Smol, J. P., Birks, H. J. B., Last, W.M. (Eds.), Tracking Environmental Change Using Lake Sediments. Volume 3: Terrestrial, Algal, and Siliceous Indicators. Kluwer Academic Publishers, Dordrecht, pp. 49–65. https://doi.org/10.1016/B978-0-12-409548-9.10499-3.

Birks, H.H., Van Dinter, M., 2010. Lateglacial and early Holocene vegetation and climate gradients in the Nordfjord - Ålesund area, western Norway. Boreas 39, 783–798. https://doi.org/10.1111/j.1502-3885.2010.00161.x.

Blaauw, M., van Geel, B., van der Plicht, J., 2004. Solar forcing of climatic change during the mid-Holocene: indications from raised bogs in the Netherlands. Holocene 14 (1), 35–44. https://doi.org/10.1191/0959683604hl687rp.

Bragazza, L., 2006. A decade of plant species changes on a mire in the Italian Alps vegetation-controlled or climate-driven mechanisms. Clim. Change 77 (3-4), 415–429. https://doi.org/10.1007/s10584-005-9034-x.

Bu, Z.J., Rydin, H., Chen, X., 2011. Direct and interaction-mediated effects of environmental changes on peatland bryophytes. Oecologia 166 (2), 555–563. https://doi.org/10.1007/s00442-010-1880-1.

Cao, X.Y., Herzschuh, U., Telford, R.J., Ni, J., 2014. A modern pollen - climate dataset from China and Mongolia: Assessing its potential for climate reconstruction. Rev. Palaeobot. Palynol. 211, 87–96. https://doi.org/10.1016/j.revpalbo.2014.08.007.

Castro, D., Souto, M., Garcica-Rodeja, E., Pontevedra-Pombal, X., Fraga, M.I., 2015. Climate change records between the mid- and late Holocene in a peat bog from Serra do Xistral (SW Europe) using plant macrofossils and peat humification analyses. Palaeogeogr. Palaeoclimatol. Palaeoecol. 420, 82–95. https://doi.org/10.1016/j. palaeo.2014.12.005.

Chambers, F.M., Charman, D.J., 2004. Holocene environmental change: contributions from the peatland archive. Holocene 14 (1), 1–6. https://doi.org/10.1191/ 0959683604hl684ed.

Charman, D.J., Hendon, D., Woodland, W.A., 2000. The identification of testate amoebae (Protozoa: Rhizopoda) in peats. QRA technical guide no. 9. https://doi.org/ 10.1016/j.quascirev.2004.03.008.

Dise, B.N., 2009. Peatland response to global change. Science 326 (5954), 810–811. https://doi.org/10.1126/science.1174268.

Feurdean, A., Gałka, M., Florescu, G., Diaconu, A.-C., Tant¸au, I., Kirpotin, S., Hutchinson, S.M., 2019. 2000 years of variability in hydroclimate and carbon accumulation in western Siberia and the relationship with large-scale atmospheric circulation: a multi-proxy peat record. Quat. Sci. Rev. 226, 1–15. https://doi.org/ 10.1016/j.quascirev.2019.105948.

Ghosh, R., Bruch, A.A., Portmann, F., Bera, S., Paruya, D.K., Morthekai, P., Ali, S.N., 2017. A modern pollen - climate dataset from the Darjeeling area, eastern Himalaya: assessing its potential for past climate reconstruction. Quat. Sci. Rev. 174, 63–79. https://doi.org/10.1016/j.quascirev.2017.09.002.

Goud, E.M., Watt, C., Moore, T.M., 2018. Plant community composition along a peatland margin follows alternate successional pathways after hydrologic disturbance. Acta Oecologica 91, 65–72. https://doi.org/10.1016/j.actao.2018.06.006.

Hédl, R., Bernhardt-Römermann, M., Grytnes, J.-A., Jurasinski, G., Ewald, J., 2017. Resurvey of historical vegetation plots: a tool for understanding long-term dynamics of plant communities. Appl. Veg. Sci. 20 (2), 161–163. https://doi.org/10.1111/

avsc.12307.

Hong, B., Liu, C.Q., Lin, Q.H., Shibata, Y., Leng, X.T., Wang, Y., Zhu, Y.X., Hong, Y.T., 2009. Temperature change recorded by $\delta^{18}O$ in Hani peat since 14000 a BP. Sci. China Ser. D Earth Sci. 39, 626–637. https://doi.org/10.1007/s11430-009-0086-z.

Jiroušek, M., Poulíčková, A., Kintrová, K., Opravilová, V., Hájková, P., Rybníček, K., Kočí, M., Bergová, K., Hnilica, R., Mikulášková, E., Králová, Š., Hájek, M., 2013. Long-term and contemporary environmental conditions as determinants of the species composition of bog organisms. Freshw. Biol. 58 (10), 2196–2207.

Juggins, S., 2013. Rioja: analysis of quaternary science data, R Package version 0.8-4.

Kapfer, J., Hédl, R., Jurasinski, G., Kopecký, M., Schei, F.H., Grytnes, J.-A., Bernhardt-Römermann, M., 2017. Resurveying historical vegetation data - opportunities and challenges. Appl. Veg. Sci. 20 (2), 164–171.

Kokkonen, N.A.K., Laine, A.M., Laine, J., Vasander, H., Kurki, K., Gong, J., Tuittila, E.-S., Collins, B., 2019. Responses of peatland vegetation to 15-year water level drawdown as mediated by fertility level. J. Veg. Sci. 30 (6), 1206–1216. https://doi.org/ 10.1111/jvs.12794.

Krashevska, V., Tsyganov, A.N., Esaulov, A.S., Mazei, Y.A., Hapsari, K.A., Saad, A., Sabiham, S., Behling, H., Biagioni, S., 2020. Testate amoeba species- and trait-based transfer functions for reconstruction of hydrological regime in tropical peatland of Central Sumatra, Indonesia. Front. Ecol. Evol. 8 (225) https://doi.org/10.3389/ fevo.2020.00225.

Kurina, I.V., Li, H., 2019. Why do testate amoeba optima related to water table depth vary? Microb. Ecol. 77 (1), 37–55. https://doi.org/10.1007/s00248-018-1202-4.

Laine, A.M., Selänpää, T., Oksanen, J., Seväkivi, M., Tuittila, E.-S., 2018. Plant diversity and functional trait composition during mire development. Mires Peat 21 (02), 1–19.

Lamentowicz, M., Gałka, M., Marcisz, K., Słowin´ski, M., Kajukało-Drygalska, K., Dayras, M.D., Jassey, V.E.J., 2019. Unveiling tipping points in long-term ecological records from Sphagnum-dominated peatlands. Biol. Lett. 15 (4), 20190043. https://doi.org/10.1098/rsbl.2019.0043.

Lepš, J., Smilauer, P., 2003. Multivariate analysis of ecological data using CANOCO. Cambridge University Press, Cambridge, p. (pp. 284).

Li, H., Wang, S., Zhao, H., Wang, M., 2015. A testate amoebae transfer function from Sphagnum-dominated peatlands in the Lesser Khingan Mountains, NE China. J. Paleolimnol. 54 (2-3), 189–203. https://doi.org/10.1007/s10933-015-9846-2.

Liu, C., Bu, Z.-J., Mallik, A., Rochefort, L., Hu, X.-F., Yu, Z., 2020. Resource competition and allelopathy in two peat mosses: implication for niche differentiation. Plant Soil 446 (1-2), 229–242. https://doi.org/10.1007/s11104-019-04350-0.

Lou, Y.J., Gao, C.Y., Pan, Y.W., Xue, Z.S., Liu, Y., Tang, Z.H., Jiang, M., Lu, X.G., Rydin, H., 2018. Niche modelling of marsh plants based on occurrence and abundance data. Sci. Total Environ. 616–617, 198–207. https://doi.org/10.1016/j.scitotenv.2017.10.300.

Lu, H.-Y., Wu, N.-Q., Yang, X.-D., Jiang, H., Liu, K.-B., Liu, T.-S., 2006. Phytoliths as quantitative indicators for the reconstruction of past environmental conditions in China I: phytolith-based transfer functions. Quat. Sci. Rev. 25 (9-10), 945–959. https://doi.org/10.1016/j.quascirev.2005.07.014.

Ma, J.Z., Chen, X., Malik, A., Bu, Z.J., Zhang, M.M., Wang, S.Z., Sundberg, S., 2020. Environmental together with interspecific interactions determine bryophyte distribution in a protected mire of Northeast China. Front. Earth. Sci. 8 (32) https://doi.org/10.3389/feart.2020.00032.

Malhotra, A., Roulet, N.T., Wilson, P., Giroux-Bougard, X., Harris, L.I., 2016. Ecohydrological feedbacks in peatlands: an empirical test of the relationship among vegetation, microtopography and water table. Ecohydrology 9 (7), 1346–1357. https://doi.org/10.1002/eco.1731.

Mauquoy, D., Barber, K., 2002. Testing the sensitivity of the palaeoclimatic signal from ombrotrophic peat bogs in northern England and the Scottish Borders. Rev. Palaeobot. Palynol. 119 (3-4), 219–240. https://doi.org/10.1016/S0034-6667(01)00099-9.

Mauquoy, D., van Geel, B., 2010. Plant macrofossil methods and studies: mire and peat Macros. In: Elias, S.A. (Ed.), Encyclopedia of Quaternary Science, pp. 2315–2336.

Mitchell, E.A.D., Charman, D.J., Warner, B.G., 2008. Testate amoebae analysis in ecological and paleoecological studies of wetlands: past, present and future. Biodivers. Conserv. 17 (9), 2115–2137. https://doi.org/10.1007/s10531-007-9221-3.

Mitchell, E.A.D., Payne, R.J., van der Knaap, W.O., Lamentowicz, Ł., Gąbka, M., Lamentowicz, M., 2013. The performance of single- and multi-proxy transfer functions (testate amoebae, bryophytes, vascular plants) for reconstructing mire surface wetness and pH. Quat. Res. 79 (1), 6–13. https://doi.org/10.1016/j. yqres.2012.08.004.

Payne, R.J., Telford, R.J., Blackford, J.J., Blundell, A., Booth, R.K., Charman, D.J., Lamentowicz, Ł., Lamentowicz, M., Mitchell, E.AD., Potts, G., Swindles, G.T., Warner, B.G., Woodland, W., 2012. Testing peatland testate amoeba transfer functions: appropriate methods for clustered training-sets. Holocene 22 (7), 819–825. https://doi.org/10.1177/0959683611430412.

Piilo, S.R., Korhola, A., Heiskanen, L., Tuovinen, J.-P., Aurela, M., Juutinen, S., Marttila, H., Saari, M., Tuittila, E.-S., Turunen, J., Va¨liranta, M.M., 2020. Spatially varying peatland initiation, Holocene development, carbon accumulation patterns and radiative forcing within a subarctic fen. Quat. Sci. Rev. 248, 106596. https:// doi.org/10.1016/j.quascirev.2020.106596.

Potvin, L.R., Kane, E.S., Chimner, R.A., Kolka, R.K., Lilleskov, E.A., 2015. Effects of water table position and plant functional group on plant community, aboveground production, and peat properties in a peatland mesocosm experiment (PEATcosm). Plant Soil 387 (1-2), 277–294. https://doi.org/10.1007/s11104-014-2301-8.

Qin, Y.M., Li, H.K., Mazei, Y., Kurina, I., Swindles, G.T., Bobrov, A., Tsyganov, A.N., Gu, Y.S., Huang, X.Y., Xue, J.T., Lamentowicz, M., Marcisz, K., Roland, T., Payne, R. J., Mitchell, E.A.D., Xie, S.C., 2021. Developing a continental-scale testate amoeba hydrological transfer function for Asian peatlands. Quat. Sci. Rev. 258, 1–17. https://doi.org/10.1016/j.quascirev.2021. 106868.

R Development Core Team, 2020. R: a language and environment for statistical computing. https://www.r-project.org.

Rydin, H., Jeglum, J.K., 2013. The Biology of Peatlands, second ed. Oxford University press, Oxford, UK.

Schröder, C., Thiele, A., Wang, S.Z., Bu, Z.J., Joosten, H., 2007. Hani mire – A percolation mire in Northeast China. Peatland Int. 2, 20–24.

Seddon, A.W.R., Mackay, A.W., Baker, A.G., Birks, H.J.B., Breman, E., Buck, C.E., Ellis, E. C., Froyd, C.A., Gill, J.L., Gillson, L., Johnson, E.A., Jones, V.J., Juggins, S., Macias- Fauria, M., Mills, K., Morris, J.L., Nogués-Bravo, D., Punyasena, S.W., Roland, T.P., Tanentzap, A.J., Willis, K.J., Aberhan, M., Asperen, E.N., Austin, W.E.N., Battarbee, R.W., Bhagwat, S., Belanger, C.L., Bennett, K.D., Birks, H.H., Bronk Ramsey, C., Brooks, S.J., Bruyn, M., Butler, P.G., Chambers, F.M., Clarke, S.J., Davies, A.L., Dearing, J.A., Ezard, T.H.G., Feurdean, A., Flower, R.J., Gell, P., Hausmann, S., Hogan, E.J., Hopkins, M.J., Jeffers, E.S., Korhola, A.A., Marchant, R., Kiefer, T., Lamentowicz, M., Larocque-Tobler, I., López-Merino, L., Liow, L.H., McGowan, S., Miller, J.H., Montoya, E., Morton, O., Nogué, S., Onoufriou, C.,Boush, L.P., Rodriguez-Sanchez, F., Rose, N.L., Sayer, C.D., Shaw, H.E., Payne, R., Simpson, G., Sohar, K., Whitehouse, N.J., Williams, J.W., Witkowski, A., McGlone, M., 2014. Looking forward through the past: identification of 50 priority research questions in palaeoecology. J. Ecol. 102 (1), 256–267.

Swindles, G.T., Amesbury, M.J., Turner, T.E., Carrivick, J.L., Woulds, C., Raby, C., Mullan, D., Roland, T.P., Galloway, J.M., Parry, L.E., Kokfelt, U., Garneau, M., Charman, D.J., Holden, J., 2015a. Evaluating the use of testate amoebae for palaeohydrological reconstruction in permafrost peatlands. Palaeogeogr. Palaeoclimatol. Palaeoecol. 424, 111–122. https://doi.org/10.1016/j. palaeo.2015.02.004.

Swindles, G.T., Holden, J., Raby, G.L., Turner, T.E., Blundell, A., Charman, D.J., Menberu, M.W., Kløve, B., 2015b. Testing peatland water-table depth transfer functions using high-resolution hydrological monitoring data. Quat. Sci. Rev. 120, 107–117. https://doi.org/10.1016/j.quascirev.2015.04.019.

Telford, R.J., Birks, H.J.B., 2009. Evaluation of transfer functions in spatially structured environments. Quat. Sci. Rev. 28 (13-14), 1309–1316. https://doi.org/10.1016/j. quascirev.2008.12.020.

Telford, R.J., Birks, H.J.B., 2011. Effect of uneven sampling along an environmental gradient on transfer-function performance. J. Paleolimnol. 46 (1), 99–106. https:// doi.org/10.1007/s10933-011-9523-z.

ter Braak, C.J.F., Šmilauer, P., 2012. CANOCO Reference Manual and User's Guide: Software for Ordination (Version 5). Ithaca, Microcomputer Power.

Thompson, R.S., Anderson, K.H., Bartlein, P.J., 2008. Quantitative estimation of bioclimatic parameters from presence/absence vegetation data in North America by the modern analog technique. Quat. Sci. Rev. 27 (11-12), 1234–1254. https://doi. org/10.1016/j.quascirev.2008.02.014.

Tierney, J.E., Poulsen, C.J., Montañez, I.P., Bhattacharya, T., Feng, R., Ford, H.L., Hönisch, B., Inglis, G.B., Petersen, S.V., Sagoo, N., Tabor, C.R., Thirumalai, K., Zhu, J., Burls, N.J., Foster, G.L., Goddéris, Y., Huber, B.T., Ivany, L.C., Turner, S.K.,

Lunt, D.J., McElwain, J.C., Mills, B.J.W., Otto-Bliesner, B.L., Ridgwell, A., Zhang, Y. G., 2020. Past climates inform our future. Science 370 (6517). https://doi.org/ 10.1126/science.aay3701.

Turner, T.E., Swindles, G.T., Charman, D.J., Blundell, A., 2013. Comparing regional and supra-regional transfer functions for palaeohydrological reconstruction from Holocene peatlands. Palaeogeogr. Palaeoclimatol. Palaeoecol. 369, 395–408. https://doi.org/10.1016/j.palaeo.2012.11.005.

Van bellen, S., Mauquoy, D., Payne, R.J., Roland, T.P., Daley, T.J., Hughes, P.D.M., Loader, N.J., Street-perrott, F.A., Rice, E.M., Pancotto, V.A., 2014. Testate amoebae as a proxy for reconstructing Holocene water table dynamics in southern Patagonian peat bogs. J. Quat. Sci. 29 (5), 463–474. https://doi.org/10.1002/jqs.2719.

Väliranta, M., Korhola, A., Sepp¨a, H., Tuittila, E.-S., Sarmaja-Korjonen, K., Laine, J., Alm, J., 2007. High-resolution reconstruction of wetness dynamics in a southern boreal raised bog, Finland, during the late Holocene: a quantitative approach. Holocene 17 (8), 1093–1107. https://doi.org/10.1177/0959683607082550.

Väliranta, M., Blundell, A., Charman, D.J., Karofeld, E., Korhola, A., Sillasoo, Ü., Tuittila, E.S., 2012. Reconstructing peatland water tables using transfer functions for plant macrofossils and testate amoebae: A methodological comparison. Quat. Int. 268, 34–43. https://doi.org/10.1016/j.quaint.2011.05.024.

Vicherová, E., Hájek, M., Šmilauer, P., Hájek, T., 2017. Sphagnum establishment in alkaline fens: Importance of weather and water chemistry. Sci. Total Environ. 580, 1429–1438. https://doi.org/10.1016/j.scitotenv.2016.12.109.

Wen, R.L., Xiao, J.L., Ma, Y.Z., Feng, Z.D., Li, Y.C., Xu, Q.H., 2013. Pollen-climate transfer functions intended for temperate eastern Asia. Quat. Int. 311, 3–11. https:// doi.org/10.1016/j.quaint.2013.04.025.

Xing, W., Bao, K.S., Gallego-Sala, A.V., Charman, D.J., Zhang, Z.Q., Gao, C.Y., Lu, X.G., Wang, G.P., 2015. Climate controls on carbon accumulation in peatlands of Northeast China. Quat. Sci. Rev. 115, 78–88. https://doi.org/10.1016/j. quascirev.2015.03.005.

Xu, J., Morris, P.J., Liu, J., Holden, J., 2018. PEATMAP: Refining estimates of global peatland distribution based on a meta analysis. Catena 160, 134–140. https://doi. org/10.1016/j.

Yang, Q.N., Li, H.C., Zhao, H.Y., Li, H.K., Bu, Z.J., Wang, S.Z., Chou, C.Y., Liu, Z.P., 2019. Hydroclimate controls of the distribution and abundance of mosses in Hani mire, Northeast China: Modern vegetation survey and peat-core analysis. Quat. Int. 528, 30–40. https://doi.org/10.1016/j.quaint.2019.09.026.

Yu, Z., Loisel, J., Brosseau, D.P., Beilman, D.W., Hunt, S.J., 2010. Global peatland dynamics since the Last Glacial Maximum. Geophys. Res. Lett. 37 (13), n/a–n/a. https://doi.org/10.1029/2010GL043584.

Zhang, H., Amesbury, M.J., Ronkainen, T., Charman, D.J., Gallego-Sala, A.V., VÄliranta, M., 2017. Testate amoeba as palaeohydrological indicators in the permafrost peatlands of north-east European Russia and Finnish Lapland. J. Quat. Sci. 32 (7), 976–988. https://doi.org/10.1002/jqs.2970.

Zhang, M.M., Bu, Z.J., Jiang, M., Wang, S.Z., Liu, S.S., Chen, X., Hao, J.N., Liao, W.Y., 2019. The development of Hani peatland in the Changbai mountains (NE China) and its response to the variations of the East Asian summer monsoon. Sci Total Environ. 692, 818–832. https://doi.org/10.1016/j.scitotenv.2019.07.287.

Zhang, M., Bu, Z., Wang, S., Jiang, M., 2020. Moisture changes in Northeast China since the last deglaciation: Spatiotemporal out-of-phase patterns and possible forcing mechanisms. Earth-Sci Rev. 201, 102984. https://doi.org/10.1016/j.earscirev.2019.102984.

Zhou, W., Zheng, Y., Meyers, P.A., Jull, A.J.T., Xie, S., 2010. Postglacial climate change record in biomarker lipid compositions of the Hani peat sequence, Northeastern China. Earth Planet. Sci. Lett. 294 (1-2), 37–46. https://doi.org/10.1016/j.epsl.2010.02.035.